Benthic biodiversity, fish community and nursery function of Lac, Bonaire

WAGENINGEN UNIVERSITY
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MSc Thesis Aquaculture and Marine Resource Management
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Report no: 007/2012

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Supervision:
Dr. R.M.M. Roijackers
Dr. A.O. Debrot

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Cover photos:
Lac, photo taken from Cai
French grunt (Haemulon flavolineatum), mangroves in Lac and Schoolmasters (Lutjanus apodus)

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Preface

20 March 2012

This thesis is conducted for our MSc Aquaculture and Marine Resource Management at the Aquatic Ecology and Water Quality Management group of Wageningen University. The project is performed with IMARES, the Wageningen University Research Center's Institute of Marine Research and Ecosystem Studies, and guided by Dolfi Debrot. All fieldwork was done in Bonaire, were local support was provided by STINAPA, the National Parks Foundation.

In Lac, a tropical mangrove lagoon in the southeast of Bonaire, the habitats are continuously changing. Mangroves are growing seawards, enclosing pools and reducing open bay habitat. The death of many mangrove trees, caused by reduced water circulation and hyper saline conditions, resulted in backwaters at the landward site of the mangroves. Our study is intended to quantitatively describe the benthic biodiversity of Lac's central bay, bay border, mangrove pool and backwater habitats. Further on, Lac's fish community and nursery function is assessed. The results can serve as a baseline study and future studies may be compared with it. This way it is possible to monitor changes in Lac and eventually take management actions.

At the request of IMARES, the results from our research are presented as two separate articles, which hopefully will lead to publications. Our supervisor from Wageningen University, Rudi Roijackers, generously agreed to accept the separate studies as our thesis. Preparation, field work and thesis writing for the benthic biodiversity study as well as the fish biodiversity and nursery function study were done together. Therefore one single thesis, consisting of two articles, is presented as end product for the both of us.

We thank the STINAPA staff, in particular Ramon de Léon, Sabine Engel and Gevy Soliana, for their advice, cooperation and assistance. Rita Peachey allowed us to use the CIEE Bonaire laboratory facilities and Albert Bianculli provided equipment and advice for the irradiance measurements. We thank Elly Albers and the Mangrove info center for providing us with kayaks. Erik Meesters provided statistical assistance and performed the cluster analysis. Ellard Hunting from the University of Amsterdam identified the unknown sponges and W. F. Prudhomme van Reine from the University of Leiden identified unknown algae and confirmed the discovery of *H. stipulacea* in Lac. Last, but not least, we thank Dolfi Debrot and Rudi Roijackers for advice and reviewing.

Alwin Hylkema
Willem Vogelaar

Abstract

Lac, Bonaire, is a tropical lagoon fringed with mangroves. Lac contains a diversity of interconnected habitats ranging from algal beds, seagrass beds, mangrove pools, mangrove fringes and backwaters. The mangroves are expanding seawards, overgrowing bay habitat and enclosing pools. Some pools are directly connected to the bay, others are more isolated. To assess the benthic biodiversity, the percentage cover per species was estimated on 98 randomly chosen survey sites in the central bay, bay border and mangrove pools of Lac. Isolated mangrove pools are significantly lower in total cover, species richness and biodiversity than other habitats. The non-native seagrass species *Halophila stipulacea* covers large areas in Lac's central bay habitat. The effect on native seagrass growth is not known, but it is possible that *H. stipulacea* interferes with native seagrass succession or invades existing seagrass beds.

The fish community and nursery function of Lac were investigated using visual censuses and cast net throws. Central bay, seagrass and mangroves fringe biotopes have a higher fish density, species richness and diversity than the algal beds and the non-vegetated biotopes in the central bay and mangrove pools. The more isolated mangrove pools and backwaters have the lowest species richness. *Halichoeres bivittatus, Sparisoma radians* and 4 Gerreidae are common species, which stay their entire life history in the Lac biotopes. Lac's seagrass beds are a nursery for *Acanthurus chirurgus, Caranx crysos, Haemulon sciurus, Lutjanus apodus, Lutjanus griseus, Ocyurus chrysurus* and *Scarus iseri*. *Chaetodon capistratus, Haemulon flavolineatum, Haemulon sciurus, Lutjanus apodus, Lutjanus griseus, Scarus guacamaia, Scarus iseri* and *Sphyraena barracuda* principally utilize the mangroves as nursery. The backwater biotope, at the landside of the mangroves, has a different fish community without nursery species. If the mangroves expand further into the bay, which is happening at the moment, more isolated biotopes might be created. Seagrass beds, mangrove fringes and open bay habitat the most valuable nursery biotopes with the highest density, species richness and diversity, might decrease in size.

The changing bay biotopes of Lac, Bonaire; a quantitative study of the distribution of seagrass and algal beds in a tropical mangrove lagoon

Introduction

Shallow water bay biotopes provide habitat, nursery and feeding grounds for many fish (Parrish, 1989; Nagelkerken *et al.*, 2000; Nagelkerken *et al.*, 2000b; Laegdsgaard & Johnson, 2001) and invertebrate (Haywood *et al.*, 1995; Loneragan *et al.*, 1998) species. Lac is an approximately 7 km^2 lagoon in the southeast of Bonaire, and contains many of these bay biotopes. Seagrass beds, algal beds, mixed vegetation, non-vegetated areas and mangroves can all be found here (van Moorsel & Meijer, 1993; Lott, 2000; Engel, 2008). The bay is an important habitat for the endangered queen conch (*Strombus gigas*) (Lott, 2000; Engel, 2008) and the protected green turtle (*Chelonia mydas*) (Debrot *et al.*, 2010). The seagrass beds and mangroves of Lac function as habitat and nursery for many fish species (van Moorsel & Meijer, 1993; Nagelkerken *et al.*, 2002).

The habitats in Lac are continuously changing. The Lac lagoon is fringed with the red mangrove *Rhizophora mangle*, while the black mangrove, *Avicennia germinans* covers large areas at the land side of Lac (van Moorsel & Meijer, 1993; Lott, 2001). In F*ig. 1* the changes in mangrove cover between 1961 and 1996 can be seen. At the landward side of the bay there has been a big decrease in mangrove cover (Erdmann & Scheffers, 2006). This die-off is a (semi-) natural process, caused by the mangroves themselves. As mangroves grow and extend seaward, they trap sediment and organic matter between their roots, which results in accretion of land, reduced water flow and hypersaline conditions. In dry periods many mangrove trees die in areas isolated from circulation and prone to drying and hypersalinity (Wagenaar Hummelinck & Roos, 1970; Lott, 2000). Reduction in freshwater inflow, caused by the construction of a dam and the road to Cai (*Fig. 1*) which were both built in the period 1951-1952, may have accelerated the die-off process (Wagenaar Hummelinck & Roos, 1970). The death of mangrove trees has created zones of muddy backwaters behind the mangroves. In the process of *R. mangle* growing further into the bay, the surface area of open bay habitat has been reduced. Mangrove growth into the bay is facilitated by banks of *Halimeda* algae, which produce calcareous sediment (Bach, 1979; Bosence, 1989) and thereby reduce water depth locally. If the water is shallow enough, *R. mangle* overgrows the *Halimeda* banks, forming a new Lac habitat: mangrove pools (van Moorsel & Meijer, 1993).

Halophila stipulacea is an invasive seagrass species in the Caribbean (Willette & Ambrose, 2009) which was first reported in Grenada in 2002 (Ruiz & Ballantine, 2004). *H. stipulacea* is not reported in the seagrass characterization studies which were performed in Lac in 2000 and 2007 (Lott, 2000; Engel, 2008), but now covers areas in the central bay and the mangrove pools (personal observation).

The expansion of *R. mangle* into the bay and the invasion of *H. stipulacea* may cause big changes to the Lac habitats, which makes it important to closely monitor the area. Several studies have been conducted on the benthic communities in Lac (Wagenaar Hummelinck & Roos, 1970; Hoek *et al.*, 1972; van Moorsel & Meijer, 1993; Lott, 2000; Engel, 2008), but these are all qualitative. Our study is intended to quantitatively describe the benthic biodiversity of Lac's central bay, bay border and mangrove pool habitats. The results can serve as a baseline study and future studies may be compared with it. This way it is possible to monitor changes in Lac and eventually take management actions. The data for this study are collected using the following research questions:

1. ***What are the characteristic benthic assemblages of the different areas (central bay, bay border, blue mangrove pools and dark mangrove pools) of Lac, Bonaire?***
2. ***Do the blue and dark mangrove pools contain a different benthic biodiversity compared to the central bay and the bay border?***
3. ***To what extent has the invasive seagrass species H. stipulacea colonized Lac?***

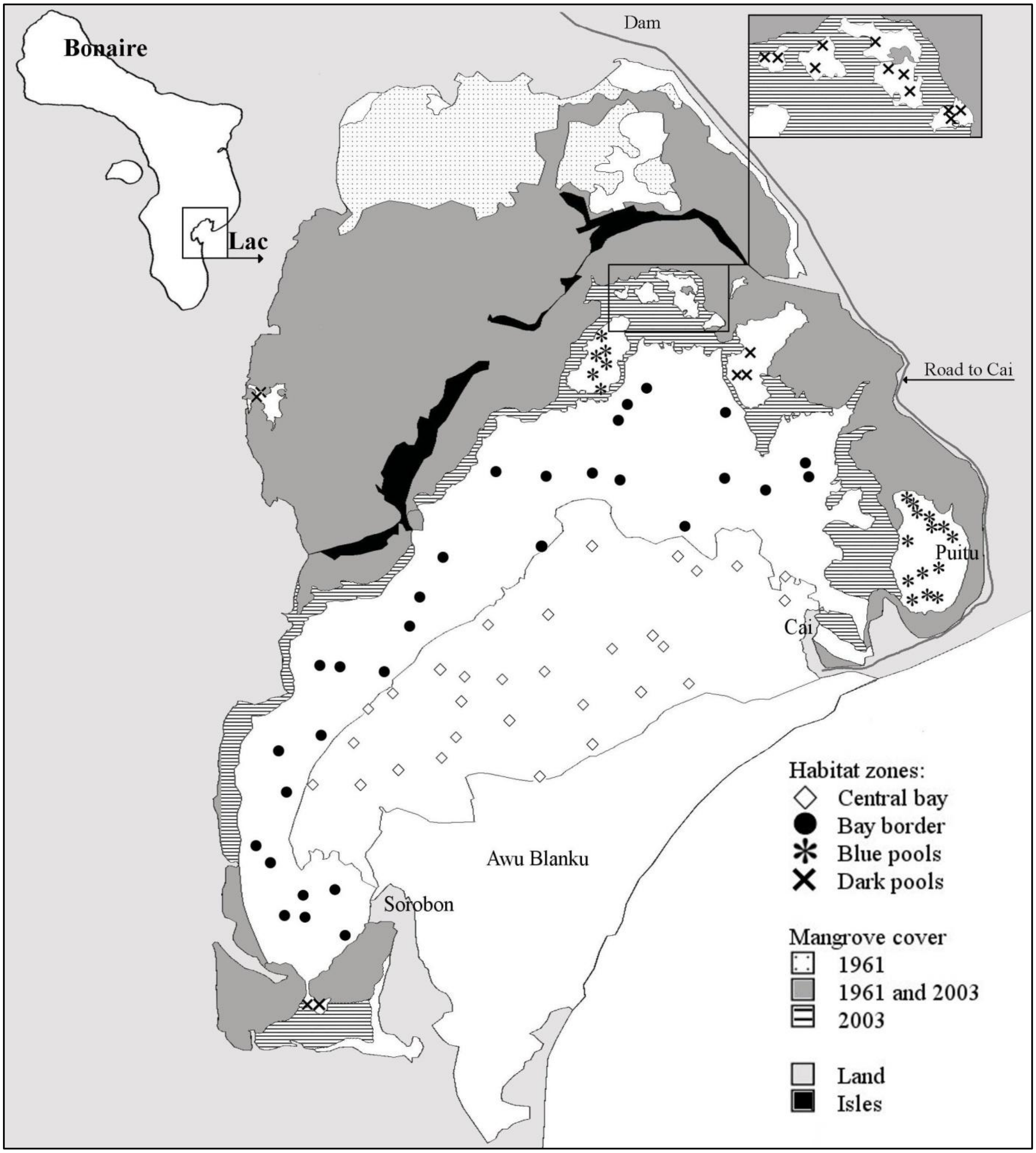

Figure 1: The survey points per habitat zone and the changes in mangrove cover between 1961 and 1996 (Erdmann & Scheffers, 2006; © Google 2003).

Materials & methods

Site selection

Using satellite images from 2003, Lac was divided in four principal habitat zones: central bay, bay border, blue mangrove pools and dark mangrove pools (*Fig. 1*). The mangrove pools were divided in two habitat zones because some pools appeared blue and others appeared dark on the satellite images, which might indicate a different vegetation growth. Sample sites were chosen using a random location generator [1]. The amount of sites per habitat zone differed; 18 sites in the dark mangrove pools, 20 sites in the blue mangrove pools, 30 sites in the bay border and 30 sites in the central bay. Each site was visited once, between September and December 2011.

Site survey

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 are not taken into account. Taxa moving only when seriously disturbed such as upside-down jellyfish, *Cassiopea* sp., were considered sessile. Survey sites were reached by boat or kayak using a Garmin GPS 12 XL device. At each survey site the percentage cover per species was estimated using a 1 m^2 PVC quadrant. The quadrant was further divided with thin lines in squares of 10 by 10 cm, each square representing one percent. If taxa occupied less than 1 percent, their presence was noted as 0.01 % cover. The survey area was determined using the calculations of Kuenen & Debrot (1995) who performed a comparable quantitative descriptive study in the Spaanse Water bay in Curacao. Kuenen & Debrot (1995) concluded that the minimal sample area for significant results was 3 m^2. In this study 4 m^2 was surveyed, so the area was big enough to get representative results. This means the quadrant was placed four contiguous times at each site. The percentage cover estimations were done by one of the two researchers performing this study, using SCUBA or snorkeling gear.

Identification

Identification was done up to the lowest possible taxonomic level. Unknown taxa were collected in small plastic tubes with seawater and determined the same day using identification guides (Littler *et al.*, 1989; Littler & 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 and identified by experts in The Netherlands in January 2012.

Abiotic variables

Physical variables were taken at every survey site. Temperature was measured with a dive computer (Suunto Zoop) to one degree precision. Field measurements were calibrated by comparing temperature measurements of the dive computer with temperature measurements of an adjusted 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 site, 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 levels at the bottom and at the surface were measured to calculate the percentage of light reaching the bottom of the survey site. 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. Measurements were taken in duplicate for 3 minutes but only the data from 1m00s-2m40s was taken into account. 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; very easily disturbed by a moving hand. Silt was defined as very small particles of the same size; sediment is disturbed by a moving hand. Sand was defined as small particles of the same size; sediment is not disturbed by a moving hand. In some sites calcified *Halimeda* sediment was found, this consisted of remnants from the calcareous *Halimeda* algae.

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 sites based on percentage cover per taxon was performed to identify different biotic assemblages using the statistical package Primer 6. A resemblance method was chosen combining a 4th root transformation with the Bray Curtis similarity coefficient. Assemblages were discerned based on the SIMPROF analysis (Clarke *et al.*, 2008). In this analysis the structure of the permutations is tested against random permutation structures. Assemblages were discerned at a 95% confidence level ($P<0.05$).

The structure of each assemblage was analyzed in Excel 2007 using species richness (S) and Shannon index for diversity (H'). At each site 4 m^2 is sampled, so S and H' are 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 and therefore will be named mean taxon richness from now on. Percentage cover per taxonomic group and total biotic cover were calculated per m^2. For each assemblage, taxa were considered common when occurring in 50-66% of the sites and taxa were considered typical when occurring in >67% of the sites. Typical taxa having a mean cover of 30% were considered dominant (Kuenen & Debrot, 1995). Several assemblages lacked a normal distribution so a Kruskal-Wallis non-parametric test was performed in the statistical package SPSS 19.0 to identify significant differences in percentage biotic cover, taxon richness and Shannon index of diversity.

Results

The results of the cluster analysis are shown in the dendrogram of *Fig. 2*. Seven clusters can be distinguished, which are labeled A-G. Clustering is done based on percentage biotic cover per taxon, so the clusters can be regarded to as different assemblages. The location of the survey sites of each assemblage are shown in *Fig. 3*. The five main assemblages are named after the location of their sites or their main vegetation cover. Most of the sites in assemblage A, the dark pool assemblage, are located in the dark mangrove pools. Assemblage C, the blue pool assemblage, consists mainly of sites in the blue mangrove pools. Sites of assemblage D, the central bay assemblage, are mostly located in the central bay. Sites of assemblages F and G are located in the bay border, although some of the central bay sites belong to assemblage F. Assemblage F and G both have a high biotic cover. In assemblage F, the *Thalassia* assemblage, this cover consists mainly of *Thalassia testudinum*. Assemblage G, the *Thalassia/Halimeda* assemblage, has a high *T. testudinum* cover, but the calcareous algae of the genus *Halimeda* also cover large areas as well. Assemblage B and assemblage E consist both of only 2 sites and are therefore not named.

To describe each assemblage, several abiotic and biotic variables are used. Depth, horizontal SDD, bottom irradiance, temperature, salinity and sediment type can be found in *Table 1*. Mean taxon richness per 4 m^2, by taxon and in total, can be found in *Table 2*. *Table 3* shows the biotic cover of each assemblage, per taxon and in total, and *Table 4* shows the taxa which are found in each assemblage. The differences in biotic cover, taxon richness and Shannon index of diversity between the assemblages are clearly visible in *Fig. 4, 5* and *6*. In *Table 5* the assemblages where *Halophila stipulacea* is found are listed with their mean and maximum cover per m^2.

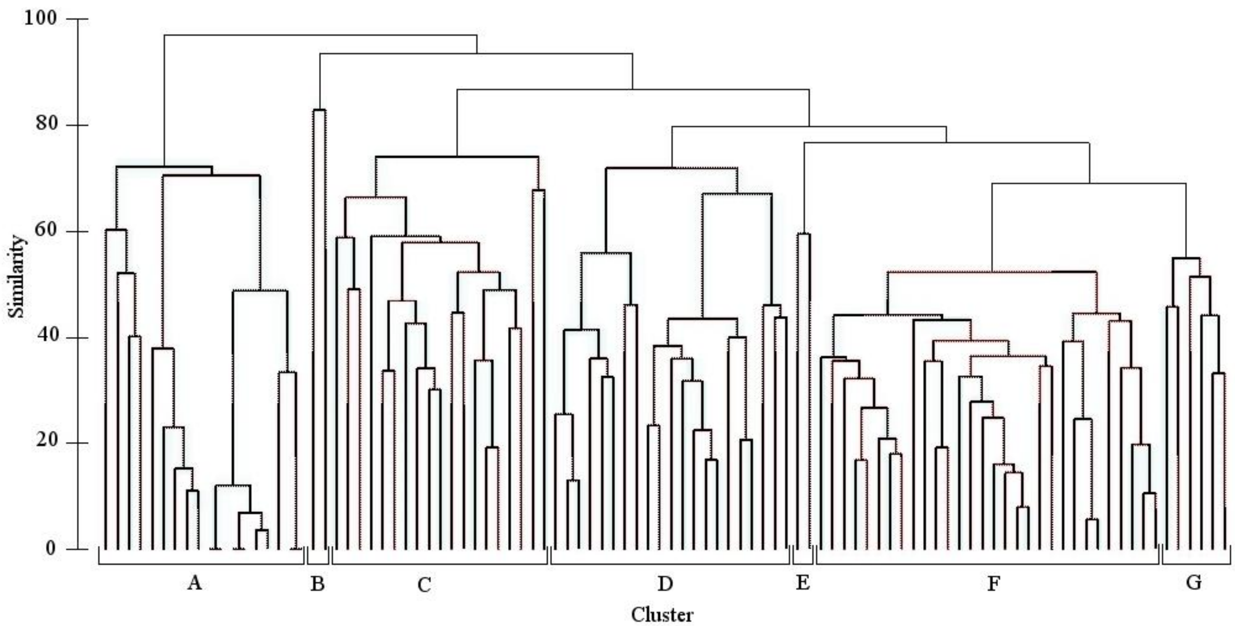

Figure 2: Dendrogram obtained by cluster analysis. Assemblages are labeled A-G.

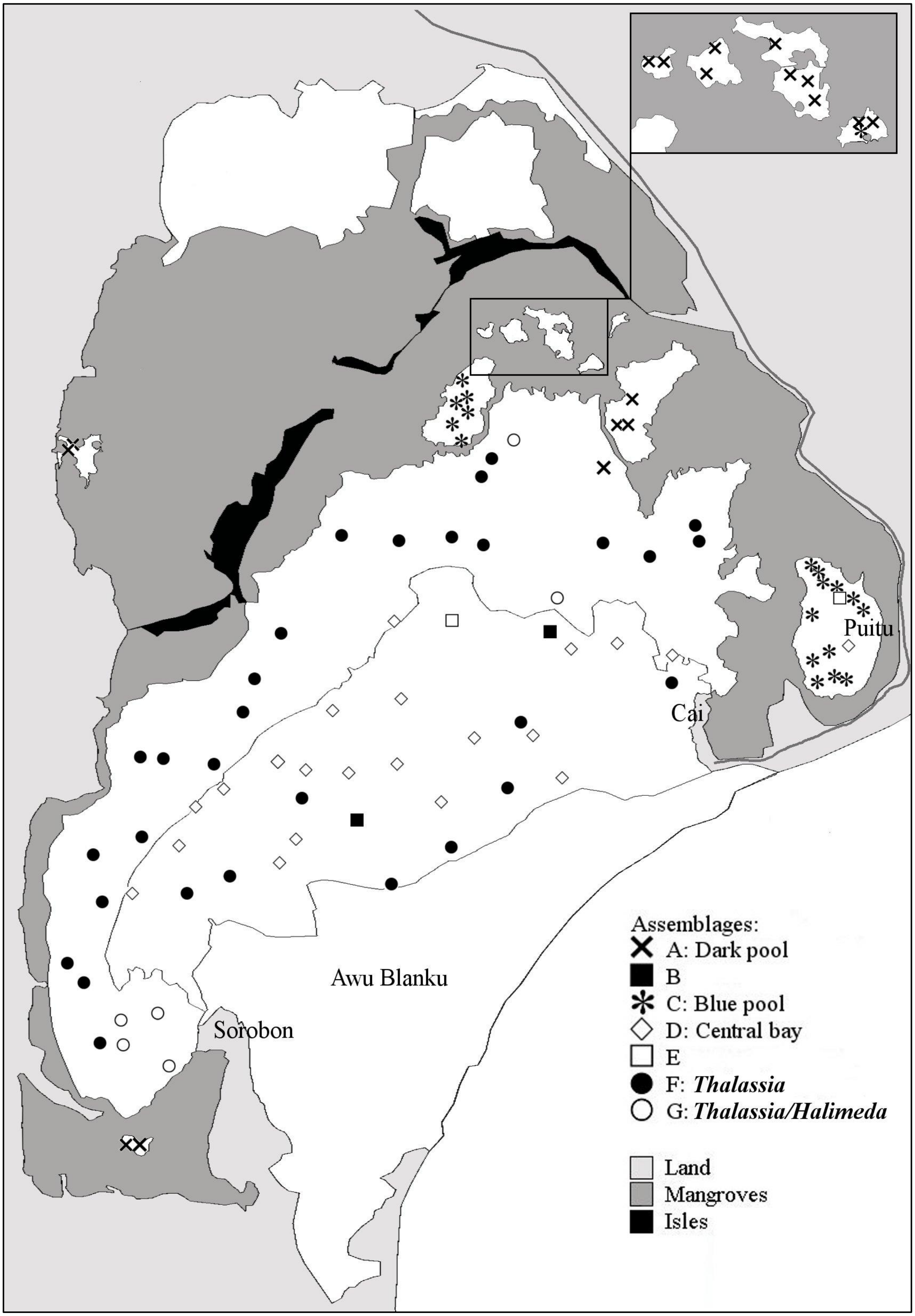

Figure 3: The survey points per assemblage (© Google 2003).

Table 1: Mean abiotic variables (number of sites, depth, horizontal SDD, bottom irradiance, temperature, salinity and sediment type) per assemblage (±SD). nd=no data

		A Dark pool	B	C Blue pool	D Central bay	E	F *Thalassia*	G *Thalassia/* *Halimeda*
N:		18	2	19	21	2	30	6
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
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
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
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
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
Sedement type (%):	organic matter	94.4±23.6	-	5.3±22.9	-	-	-	-
	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
	sand	-	75.0±0.0	13.2±17.4	76.2±25.6	50±35.4	71.4±16.3	42.9±34.5
	calcified *Halimeda*	-	-	-	-	-	-	28.6±48.8

Table 2: Mean taxon richness (S), by taxon and in total, per 4 m² in each assemblage (±SD).

	A Dark pool	B	C Blue pool	D Central bay	E	F *Thalassia*	G *Thalassia/Halimeda*
N	18	2	19	21	2	30	6
Cyanobacteria	0.1±0.2	-	0.8±0.4	0.9±0.4	1.0±0.0	0.2±0.4	0.3±0.5
Phaeophyceae	-	-	-	0.3±0.6	0.5±0.7	0.2±0.5	0.8±0.8
Rhodophyceae	-	2.0±1.4	0.3±0.6	0.9±1.0	2.5±0.7	0.2±0.5	0.5±0.8
Chlorophyceae	1.3±0.7	0.5±0.7	3.4±1.5	0.8±0.9	4.0±0.0	1.6±1.2	4.2±1.0
Angiospermae	0.1±0.2	-	0.4±0.6	1.5±0.9	0.5±0.7	1±0.2	0.8±0.4
Porifera	-	0.5±0.7	0.5±0.6	0.4±0.6	2.5±0.7	0.8±0.9	2.2±1.0
Cnidaria	0.3±0.5	-	1.2±0.4	0.1±0.4	0.5±0.7	0.3±0.4	0.5±0.5
Mollusca	-	-	-	0.1±0.3	0.5±0.7	0.0±0.2	-
Annelida	-	1.0±0.0	0.6±0.7	1.0±0.4	-	0.7±0.8	1.0±0.6
Echinodermata	-	-	-	-	-	0.0±0.2	-
S Total	1.8±1.1	4.0±1.4	7.2±2.9	5.9±1.8	12.0±2.8	5.0±2.2	10.3±2.0

Table 3: Mean biotic cover per m², by taxon and in total, in each assemblage (±SD).

	A Dark pool	B	C Blue pool	D Central bay	E	F *Thalassia*	G *Thalassia/* *Halimeda*
N	18	2	19	21	2	30	6
Cyanobacteria	0.0±0.1	-	3.4±4.5	11.4±10.6	3.5±2.1	3.6±13.3	0.8±2
Phaeophyceae	-	-	0±0	0.8±3.2	7.8±11.0	0.0±0.1	2.0±2.8
Rhodophyceae	-	0.4±0.5	1.9±8.4	2.1±5.0	8.3±7.4	0.4±1.8	0.8±1.2
Chlorophyceae	11.9±20.5	-	8.0±8.8	2.6±10.2	21.6±2.7	6.7±9.1	34.4±13
Angiospermae	0.0±0.1	-	1.7±3.9	34.9±32.2	6.6±9.4	51.0±20.2	4.8±10.3
Porifera	-	-	0.1±0.1	0.3±0.5	0.4±0.2	0.3±0.7	1.0±0.5
Cnidaria	0.3±0.9	-	3.9±3.6	0.0±0.1	1.6±2.3	0.1±0.3	0.1±0.1
Mollusca	-	-	-	0.1±0.2	0.3±0.4	-	-
Annelida	-	-	-	-	-	-	0.1±0.1
Echinodermata	-	-	-	-	-	0.0±0.1	-
Total cover	12.3±20.5	0.4±0.5	19.0±17.1	52.2±26.5	50.0±10.6	62.3±20.7	44.0±16.1

Table 4: Taxa present in Lac's assemblages. **=present in at least one site of the assemblage, C=common (present in more than 50% of the sites of the assemblage), T=typical (present in more than 66% of the sites of the assemblage) and D=dominant (typical taxon with a mean cover of 30% or more).*

		A Dark pool	B	C Blue pool	D Central bay	E	F *Thalassia*	G *Thalassia/* *Halimeda*
Cyanobacteria	Cyano brown	*		T	T	T	*	*
Phaeophyceae	*Dictyota divaricata*				*		*	*
	Dictyota sp.				*	C	*	C
Rhodophyceae	*Acanthophora spicifera*		C	*	*	T	*	*
	Amphiroa sp.		C					
	Ceramium sp.		C		*		*	
	Daysya sp. unknown 3				*	C		
	Hypnea sp.			*	*	C	*	*
	Laurencia intricata				*			
	Super fuzzy bruin/rood 12				*		*	*
	Wrangelia argus		C		*	C	*	
Chlorophyceae	*Acetabularia* sp.			T	*			*
	Avrainvillea rawsonii						*	
	Avrainvillea sp.	*		*	*	C	*	*
	Batophora oestedii	T		*				*
	Caulerpa cupressoides					C	*	
	Caulerpa mexicana			*		C		
	Caulerpa racemosa			*		C		
	Caulerpa sertularoides	*				T	*	*
	Chaetomorpha linium			*	*			
	Derbesia sp.		C	*	*		*	
	Dictyosphaeria cavernosa						*	*
	Green fibers 4				*			
	Halimeda incrassata			C	*	T	C	T
	Halimeda opuntia			*			*	T
	Penicillus sp.			*	*		*	*
	Udotea flabellum				*		*	*
	Valonia ventricosa						*	C
Angiospermae	*Halophila stipulacea*			*	C			
	Ruppia maritima	*		*				
	Syringodium filliforme			*	*		*	
	Thalassia testudinum			*	T	C	D	T
Porifera	*Amphimedon compressa*		C					
	Chalinula molitba			*			*	
	Chondrilla nucula						*	
	Dysidea etheria					C	*	*
	Haliclona tubifera						*	
	Haliclona twincayensis			*	*	T	*	C
	Hyrtios proteus						*	
	Strongylamma baki				*			
	Tedania ignis			*	*	T	*	*
	Verongula rigida						*	*
Cnidaria	*Cassiopeia frondosa*	*		*	*	C	*	
	Cassiopeia xamachana	*		T	*			
	Condylactis gigantea				*		*	C
	Porites porites						*	
Mollusca	*Strombus gigas*				*	C	*	
	Pina carnea				*			
Annelida	*Arenicola cristata*		T	*	T		C	*
	Eupolymnia sp.						*	
	Fanworm (Sabellidae)			*	*		*	T
Echinodermata	*Holothuria mexicana*						*	

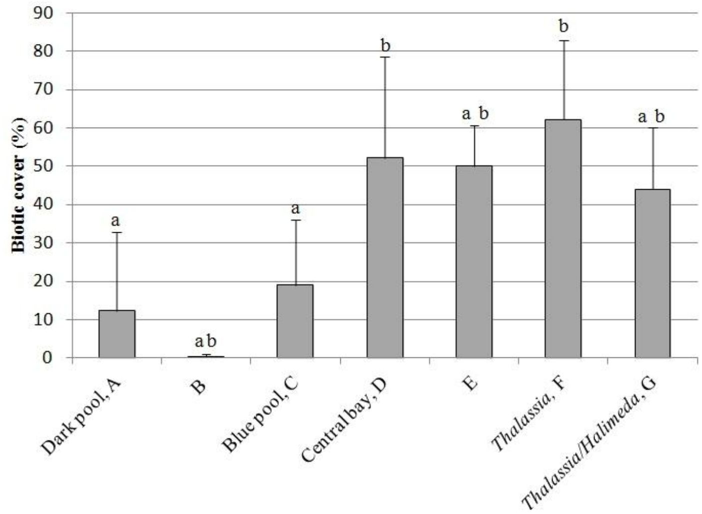

Figure 4: Mean biotic cover in percentages for each assemblage (+SD). Letters above error bars indicate statistically similar assemblages

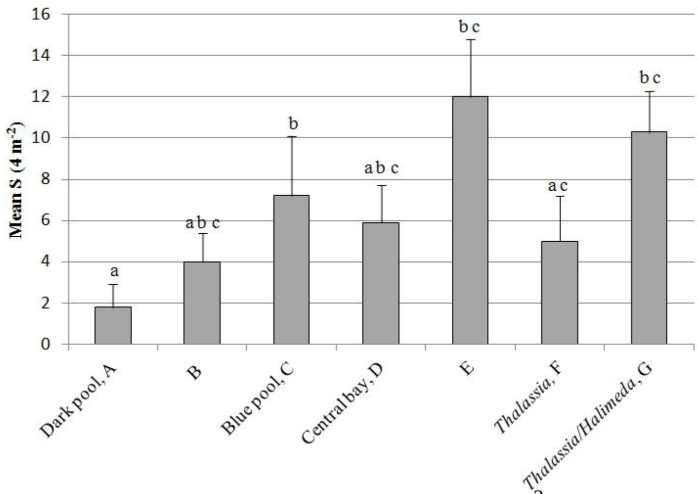

Figure 5: Mean taxon richness (S) per 4 m^2 in each assemblage (+SD). Letters above error bars indicate statistically similar assemblages.

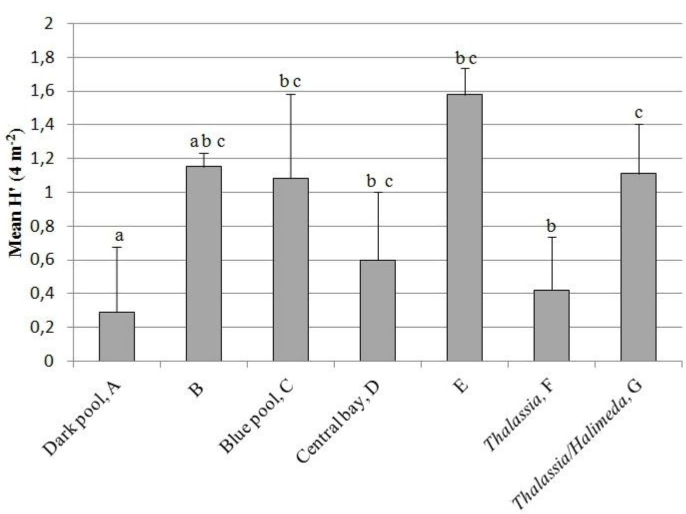

Figure 6: Mean values of Shannon index of diversity (H') per 4 m^2 in each assemblage (+SD). Letters above error bars indicate statistically similar assemblages.

Table 5: Sites per assemblage where H. stipulacea grows, mean H. stipulacea cover if present and highest H. stipulacea cover.

	C Blue pools	D Central bay
Total sites	19	21
Sites with *H. stipulacea*	5	13
Mean *H. stipulacea* cover if present	5.3	39.7
Highest *H. stipulacea* cover	15.8	81.5

Assemblage descriptions

Assemblage A, the dark pool assemblage, is formed by 18 sites: 17 sites in the dark mangrove pools and one site in the bay border. The assemblage is shallow with a mean depth of 1.4 m and the bottom consists mostly of organic matter (>94 %). The horizontal Secchi disc distance (SDD) is 4.3 m and mean temperature is 29.6 °C. The dark pool assemblage is characterized by a saline environment (40.6 ppt) compared to conditions in the Caribbean Sea, which are around 36 ppt (Froelich *et al.*, 1978). Sites in the dark pool assemblage have a mean biotic cover of 12%. The number of taxa per m^2 and Shannon index of diversity are very low (S=1.8, H'=0.29) compared to other assemblages. A typical taxon for this assemblage is *Batophora oestedii*. Other algal taxa are present on several sites but always in low quantities, except for *Avrainvillea* sp. which occurs in dense patches in a few sites.

Assemblage B is composed of 2 sites, both situated in the central bay area. The sediment is a mixture of sand (75%) and silt (25%). The mean depth is 3.4 m, while mean salinity is 36.9 ppt. The mean temperature is 30 °C and mean horizontal SDD is 7.8 m. Biotic cover is low (<1%) and a mean number of 4 taxa per m^2 was found in this assemblage. Shannon index of diversity is 1.15. The burrow worm *Arenicola cristata* is a typical taxon for this assemblage. The sponge *Amphimedon compressa*, the green algae *Derbesia* sp. and the red algae *Acanthophora spicifera*, *Amphiroa* sp., *Ceramium* sp. and *Wrangelia argus* were also found in assemblage B.

Assemblage C, the blue pool assemblage, contains 18 sites in the blue mangrove pools and 1 site 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 is high, 37.9 ppt, compared to open water conditions. Sediment type in this assemblage consists mostly of silt (81.6%) with a smaller fraction of sand. The blue pool assemblage displays a mean biotic cover of 19%, mean taxon richness of 7.2 and a Shannon index of diversity of 1.09. A brown form of cyanobacterial growth, referred to as "Cyano brown" in this study, and the green algae *Acetabularia sp.* are typical taxa for this assemblage. Less frequently observed, but still common taxa are the mangrove upside-down jellyfish *Cassiopea xamanchana* and the calcareous green algae *Halimeda incrassata*.

Assemblage D, the central bay assemblage, consists of 19 sites located in the central bay, 1 site located in the blue pool Puitu and 1 site located in the bay border. This assemblage is deep (3.7 m) and clear (horizontal SDD = 9.2 m). The mean temperature is 28.9 °C and mean salinity is 36.9 ppt. Its bottom consists of sand (76%) and silt (24%). Mean taxon richness is 5.9 and total biotic cover is 52%. Shannon index of diversity is 0.6. Typical taxa found in this assemblage are the burrow worm *A. cristata*, turtle grass *T. testudinum* and "Cyano brown". A taxon considered common is the non-native seagrass *Halophila stipulacea*.

Assemblage E is represented by two sites; one in the central bay and one in the blue pool Puitu. Mean depth is 2.2 m and horizontal SDD is 5.5 m. Mean temperature is 29.5 °C and mean salinity is 36.9 ppt. Assemblage E has a mean taxon richness of 12, Shannon index of diversity of 1.58 and biotic cover of 50%. Typical taxa for this assemblage are the fire sponge *Tedania ignis* and *Haliclona twincayensis*, the green algae *Caulerpa sertularoides* and *H. incrassata* and the red algae *A. spicifera*. Taxa observed as common are the upside-down jellyfish (*Cassiopea frondosa*), the mollusc *Strombus gigas* and the sponge *Dysidea etheria*. The marine angiosperm *T. testudinum*, the brown algae *Dictyota* sp., the green algae

Avrainvillea sp., *Caulerpa cupressoides*, *Caulerpa mexicana* and *Caulerpa racemosa* and the red algae *Daysya* sp., *Hypnea* sp. and *Wrangelia argus* were observed to be common taxa as well.

Assemblage F, the *Thalassia* assemblage, consists of 22 sites situated in the bay border and 8 in the central bay. Mean depth is 2 m and horizontal SDD is 6.3 m. Mean temperature is 29.3 °C and mean salinity is 36.9 ppt. The sediment type of the *Thalassia* assemblage consists of sand (71%) and silt (29%). Sites in assemblage F display a mean taxon richness of 5. Shannon index of diversity is 0.42. Biotic cover is 62%. Sea grass beds made up of *T. testudinum* dominate the benthic community and represent almost 35% of the total cover. Common taxa amongst these sea grass beds are the burrow worm *A. cristata* and the calcareous green algae *H. incrassata*.

Assemblage G, the *Thalassia/Halimeda* assemblage, consists of 6 sites located in the bay border. It is 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 is 5.9, mean temperature is 29.3 °C and salinity is 36.8 ppt. Mean taxon richness is 10.3 and Shannon index of diversity is 1.11. Biotic cover is 44%. Typical taxa for this assemblage are *T. testudinum, H. incrassate*, *H. opuntia* and fanworms (*Polychaeta*). Common taxa are the Caribbean giant sea anemone *Condylactis gigantea*, the sponge *H. twincayensis*, the brown algae *Dictyota* sp. and the green algae *Valonia ventricosa*.

Discussion

Comparison between Lac assemblages

This study is performed in four habitat zones of Lac: central bay, bay border, blue mangrove pools and dark mangrove pools. Cluster analysis reveals that, based on taxon composition, there are 5 main assemblages. By comparing these assemblages, differences between Lac's habitats become clear. Assemblage B and E consist of only two sites each, and are therefore not taken into account in this discussion.

The dark en blue pool assemblages have a significant lower biotic cover than the central bay and *Thalassia* assemblages. Within the mangrove pools, the dark pool assemblage has a lower total cover than the blue pools assemblage, but this difference is not significant. The highest biotic cover is found in the *Thalassia* assemblage, consisting of bay border and central bay sites. The dark pool assemblage has the lowest taxon richness. The blue pool and *Thalassia*/*Halimeda* assemblages have a significant higher taxon richness. The central bay and *Thalassia* assemblages also display a higher taxon richness but do not significantly differ from the other assemblages. Sites in the dark pool assemblage have a significant lower Shannon index of diversity than all other assemblages. The Shannon index of the *Thalassia* assemblage is significant lower than the *Thalassia*/*Halimeda* assemblage; this is caused by the dominant presence of *Thalassia testudinum* in the communities of the *Thalassia* assemblage.

The comparisons between the assemblages show that the dark pool assemblage is lower in total cover, mean taxon richness and diversity than all other assemblages. The dark pool assemblage represents the dark mangrove pools which are formed as a result of expanding *Rhizophora mangle* trees. Dark pools are located further into the mangroves than blue pools and have a less direct connection to the bay. If the mangroves expand further into the bay, blue pools will lose their direct connection, decrease in surface area and will probably become dark pools. New blue pools will be formed by the seaward growth of *R. mangle* into the bay. This means that the presence of the dark pool assemblage relative to the other assemblages might increase in the future. An increase of the dark pool assemblage will probably result in a (partial) loss of the central bay, *Thalassia*, *Thalassia*/*Halimeda* and blue pool assemblages, which are more valuable in terms of biodiversity, biotic cover and mean taxon richness.

The impact of Halophila stipulacea

In the central bay assemblage the seagrass *Halophila stipulacea* is found in 13 of the 21 central bay sites. The mean cover in these sites is 40%, but sometimes cover is as high as 80%. *H.* stipulacea is also found in five sites in the mangrove pool Puitu. The mean cover in these sites, which belong to the blue pool assemblage, is 5%.

H. stipulacea is not reported in the seagrass characterization studies which are performed in Lac in 2000 and 2007 (Lott, 2000; Engel, 2008). This means that all *H. stipulacea* growth took place within the last four years, there are no data of the first discovery in Lac. *H. stipulacea* originate from the Red Sea and East Africa and is invasive in the Mediterranean Sea since the opening of the Suez Canal (Green & Short, 2003). The first report of *H. stipulacea* in the Caribbean was in Grenada, 2002 (Ruiz & Ballantine, 2004). In 2007 it was found in Dominica and in St. Lucia (Willette & Ambrose, 2009), there are no known other publication about the expansion of *H. stipulacea* in the Caribbean. In the Gazi Bay, Kenya, *H. stipulacea* behaves as a pioneer species (Coppejans *et al.*, 1992). Bare sand and disrupted areas are quickly colonized by this fast growing seagrass, where after other seagrass 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 the observations of Coppejans *et al.* (1992), *H. stipulacea* seems to colonize bare sand flats in Lac. It is unclear of the same succession process will occur as in East Africa, but if it does *H. stipulacea* might help the succession of bare ground by *T. testudinum*. It is however also possible that *H. stipulacea* interferes with local seagrass succession or invades existing seagrass beds (Willette & Ambrose, 2009), which in Lac mainly consist of *T. testudinum*. In Flamingo bay, Grenada, no other seagrass species were found after the invasion of *H. stipulacea*, while neighboring bays where home to

Syringodium filiforme and *T. testudinum* (Ruiz & Ballantine, 2004). Although there is no evidence for a relation, it is possible that the other seagrass species were outcompeted by *H. stipulacea*. If *H. stipulacea* replaces other seagrass species it might result in a loss of *T. testudinum* cover, which might result in a change in species composition (Blaber *et al.*, 1992; Loneragan *et al.*, 1998; Nagelkerken *et al.*, 2000). *T. testudinum* is an important species for the queen conch, *Strombus gigas*, which grazes on *T. testudinum* epiphytes, and the green turtle, *Chelonia mydas*, which eats the leaves itself. Further on, *T. testudinum* beds are recognized as an important nursery habitat for reef fish species (Nagelkerken *et al.*, 2000; Nagelkerken *et al.*, 2002). Expansion of *H. stipulacea* might therefore have severe effects on the Lac biotopes.

Comparison with other data

Central bay and bay border

Wagenaar Hummelinck & Roos (1970) performed the first research to the benthic communities of Lac in 1967. The seagrass taxa described in their study are also found in the present study, except for *Halodule beaudetti*. More recent studies do not described *H. beaudetti* either (van Moorsel & Meijer, 1993; Lott, 2000) but the species is found in small quantities in 2007 (Engel, 2008). It is therefore possible that *H. beaudetti* is still present in Lac. Another striking difference between Wagenaar Hummelinck & Roos (1970) and the present study concerns the starfish *Oreaster reticulates*. *O. reticulates* occurred in Lac's seagrass beds in 1967 (Wagenaar Hummelinck & Roos, 1970), but was not found during this research. Other studies to 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 (van Moorsel & Meijer, 1993; Engel, 2008). The reason behind this disappearance is not known. Wagenaar Hummelinck & Roos (1970) described only four algae taxa, *Halimeda opuntia, Avrainvillea nigricans, Acetabularia crenulata* and *Batophora oestedii,* which are still present in Lac.

Van Moorsel & Meijer (1993) described many algae taxa which are not found in the present study. Most of these taxa are found in the station "Secu di Sorobon" (van Moorsel & Meijer, 1993), which is part of the Awa Blanku area (*Fig. 1*). No survey sites of this study were in this area, so the difference might be explained by different research area.

Mangrove pools

Van den Hoek *et al.* (1972) and van Moorsel & Meijer (1993) did the first observations in the mangrove pools of Lac. Both studies revealed the limited amount of taxa in more isolated pools, compared to pools with a more open connection to the bay. This is in accordance to the conclusion of this study: blue pools have a higher taxon richness than dark pools. *Avrainvillea nigricans* and *Batophora oestedii* are found to be the most common taxa of the isolated (dark) mangrove pools in the past and present. The main difference between the observations of van den Hoek *et al.* (1972), van Moorsel & Meijer (1993) and this study are high quantities of *T. testudinum* in some mangrove pools in 1972 and 1992, while mangrove pools have a very low or non *T. testudinum* cover in 2011. This might be explained by *R. mangle* growth into the bay, which increases the isolation of the pools and reduces the water flow.

Similar habitats

Though the worldwide amount of comparable studies is limited, a quantitative study was performed at the Spaanse Water, Curacao (Kuenen & Debrot, 1995). The Spaanse Water is an inland bay about half the size of Lac. A higher number of taxa was found in the Spaanse Water (121 taxa) compared to Lac (54 taxa), even though the smaller size. A possible reason for this is the bigger sample area in the Spaanse Water. In the Spaanse Water a total surface of 906 m^2 was studied, compared to 392 m^2 in Lac. Another possible reason is the presence of hard substrate in the sample stations at the Spaanse Water. Though areas with hard substrate are present in Lac (van Moorsel & Meijer, 1993), no hard substrate was found in the sample sites of this study. One of the areas with a high amount of hard substrate is the Awa Blanku area, particularly the part adjacent to the coral dam, which is not taken into account in this study. The absence of hard substrate in the samples sites explains the relative low quantities of coral cover in Lac, one of the main differences between the studies. The Spaanse Water study also recorded all taxa with a

second shortest dimension of 0.5 cm or larger whereas in this study a second shortest dimension of 1 cm was used as definition for macro flora and fauna.
Assemblage B and C in the Spaanse Water are comparable with the *Thalassia*/*Halimeda* assemblage in Lac, a shallow bay border assemblage. All three assemblages consist of *T. testudinum* beds mixed with *H. opuntia* and have a relatively high biotic cover (>44%). Other taxa are present in lower numbers in assemblage B and C in the Spaanse Water. Some of these taxa are found in Lac too, others are not. The main difference is the presence of *H. incrassata* in relative high quantities in the *Thalassia*/*Halimeda* assemblage compared to the two Spaanse Water assemblages. There are more taxa present in the two Spaanse Water assemblages, but this is an overall difference as mentioned above. Mean depth of the *Thalassia*/*Halimeda* assemblage is comparable to assemblage C in the Spaanse Water, but the substrate composition displays more similarities with assemblage B in the Spaanse Water.
Assemblage D in the Spaanse Water displays some resemblance with the blue pool assemblage in Lac. These assemblages are characterized by relatively high quantities of *H. incrassata* and relatively low quantities of *T. testudinum*. Biotic cover is of an average level (15-20%). Besides the taxa mentioned above the benthic community consists out of a mix of mainly green algae and sponges.
Assemblage L in the Spaanse Water is a typical seagrass meadow dominated by *T. testudinum*. The *Thalassia* assemblage is a similar environment in Lac. This assemblage is situated in the bay border and central part of the bay. Both assemblages are characterized by an average depth (1.5-2 m). This distinguishes them from the deep (3.7 m) central bay assemblage in Lac which is also characterized by the presence of *T. testudinum*. Shannon index of diversity displays low values (>0.5) in both assemblages. Biotic cover is high in both assemblages, compared to other assemblages in the same study. Biotic cover in the *Thalassia* assemblage (62%) was a lot higher than in assemblage L in the Spaanse Water (30%) though.

Conclusion

The continuous seaward growth of mangroves will result in more isolated mangrove pools and a loss of bay habitat. This means that the benthic biodiversity, biotic cover and species richness of Lac will decrease, which might negatively affect its habitat, nursery and feeding function. The non-native seagrass *H. stipulacea* is also changing the bay habitats, although it is not known if this invasion will have a positive or negative effect on the percentage cover of native seagrass species and consequently on the habitat, nursery and feeding function of Lac.

The importance of the shallow water biotopes of mangrove lagoon Lac, Bonaire, as habitat and nursery for fish species

Introduction

Tropical shallow water bay biotopes as seagrass beds and mangroves contain high densities of juvenile fish (Parrish, 1989; Nagelkerken *et al.*, 2001). The presence of these bay biotopes enhance the diversity, density and biomass of fish populations of nearby reef ecosystems (Nagelkerken *et al.*, 2002; Dorenbosch *et al.*, 2004; Mumby *et al.*, 2004), indicating that the seagrass beds and mangroves are an important nursery habitat for reef fish species. Recent otolith studies on French grunt, *Haemulon flavolineatum,* (Chittaro *et al.*, 2004) and yellowtail snapper, *Ocyurus chrysurus,* (Verweij *et al.*, 2008) show the life-cycle migration of fish species from the seagrass beds and mangroves to the reef, providing more evidence for the nursery hypothesis. High food abundance, low predation pressure through structure and shade and a good environment to intercept fish larvae are the main explanations for the nursery function of seagrass beds and mangroves (Parrish, 1989; Laegdsgaard & Johnson, 2001; Verweij *et al.*, 2006). Besides this nursery function for certain species, bay biotopes function as a permanent habitat for other fish species which stay their entire life history cycle in the mangroves, seagrass beds and algal beds (Nagelkerken *et al.*, 2000b).

Lac, a 7 km^2 lagoon in the southeast of Bonaire (*Fig. 1*), contains many of these shallow water bay biotopes (Moorsel & Meijer, 1993; Lott, 2001; Engel, 2008). The nursery function of Lac's seagrass beds and mangroves was investigated in 1982 (Nagelkerken *et al.*, 2000). Size frequency data of sixteen selected fish species were collected using visual censuses. Nagelkerken *et al.* (2000) concluded that the mangroves and seagrass beds in Lac have an important nursery function for 12 of the 16 species. However, the habitats in Lac are continuously changing. The mangroves are growing seawards, reducing the surface area of open bay habitat in Lac. Mangrove growth into the bay is facilitated by banks of *Halimeda* algae, which produce calcareous sediment (Bach, 1979; Bosence, 1989) and thereby reduce water depth locally. If the water is shallow enough, *R. mangle* overgrows the *Halimeda* banks, forming mangrove pools (Moorsel & Meijer, 1993). Some pools appear dark on satellite images, while others appear blue. At the landward side of the mangroves there has been a big decrease in mangrove cover. This decades-long die-off is a (semi-) natural process, caused by the mangroves themselves but could have consequences on nursery habitat quality and availability. As mangroves grow and extend seaward, they trap sediment and organic matter between their roots. This results in accretion of land, reduced water flow, hyper-saline conditions in dry periods and the death of many mangrove trees in areas isolated from circulation and prone to drying and hyper salinity (Wagenaar Hummelinck & Roos, 1970; Lott, 2000). Reduction in freshwater inflow, caused by the construction of a dam and the road to Cai (*Fig. 1*) which were both built in the period 1951-1952, may have accelerated the die-off process (Wagenaar Hummelinck & Roos, 1970). The death of mangrove trees has created zones of muddy backwaters behind the mangroves, forming a new Lac biotope which might or might not be suitable for fish.

It is possible that the changing Lac biotopes affect its nursery and habitat function (Blaber *et al.*, 1992; Loneragan *et al.*, 1998; Nagelkerken *et al.*, 2000b). The fish biodiversity of the mangrove pools in Lac is never quantitatively described and there are no data about the species composition in the backwaters. More than 100 fish species have been observed in Lac (Moorsel & Meijer, 1993). Although many of them might be incidental observations, it is possible that the Lac biotopes are important for some of these species.

To provide further insight into the function of the Lac biotopes, size frequency data were collected of all encountered fish species in each habitat, using visual census. Visual census has the advantages that it is non-destructive, repeatable in time and inexpensive. Moreover the results are comparable with many other studies (Nagelkerken *et al.*, 2000b). With the collected data, the following questions will be answered:

1. **Which biotopes of Lac are used by which fish species?**
2. **Do the encountered fish species use the biotopes as a nursery habitat?**

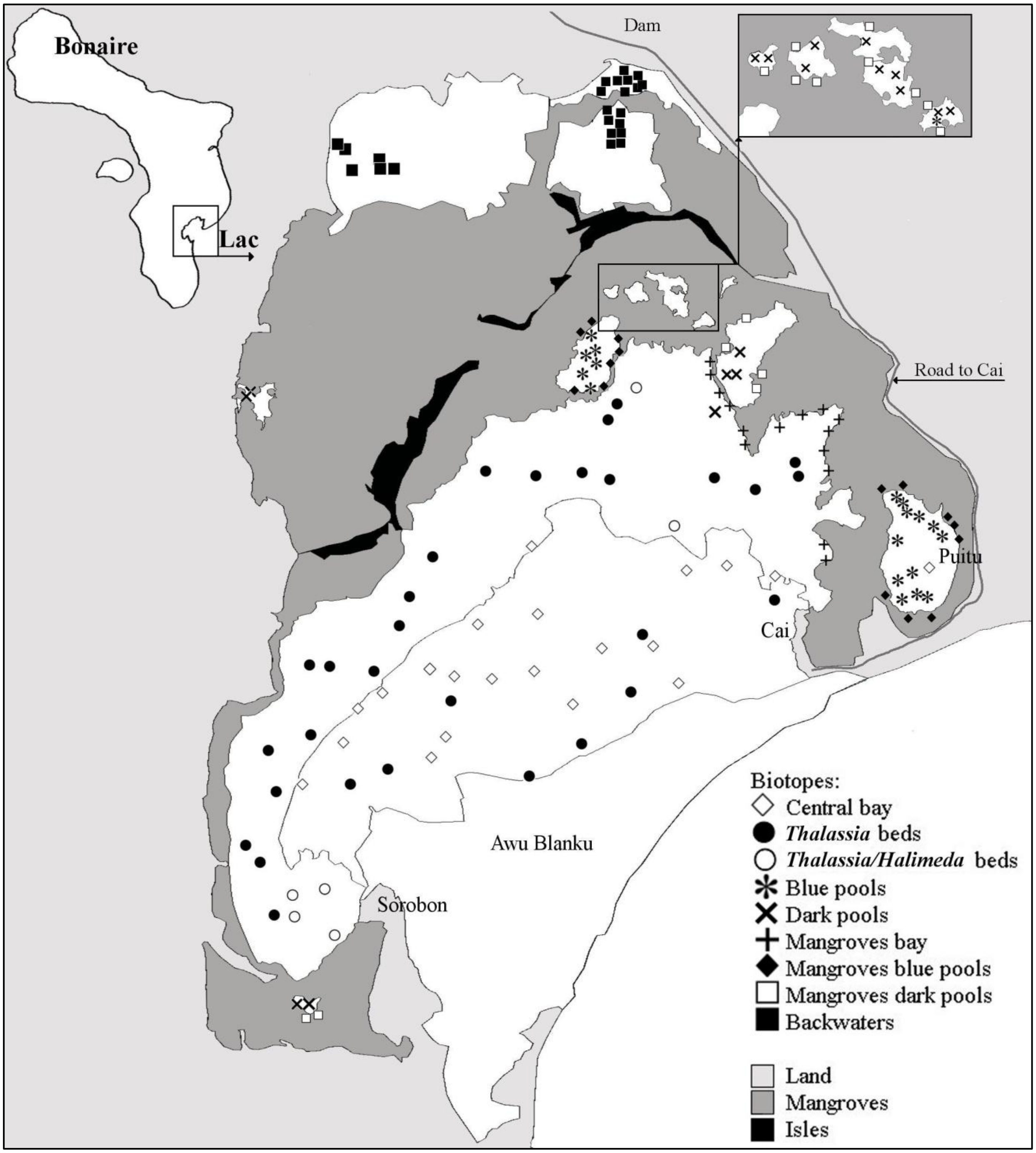

Figure 1: Lac, Bonaire. Survey sites are indicated per biotope.

Material & methods

Biotope description

In Lac, Bonaire, nine different biotopes can be distinguished. A study of the benthic biodiversity in Lac revealed that there are 5 main vegetation assemblages in the central bay, the bay border and the mangrove pools. These benthic assemblages can be regarded as different biotopes. The "central bay biotope", in which study sites are mostly located in the deeper part of Lac, has a low biotic cover which consists of a mixed vegetation of algae and the invasive seagrass *Halophila stipulacea* (*Fig. 1*). The "*Thalassia* biotope" is predominant in the bay border and the central bay and has a high biotic cover of *Thalassia testudinum*. Sometimes *T. testudinum* forms a mixed vegetation with *Halimeda* sp., this is referred to as the "*Thalassia/Halimeda* biotope". A fourth biotope, "blue pools", is mainly present in mangrove pools which appear blue on the satellite images. The benthic biodiversity here consists of algal species and upside-down jellyfish, *Cassiopeia* sp.. The fifth biotope is especially present in the dark pools. This "dark pools biotope" has a low biotic cover, mainly consisting of green algae of the genera *Batophora* and *Avrainvillea*. The bay and the blue and dark pools are all fringed with mangroves, forming three more Lac biotopes. The backwaters, created by the death of mangrove trees at the land side of Lac, form the ninth biotope. Awa Blanku is a shallow sandy platform of 1-2 meters deep, covering one third of the open bay (*Fig. 1*). Except for a few small and shallow seagrass beds near Sorobon there is almost no vegetation growing on Awa Blanku. Therefore this area is not taken into account for this research.

Mean biotic variables per biotope can be found in *Table 1*. Mean depth in the central bay biotope is 3.7 m, while the *Thalassia* and *Thalassia/Halimeda* beds have a mean depth of respectively 2 and 1.7 m. Blue pools are on average 2.5 m deep. Dark pool and mangrove fringe biotopes have a mean depth around 1 m. The backwaters average 0.4 m and are relatively shallow. Mean salinity in all biotopes, except the backwaters, ranged between 36.9 and 40.6 ppt. More landwards situated biotopes like pools and the mangroves fringing the pools have in general a higher salinity than the open bay biotopes. Mean salinity in the backwaters was 52.1 ppt and was considerably higher than all other biotopes. Temperature ranges between 28.9 and 30.0 °C, except for the backwaters were the mean temperature is 32.3 °C. Measurements were taken between September and December 2011.

Site selection

Selection of the survey sites in the mangroves was based on depth (>0.5 m) and visibility (>2 m), thus making sure visual census was possible. In all other biotopes the sites were selected using a random location generator [1]. The number of survey sites per biotope can be found in *Table 1*.

Table 1: Number of survey sites (N) and depth, salinity, temperature and sediment type per biotope.

No.	Biotope	N	Depth (m)	Salinity (ppt)	Temperature (°C)
1	Central bay	21	3.7±0.7	36.9±0.5	28.9±0.4
2	*Thalassia* beds	30	2±1.3	36.9±0.7	29.3±0.8
3	*Thalassia/Halimeda* beds	6	1.7±0.5	36.8±0.6	29.3±0.5
4	Blue pools	19	2.5±0.8	37.9±0.7	30.0±0.0
5	Dark pools	18	1.4±0.4	40.6±4.7	29.6±0.5
6	Mangrove fringes bay	15	0.9±0.2	36.9±0.6	29.1±0.8
7	Mangrove fringes blue pools	15	1.1±0.2	36.4±0.9	29.6±0.5
8	Mangrove fringes dark pools	15	1.0±0.5	37.1±0.8	29.3±0.6
9	Backwaters	23	0.4±0.2	52.1±1.7	32.3±1.1
	Total:	139			

Site survey

In each biotope, except for the backwaters, size-frequency data of all the encountered fish species were collected using a visual census technique (Nagelkerken *et al*., 2000). The 139 survey sites were reached by boat or kayak using a Garmin GPS 12 XL device. Visibility was checked and the site was revisited on another day if the visibility was less than 2 meter. At each site a 25 meter transect line was anchored on the bottom with two iron poles. A period of 15 minutes was kept between placing the transect line and surveying the site, this was enough to restore the initial fish densities (personal observation). At the mangrove sites the transect line was set out parallel of the mangrove fringe. Fish swimming in the mangroves within one meter of the transect line were identified and counted via visual census, covering an area of 25 m^2. At all other sites the observers counted all fish swimming within one meter at each site of the transect line, covering an area of 50 m^2. In case the substrate was easily disturbed and would reduce the visibility to less than two meter, the data was collected immediately while setting out the transect line.

Two observers conducted the research from September till December 2011 using SCUBA or snorkeling gear. Visual census is subject to differences in interpretation of size 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 lying on the sea bottom. Test transects were practiced by both observers until size estimates were similar for both divers and data could be pooled. Size estimation was done with size categories of 5 cm. In the case of larger groups of fish, numbers were estimated in manifold of 10 or even 100 in case of bigger schools. The backwaters were too shallow and visibility was too low to perform visual censuses, so a cast net was used instead to assess the fish biodiversity in this biotope. At 23 randomly chosen sites the net was thrown 2-4 times, resulting in 50 throws in total.

Fish identification was practiced prior to the surveys by diving and snorkeling in the research area. Unknown species were photographed and identified using an identification guide (Humann & DeLoach, 1994). At the start of the research all fish in Lac could easily be identified on 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. For small baitfish species such as silversides and scads only the presence was noted. Cryptic species like blennies and gobies were not taken into account in this study.

Abiotic variables

Physical variables were taken at every survey site. Temperature was measured with a dive computer (Suunto Zoop) to one degree precision. Field measurements were calibrated by comparing temperature measurements of the dive computer with temperature measurements of an adjusted 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 site, 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.

Data analysis

The diversity of each biotope was analyzed using the mean species richness (S) and the mean Shannon index for diversity (H’). To compare S and H’ of the mangrove transects (25 m^2) with the other transects (50 m^2), each mangrove transect was pooled together with the nearest other mangrove transect of the same biotope. Per mangrove biotope 15 transects were performed, which resulted in 7 pooled transects of 50 m^2. The remaining transect was not taking into account for the S and H’ analysis. Species richness is in this study defined as the number of species per 50 m^2 per biotope. To make the density in the mangrove transects (25 m^2) comparable with other transects (50 m^2) and with other studies, the data was standardized to density per 100 m^2. The mean fish density per biotope was calculated for each species and in total.

Kruskal-Wallis non-parametric tests were performed using the statistical package SPSS 19.0 to test for significant differences between the biotopes for biotic variables S, H’ and mean fish density.

Results

Biodiversity

During this study a total of 11986 fish were encountered in 8 biotopes where visual census was possible: central bay, *Thalassia* beds, *Thalassia*/*Halimeda* beds, blue pools, dark pools and mangroves fringing the bay, blue and dark pools. A total of 45 species belonging to 16 different families were observed (*Table 2)*. Nursery species are reef fish of which the juveniles use the bay biotopes as nursery area (Nagelkerken *et al.*, 2000b). Eleven nursery species were regularly found in Lac: *Acanthurus chirurgus, Caranx crysos, Chaetodon capistratus, Haemulon flavolineatum, H. sciurus, Lutjanus apodus, L. griseus, Ocyurus chrysurus, Scarus guacamaia, Scarus iseri* and *Sphyraena barracuda*. Bay species stay their entire life cycle in the bay biotopes and are not present or occurring only in low densities on the coral reef (Nagelkerken *et al.*, 2000b). *Eucinostomus lefroyi, E. melanopterus, E. jonesi/gula, Gerres cinereus, Halichoeres bivittatus* and *Sparisoma radians* are bay species and have a relative abundance of 10 percent or more in one of the Lac biotopes. They are therefore considered dominant bay species. All dominant species, except *H. bivittatus* and *S. radians* belong to the Gerreidae family. The relative abundance of the nursery and dominant bay species is shown in *Table 3*.

The most abundant species in the central bay are *S. iseri, H. flavolineatum* and *C. crysos* (*Table 2*). The central bay is also an important biotope for *E. jonesi/gula, H. bivittatus* and the parrotfish *S. radians.* In the *Thalassia* and *Thalassia/Halimeda* biotopes *S. iseri* represents respectively 66 and 70 percent of all fish that were encountered. Other abundant species are *H. bivittatus, S. radians* and *L. griseus*. The Gerreidae family is almost absent in these biotopes. The mangrove fringe biotopes show large differences in species abundance. In the mangroves fringing the bay all nursery and dominant species, except the mojarra *E. lefroyi* are present. The parrotfish *S. iseri* and *S. guacamaia* are with respectively 55 and 10 percent the most abundant species. *S. guacamaia* is also abundant in the mangroves fringing the blue pools, but *S. iseri* is absent in this biotope. For the Gerreidae and the snappers *L. apodus* and *L. griseus* this is an important biotope. The mangroves fringing the dark pools show a comparable species abundance. In the blue and dark pool mangrove biotopes the Gerreidae have a relative abundance of respectively more than 30 and more than 50 percent. *L. griseus* is the most abundant species in the blue pool mangrove biotope and is also very abundant in the dark pool mangrove biotope.

The backwater biotope was sampled with a cast net. Fish species present in this biotope are shown in *Table 2*. *Elops saurus* and *Mugil curema* were two species exclusively found in the backwaters. Other species observed here were *Cyprinodon dearborni*, *Atherinomorus stipes* and 3 species of Gerreidae. These species were also observed in the mangrove fringe and the dark pool biotopes.

Total fish density was highest in the mangroves fringing the bay, on average 350 fish were observed here per 100 m^2 (*Fig. 2*). Although this is twice as high as the mean fish density in mangroves fringing the blue pools and the *Thalassia* biotope, they did not significantly differ. The mean fish density in the mangrove fringes and the *Thalassia* biotopes was significantly higher than the central bay and the mangrove pool biotopes. Mean species richness (S) per biotope can be seen in *Fig. 3.* On average, there are 12 (±2.83) species found per 50 m^2 in the mangroves fringing the bay, which is significantly higher than the central bay, blue pool and dark pool biotopes. The *Thalassia* biotope and mangroves fringing the blue pools also have a significantly higher species richness compared to the central bay, blue and dark mangrove pool biotopes. Species richness in the mangroves fringing the dark pools was significantly higher than species richness in the dark mangrove pool biotope, though not significantly different from the other biotopes. Shannon index for diversity (H’) is highest in the mangrove biotopes, which are significantly different from the central bay, blue and dark pool biotopes, but not from the *Thalassia* and *Thalassia/Halimeda* biotopes (*Fig. 4*).

Table 2: Mean density per 100 m^2 of all encountered fish species per biotope. P=present (not counted), -=absent

		Central Bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangroves bay	Mangroves blue pools	Mangroves dark pools	Backwaters
	Acanthuridae									
1	*Acanthurus chirurgus*, docterfish	0,9 ± 3,1	0,8 ± 2,1	-	-	-	-	3,5 ± 8	-	-
	Atherinidae									
2	*Atherinomorus stipes*, hardhead silverside	-	-	-	-	-	P	P	P	P
	Carangidae	**3,5**	**7,0**	**-**	**1,2**	**0,1**	**0,3**	**1,6**	**2,7**	
3	*Caranx crysos*, blue runner	3,5 ± 7,4	6,9 ± 20,1	-	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 ± 1,3	0,2 ± 0,8	0,3 ± 0,8	0,1 ± 0,5	-	3,5 ± 4,7	-	0,3 ± 1	-
	Cyprinodontidae									
9	*Cyprinodon dearborni*	-	-	-	-	-	-	-	P	P
	Diodontidae									
10	*Chilomycterus schoepfi*, striped burrfish	-	0,1 ± 0,4	-	-	-	-	-	-	-
	Elopidae									
11	*Elops saurus*, ladyfish	-	-	-	-	-	-	-	-	P
	Gerreidae	**2,9**	**0,5**	**2,6**	**2,8**	**5,1**	**29,5**	**51,7**	**57,3**	**P**
12	*Diapterus auratus*, Irish pompano	-	-	-	-	-	0,5 ± 2,1	0,5 ± 1,4	0,5 ± 1,4	P
13	*Eucinostomus lefroyi*, mottled mojarra	-	-	-	-	1,8 ± 7,5	-	-	-	-
14	*Eucinostomus melanopterus*, flagfin mojarra	0,1 ± 0,4	0,1 ± 0,4	-	1,4 ± 4,7	0,6 ± 1,9	16,8 ± 17,8	36,8 ± 68,5	19,2 ± 33,6	-
15	*Eucinostomus jonesi / E. gula*, silver jenny / slender mojarra	2,6 ± 11,8	0,3 ± 1,1	2,3 ± 5,7	-	-	2,9 ± 7,6	1,6 ± 5,2	-	P
16	*Gerres cinereus*, yellowfin mojarra	0,2 ± 0,6	0,1 ± 0,5	0,3 ± 0,8	1,4 ± 3,8	2,7 ± 5,1	9,3 ± 10,5	12,8 ± 14,7	37,6 ± 28	P
	Haemulidae	**3,9**	**4,9**	**-**	**-**	**-**	**19,7**	**16,3**	**0,8**	**-**
17	*Anisotremus surinamensis*, black margate	0,1 ± 0,4	1,2 ± 6,2	-	-	-	-	-	-	-
18	*Haemulon flavolineatum*, French grunt	3,8 ± 17,5	1,3 ± 7,3	-	-	-	18,4 ± 32	14,4 ± 51,4	-	-
19	*Haemulon sciurus*, bluestriped grunt	-	2,4 ± 5,4	-	-	-	1,3 ± 3,3	1,9 ± 3	0,8 ± 1,7	-
	Labridae	**3,3**	**12,5**	**12,3**	**-**	**-**	**0,5**	**-**	**-**	**-**
20	*Halichoeres bivittatus*, slippery dick	2,2 ± 4,6	12,3 ± 24,2	12 ± 16,1	-	-	0,5 ± 1,4	-	-	-
21	*Serranus tigrinus*, harlequin bass	0,1 ± 0,4	-	-	-	-	-	-	-	-
22	*Thalassoma bifasciatum*, bluehead wrasse	-	-	0,3 ± 0,8	-	-	-	-	-	-
23	*Xyrichthys martinicensus*, rosy razorfish	0,9 ± 3,9	0,1 ± 0,4	-	-	-	-	-	-	-
24	*Xyrichthys splendens*, green razorfish	0,1 ± 0,4	0,1 ± 0,7	-	-	-	-	-	-	-

		Central Bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangroves bay	Mangroves blue pools	Mangroves dark pools	Backwaters
	Lutjanidae	**0,3**	**20,4**	**3,0**	**5,0**	**3,1**	**33,6**	**60,8**	**25,6**	**-**
25	*Lutjanus apodus*, schoolmaster	-	1,5 ± 2,8	-	1,4 ± 2,6	0,4 ± 1,5	22,1 ± 15	23,5 ± 17,4	7,5 ± 8,7	-
26	*Lutjanus cyanopterus*, Cubera snapper	-	-	-	-	-	0,3 ± 1	0,5 ± 2,1	0,5 ± 1,4	-
27	*Lutjanus griseus*, grey snapper	-	15,1 ± 23,9	3 ± 3,9	3,6 ± 7,5	2,7 ± 9,4	10,9 ± 17	36,8 ± 40,3	17,6 ± 19,6	-
28	*Lutjanus mahogoni*, mahogany snapper	-	0,1 ± 0,4	-	-	-	-	-	-	-
29	*Ocyurus chrysurus*, yellowtail snapper	0,3 ± 1	3,7 ± 6,3	-	-	-	0,3 ± 1	-	-	-
	Mugilidae									
30	*Mugil curema*, white mullet	-	-	-	-	-	-	-	-	P
	Mullidae	**0,0**	**0,2**	**-**	**-**	**-**	**0,5**	**0,3**	**-**	-
31	*Mulloidichtys martinicus*, yellow goatfish	-	-	-	-	-	0,5 ± 2,1	0,3 ± 1	-	-
32	*Pseudupeneus maculatus*, spotted goatfish	-	0,2 ± 0,8	-	-	-	-	-	-	-
	Ostraciidae	**0,6**	**0,1**	**-**	**-**	**-**	**1,0**	**0,3**	**-**	-
33	*Lactophrys bicaudalis*, spotted trunkfish	-	-	-	-	-	0,5 ± 1,4	-	-	-
34	*Lactophrys triqueter*, smooth trunkfish	0,6 ± 1,8	0,1 ± 0,5	-	-	-	0,5 ± 1,4	0,3 ± 1	-	-
	Pomacentridae	**0,3**	**2,9**	**3,3**	**-**	**-**	**9,9**	**-**	**-**	-
35	*Abudefduf saxatilis*, sergeant major	-	-	-	-	-	2,4 ± 5,8	-	-	-
36	*Microspathodon chrysurus*, yellowtail damsel	-	0,1 ± 0,5	-	-	-	-	-	-	-
37	*Stegastes diencaeus*, longfin damselfish	-	0,1 ± 0,5	-	-	-	0,3 ± 1	-	-	-
38	*Stegastes leucostictus*, beaugregory	0,3 ± 0,7	2,7 ± 4,7	3,3 ± 4,1	-	-	7,2 ± 15,1	-	-	-
	Scaridae	**8,2**	**135,2**	**73,7**	**0,1**	**0,2**	**252,8**	**21,6**	**23,9**	**-**
39	*Cryptotomus roseus*, bluelip parrotfish	0,1 ± 0,4	0,1 ± 0,7	2,7 ± 3	-	-	-	-	-	-
40	*Scarus coeruleus*, blue parrotfish	-	-	0,3 ± 0,8	-	-	-	-	1,3 ± 5,2	-
41	*Scarus guacamaia*, rainbow parrotfish	-	0,1 ± 0,7	-	-	0,2 ± 0,9	34,7 ± 56,9	19,2 ± 28,6	22,1 ± 43,5	-
42	*Scarus iserti*, striped parotfish	4,9 ± 10,7	122,7 ± 144,3	66,7 ± 163,3	-	-	195,2 ± 311,9	2,4 ± 6,7	-	-
43	*Sparisoma aurofrenatum*, redband parrotfish	0,1 ± 0,4	0,1 ± 0,4	-	-	-	-	-	-	-
44	*Sparisoma radians*, bucktooth parrotfish	3,1 ± 7	11,3 ± 14,4	4 ± 4,6	0,1 ± 0,5	-	18,4 ± 35,1	-	-	-
45	*Sparisoma rubripinne*, yellowtail parrotfish	-	-	-	-	-	-	-	0,5 ± 2,1	-
46	*Sparisoma viride*, stoplight parrotfish	-	0,9 ± 1,8	-	-	-	4,5 ± 6,6	-	-	-
	Sphyraenidae									
47	*Sphyraena barracuda*, great barracuda	-	-	-	0,1 ± 0,5	-	2,4 ± 2,5	2,9 ± 2,8	1,3 ± 2,5	-

Table 3: Relative abundance (%) of selected nursery species (n) and dominant species (>10% abundance in one of the biotopes, d) in each biotope.

		Central bay	*Thalassia*	*Thalassia/ Halimeda*	Blue pools	Dark pools	Mangrove bay	Mangrove blue	Mangrove dark
Acanthurus chirurgus	n	3,7	0,4	-	-	-	-	2,2	-
Caranx crysos	n	14,5	3,7	-	12,9	-	0,1	1,0	-
Chaetodon capistratus	n	1,2	0,1	0,3	1,1	-	1,0	-	0,3
Eucinostomus lefroyi	d	-	-	-	-	21,2	-	-	-
Eucinostomus melanopterus	d	0,4	0,1	-	15,1	7,1	4,7	23,1	17,1
Eucinostomus jonesi/E. gula	d	10,7	0,2	2,4	-	-	0,8	1,0	
Gerres cinereus	d	0,8	0,1	0,3	15,1	31,8	2,6	8,1	33,5
Haemulon flavolineatum	n	15,7	0,7	-	-	-	5,2	9,1	-
Haemulon sciurus	n	-	1,3	-	-	-	0,4	1,2	0,7
Halichoeres bivittatus	d	9,1	6,7	12,6	-	-	0,1	-	-
Lutjanus apodus	n	-	0,8	-	15,1	4,7	6,2	14,8	6,7
Lutjanus griseus	n	-	8,2	3,2	38,7	31,8	3,1	23,1	15,7
Ocyurus chrysurus	n	1,2	2,0	-	-	-	0,1	-	-
Scarus guacamaia	n	-	0,1	-	-	2,4	9,8	12,1	19,7
Scarus iseri	n	20,2	66,4	70,1	-	-	55,2	1,5	-
Sparisoma radians	d	12,8	6,1	4,2	1,1	-	5,2	-	-
Sphyraena barracuda	n	-	-	-	1,1	-	0,7	1,8	1,2
Total		90,5	96,8	93,1	100,0	98,8	95,3	99,0	94,7

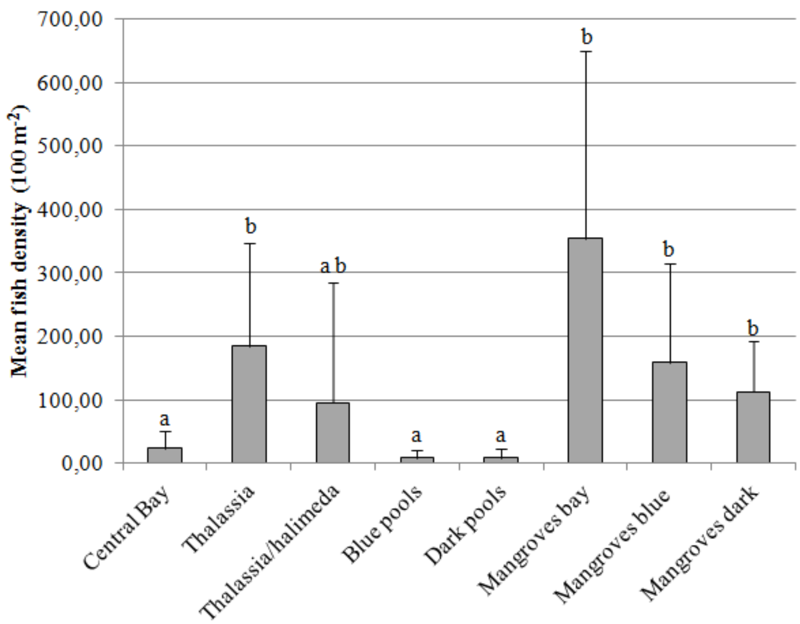

Figure 2: Mean fish density per 100 m^2 in each biotope (+SD). Letters indicate statistically similar densities.

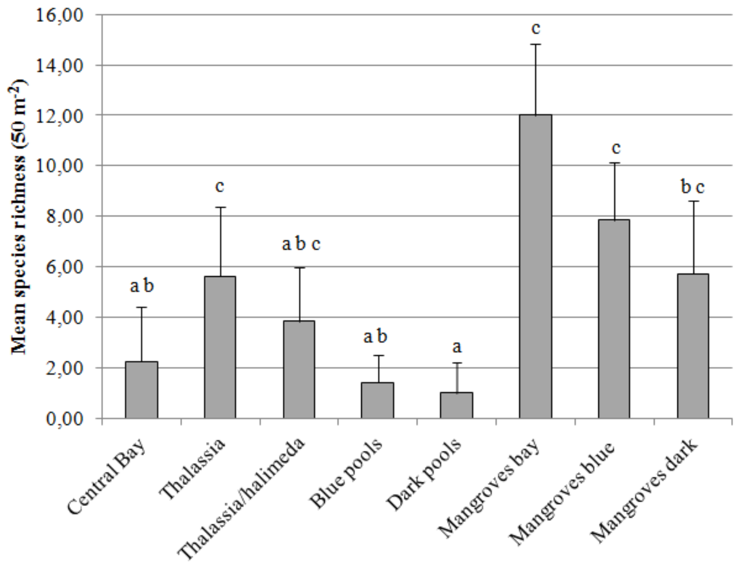

Figure 3: Mean species richness (S) per 50 m^2 in each biotope (+SD). Letters indicate statistically similar densities.

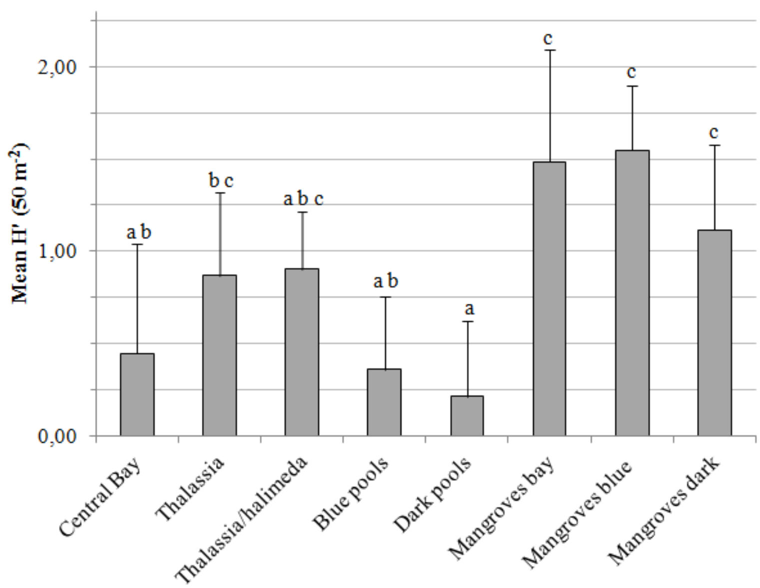

Figure 4: Mean Shannon index (H') per 50 m^2 in each biotope (+SD). Letters indicate statistically similar densities.

Nursery function

The density per size class of 11 selected nursery species can be found in *Fig. 5* and *Fig. 6.* Mean length at first maturity (L_m) of these species is presented in *Table 4.* Juveniles of *Acanthurus chirurgus* mainly used the central bay and *Thalassia* biotopes, while adults were observed in the mangrove fringes of the blue pools. All observed *Chaetodon capistratus* mainly used the mangroves fringing the bay. Mean length at first maturity is 7 cm (Bouchon-Navaro *et al.*, 2006), which makes it difficult to conclude if the observed fish in the size class 5-10 cm were large juveniles or adults. *Caranx crysos* was found in only one size class: 15-20 cm. The L_m of this species is 20 cm or more (Munro, 1983), so most observed fish probably were juveniles. *Thalassia* and central bay biotopes were the most important for *C. crysos*. L_m for *Haemulon flavolineatum* is 18.8 cm (Bouchon-Navaro *et al.*, 2006), so most encountered individuals were juveniles. Mangrove habitats of the bay and blue pools were the main biotope for this species. *Haemulon sciurus* was encountered in all mangrove fringes and in the *Thalassia* biotope. Most individuals were observed in the size class 15-20 cm, which can be regarded to as large juveniles because L_m of this species is 22 cm (Faunce & Serafy, 2007). *Sphyraena barracuda* individuals were found in all size classes up to 60 cm. According to the L_m of 58 cm (Faunce & Serafy, 2008), almost all of them were juveniles. Small juveniles, 0-20 cm, were found in mangroves fringing the bay and the blue pools, while larger juveniles mainly used the mangroves of the blue and the dark pools.

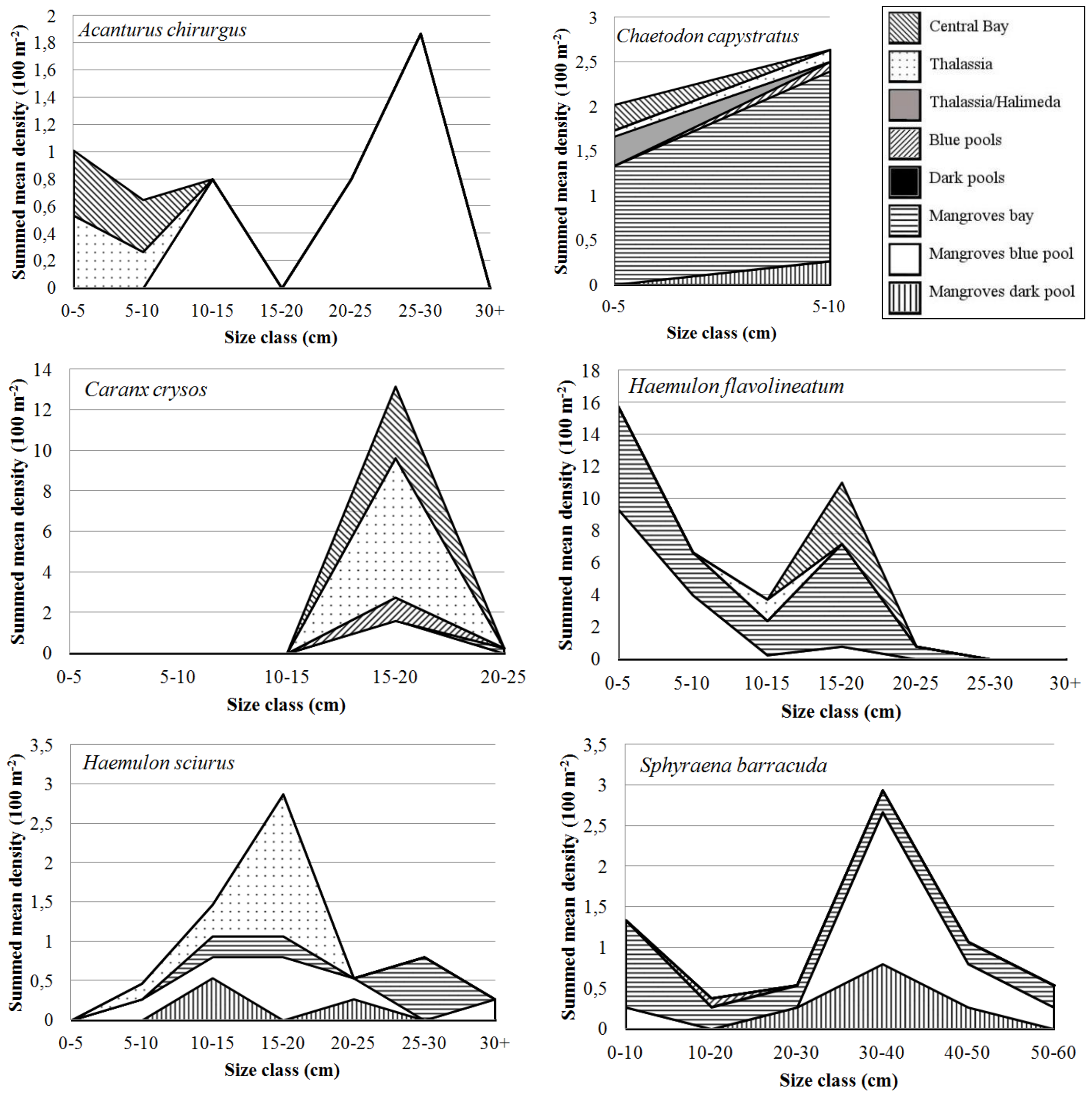

Figure 5: Summed mean densities per biotope for Acanthurus chirurgus, Caranx crysos, Chaetodon capistratus, Haemulon flavolineatum, Haemulon sciurus and Sphyraena barracuda.

The snappers *Lutjanus apodus* and *Lutjanus griseus* were both found in large numbers. Almost all individuals of *L. apodus* can be regarded as juveniles, because they were smaller than the length at first maturity (25.8 cm) (Martinez-Andrade, 2003). Most individuals of *L. griseus* were also juveniles (L_m=19 cm) (Faunce & Serafy, 2007), although adults were also regularly observed in the Lac biotopes. Juveniles of both species mainly used the mangroves fringes of bay, dark and blue pools. Juvenile *L. griseus* also used the *Thalassia* biotope and adult *L. griseus* mainly utilized the mangrove fringes of the blue and dark pools. From the third snapper species, *Ocyurus chrysurus*, the mean length at first maturity is 32.3 cm. All observed individuals were therefore juveniles and *Thalassia* beds were their most important biotope. *Scarus iseri* juveniles, all smaller than L_m=15.9 cm (Bouchon-Navaro *et al.*, 2006), were observed in the mangroves fringing the bay, *Thalassia* and *Thalassia/Halimeda* biotopes. From the parrotfish *Scarus guacamaia* no L_m data are known. However, coloration indicates that all observed individuals were juveniles. The mangrove habitats were clearly very important for this species, because they are not observed in any other biotope.

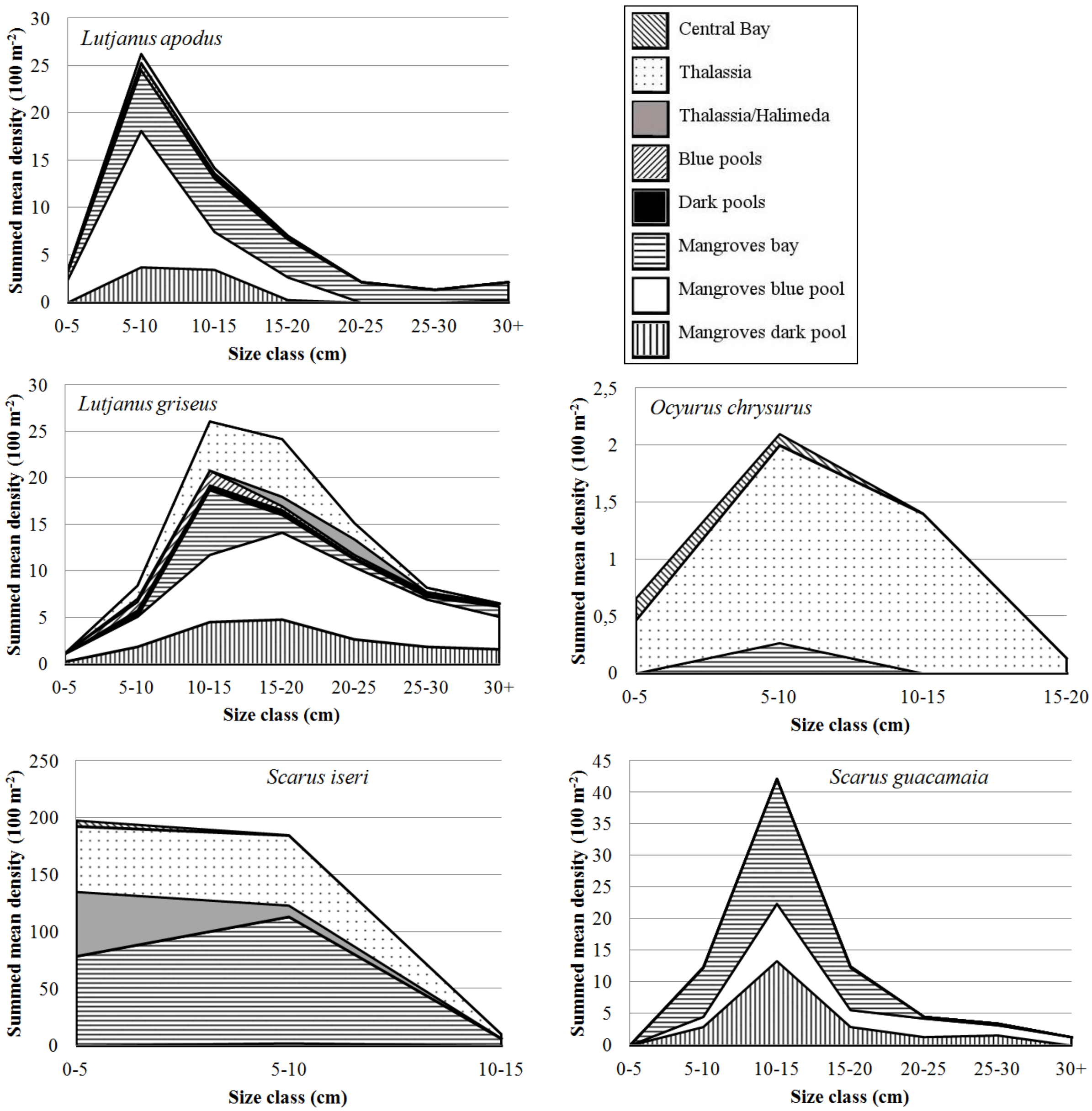

Figure 6: Summed mean densities per biotope for Lutjanus apodus, Lutjanus griseus, Ocyurus chrysurus, Scarus guacamaia and Scarus iseri.

Table 4: Mean length at first maturity (L_m) for 11 selected nursery species. Data are from Bouchon – Navaro et al. (2006), Faunce & Serafy (2007), Faunce & Serafy (2008), Martinez-Andrade (2003), Mateo & Tobias (2001) and Munro (1983). nd=no data

Species	L_m (cm)
Acanthurus chirurgus	14.0
Caranx crysos	>20
Chaetodon capistratus	7.0
Haemulon flavolineatum	18.8
Haemuleon sciurus	22.0
Lutjanus apodus	25.8
Lutjanus griseus	19.0
Ocyurus chrysurus	32.3-42.1
Scarus guacamaia	nd
Scarus iseri	15.9
Sphyraena barracuda	58

Discussion

The central bay biotope has a significantly lower species richness and fish density than the *Thalassia* beds and the mangroves fringes of the bay and blue pools. The Shannon index of diversity is significantly lower than in the mangrove fringe biotopes. This low density and diversity of fishes is possibly caused by the low biotic cover and low spatial structure in the central bay biotope, which results in less protection and feeding opportunities. Juvenile *Caranx crysos* were found in the central bay biotope and in deeper sites of the *Thalassia* biotope. Other studies have found that *Sargassum*-mats have a nursery function for small (1-13 cm) juveniles of *C. crysos* (Wells & Rooker, 2004), but no data are available about the preferred habitat of bigger juveniles. Our results suggest that tropical bay biotopes have a nursery function for bigger *C. crysos* juveniles, although the habit of *C. crysos* to follow the boat may have resulted in an overestimation of their numbers. This may also be the case with *Lactophrys triqueter*, which seemed to approach the divers out of curiosity during the survey. All other fish species do not seem to be either scared or attracted by the transect line, the boat or the observers unless closely approached.

The *Thalassia* beds have a significantly higher species richness and fish density than the blue and dark pool biotopes. This may be explained by the presence of spatial structure in the *Thalassia* beds in contrast to the much less vegetated blue and dark pools. Besides offering protection the *Thalassia* beds function as feeding grounds for juvenile Scaridae (Ogden & Ehrlich, 1977; Robblee & Zieman, 1984; Nagelkerken *et al.*, 2000a). This is confirmed by high densities of *Scarus iseri* and *Sparisoma radians* in this biotope. *S. iseri* is more abundant in the mangrove fringes of the bay than on the seagrass beds in this study. *S. radians* seems to be a resident of Lac in all life stages and was often encountered in the *Thalassia*, *Thalassia/Halimeda* and central bay biotope. Numbers of this species may have been underestimated due to their camouflage and habit to stay motionless in the *Thalassia* beds when approached. Haemulidae and Lutjanidae feed on macro-invertebrates which emerge from the *Thalassia* beds during the night (Ogden & Ehrlich, 1977; Nagelkerken *et al.*, 2000a). However, numbers of *L. apodus*, *L. griseus* and *H. flavolineatum* were relatively low compared to numbers encountered in the mangrove fringes. This difference might be caused by surveying during daytime, when these species seek cover in the mangrove fringes (Ogden & Ehrlich, 1977; Nagelkerken *et al.*, 2000a). Many juvenile *O. chrysurus* were encountered in the *Thalassia* beds. This confirms results of earlier studies that indicate their dependence on seagrass beds as nursery grounds (Robblee & Zieman, 1984; Nagelkerken *et al.*, 2000; Verweij *et al.*, 2008), although there are studies which suggest the preference of juvenile *O. chrysurus* for mangrove fringes (Cocheret de la Morinière, E. *et al.*, 2002).

The mangrove fringe biotopes have a significantly higher species richness, diversity and fish density than the open parts of the blue pools and dark pools. This is possibly caused by the absence of dense vegetation in the blue pools and dark pool biotopes, which means there are little feeding and shelter opportunities. Most of the fish found in the blue and dark mangrove pools were Gerreidae and Lutjanidae. The zoobenthivoric Gerreidae seemed to use the open parts of the blue pools and dark pools for feeding purposes. The Lac biotopes are probably a permanent habitat for Gerreidae, because both adults and juveniles were observed in high densities. The complexity of the environment in the mangrove fringe biotopes provides plenty protection possibilities (Laegdsgaard & Johnson, 2001). Gerreidae and Lutjanidae were the most observed species in these biotopes, but juvenile *Scarus guacamaia* was also found in high densities. This is in accordance with other studies which underline the dependence of *S. guacamaia* on mangroves as nursery habitat (Nagelkerken & Velde, 2003; Mumby *et al.*, 2004; Nagelkerken, 2007). The density of *S. guacamaia* was high compared to mangrove related studies in other parts of the Caribbean (Nagelkerken *et al.*, 2000b; Serafy *et al.*, 2003). Other species of Scaridae were encountered in the mangrove fringes of the bay. High numbers of these species may be a result of the presence of *Thalassia* beds up to the point at which the mangroves grow. This creates a mixed biotope containing species found in mangrove fringes and species found on the *Thalassia* beds.

Although no quantitative comparison is possible due to fact that the sampling method differed from the visual census used in the other biotopes, it is clear that the backwaters are inhabited by different fish species than the other Lac biotopes. Nursery species are not found here, but *A. stipes, C. dearborni, E. saurus, M. curema* and many species of the Gerreidae family are common in this biotope.

Comparison with prior studies

The nursery function of Lac's *Thalassia* beds and mangroves fringing the bay was investigated in 1982 (Nagelkerken *et al.*, 2000). Nagelkerken *et al.* (2000) did not examine the various pool habitats, backwater areas or central bay habitats. Size frequency data of 16 selected fish species were collected using visual censuses. Nine of these species were regularly encountered in the Lac biotopes: *Acanthurus chirurgus, Chaetodon capistratus, Haemulon flavolineatum, Haemulon sciurus, Lutjanus apodus, Lutjanus griseus, Ocyurus chrysurus, Sparisoma viride* and *Sphyraena barracuda*. These species were also observed in the present study, but most of them are found in different densities compared to 1982. *H. flavolineatum* densities in the mangroves were 3 times higher than in 1982, but densities in *Thalassia* beds are much lower. Both studies are performed during daytime, so the ontogenetic day -night pattern (Ogden & Ehrlich, 1977; Nagelkerken *et al.*, 2000a) of this species cannot be the cause of the difference. Intensified recreation in the bay biotopes (Lott, 2001) might be an explanation for the shift in biotope preference. However, higher densities of other fish species on *Thalassia* beds, compared to Nagelkerken *et al.* (2000) contradict this reasoning. Densities of *H. sciurus*, another Haemulid, were around 4 times higher in both mangrove and *Thalassia* biotopes in 2011 when compared to 1982. The same trend can be observed in the Lutjanidae family, densities of *O. chrysurus* and *L. apodus* were 2-3 times higher than in 1982. The mean density of *L. griseus* on the seagrass beds was more than 15 times higher in 2011, while in the mangroves densities are 3 times higher. *S. barracuda* densities in the mangrove biotope are 5 times higher compared to the data of 1982 but are comparable to data collected in Florida in 1999 (Eggleston *et al.*, 2004).

Part of the difference in fish density on the seagrass beds might be explained by the used methodology. Nagelkerken *et al.* (2000) used bigger transects: 300 x 3 m. The seagrass cover in Lac is patchy. Therefore it is possible that less vegetated areas, where fish densities are lower, were included in the transects in 1982, whereas we made narrower habitat distinctions. The transects in our study are 25 x 2 meter and randomly chosen. Seagrass beds are discerned from other biotopes by cluster analysis, which results in a high seagrass cover in each transect. Another difference between our study and the study of Nagelkerken *et al.* (2000) is the depth of the sampled area. Mean depth of the *Thalassia* beds in this study is 2 m, while the *Thalassia* beds of the 1982 study ranged 0.4-1.4 m. Although shallow seagrass beds do not seem to be less attractive to fish (personal observation), they are more difficult to survey. Shallow beds are more easily disturbed and the view is obstructed by *T. testudinum* leaves. It is therefore possible that part of the difference in density is explained by the shallowness of the seagrass beds in 1984. However, this leaves the differences in mangrove densities unexplained. Reduced fishing pressure, which showed a declining trend from 1987 to 1992 (Moorsel & Meijer, 1993), is likely to be responsible for the largest part of the difference in fish densities between the studies.

Nagelkerken *et al.* (2000) concluded that the seagrass beds are the most important nursery biotope for *A. chirurgus, H. flavolineatum, H. sciurus, O. chrysurus* and *S. viride*, while *C. capistratus, L. apodus, L. griseus* and *S. barracuda* rather utilized the mangrove fringes as a nursery. This is in accordance with the present study, with the exception of the biotope preference of the grunts *H. flavolineatum* and *H. sciurus*. Juvenile *H. sciurus* in this study occurred in seagrass beds and mangrove fringes in similar densities. Juvenile *H. flavolineatum* were almost absent in the seagrass beds in 2011, while they occurred in high densities in the mangroves. This was also found by a study conducted in 1998 in the Spaanse Water, Curacao, where significantly higher densities of *H. flavolineatum* and *H. sciurus* were found in mangrove fringes compared to densities in seagrass beds (Cocheret de la Morinière *et al.*, 2002).

Conclusion

The Lac biotopes have an important nursery and habitat function for many fish species. Seagrass beds and mangroves fringes have a higher fish density, species richness and diversity than the algal beds and the non-vegetated biotopes in the central bay and mangrove pools. The more isolated mangrove pools and backwaters have the lowest species richness. Lac's seagrass beds are a nursery for *Acanthurus chirurgus, Caranx crysos, Haemulon sciurus, Lutjanus apodus, Lutjanus griseus, Ocyurus chrysurus* and *Scarus iseri*. *Chaetodon capistratus, Haemulon flavolineatum, Haemulon sciurus, Lutjanus apodus, Lutjanus griseus, Scarus guacamaia, Scarus iseri* and *Sphyraena barracuda* principally utilize the mangroves as nursery. The central bay and blue pool biotopes are hardly used as nursery, while in the dark pools and the backwaters nursery species are totally absent.

If the mangroves continue to expand uncontrolled further into the bay, which is happening at the moment, more isolated biotopes such as the backwaters might be created. Seagrass beds and mangrove fringes, the most valuable nursery biotopes with the highest fish density, species richness and diversity, will decrease in size.

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[1] random location generator: www.geomidpoint.com/random/