ISSN-0034-7744

REVISTA DE
BIOLOGÍA TROPICAL

INTERNATIONAL JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

UNIVERSIDAD DE
COSTA RICA

Volume 62 (Suppl. 3) • September, 2014 • Volumen 62 (Supl.3) • Setiembre, 2014
San José, Costa Rica • www.biologiatropical.ucr.ac.cr

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Revista de Biología Tropical

EDITORIAL
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PROCEEDINGS OF THE 36TH SCIENTIFIC MEETING OF THE
MEMORIAS DE LA 36TA REUNIÓN CIENTÍFICA DE LA
ASSOCIATION OF MARINE LABORATORIES OF THE CARIBBEAN (AMLC)
ASOCIACIÓN DE LABORATORIOS MARINOS DEL CARIBE (ALMC)

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Revista de Biología Tropical • Universidad de Costa Rica • 11501-2060 San José, Costa Rica

Graphic Editor / Editor Gráfico:
Sergio Aguilar Mora

Technical Editor / Editora Técnica:
Carolina Seas Carvajal

Cover photographs / Fotografías de portada:
Photographs taken during the 36th Scientific Meeting of the Association of Marine Laboratories of the Caribbean, hosted by Discovery Bay Marine Laboratory at Sunset Jamaica, Grande Ocho Rios, Jamaica, June 17-21, 2013. Photographs by Peter Ainsworth, Dale Webber and Deana-Lee Douglas.

574.05
R Revista de Biología Tropical / Universidad de Costa Rica. —Vol. 1
(1953)– . — San José, C. R. : Editorial Universidad de
Costa Rica, 1953–
v.

ISSN–0034–7744

1. Biología – Publicaciones periódicas, 2. Publicaciones
periódicas costarricenses.

BUCR

Edición aprobada por la Comisión Editorial de la Universidad de Costa Rica

Apdo. 11501-2060 • Tel.: 2511-5310 • Fax: 2511-5257
E-mail: distribucionyventas.siedin@ucr.ac.cr • Página web: www.editorial.ucr.ac.cr

Revista de
Biología Tropical
INTERNATIONAL JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Volume 62 (Suppl. 3) • Volumen 62 (Supl. 3) September, 2014 • Setiembre, 2014

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Asociación de Laboratorios Marinos del Caribe (ALMC)

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PROCEEDINGS OF THE 36TH SCIENTIFIC MEETING OF THE ASSOCIATION OF MARINE LABORATORIES OF THE CARIBBEAN (AMLC)

PROGRAMME

Day 1: Monday June 17, 2013

Time	Presenters	Author & Title
8:00	Registration	
Opening Ceremony		
9:00	Chair: **Professor Ishenkumba Kahwa**, Dean, Faculty of Science & Technology, UWI, Mona Campus	
	Welcome & Opening Remarks. Mr. Peter Gayle, President, AMLC	
9:30	**Plenary 1** ***Why are some Caribbean coral reefs much healthier than others?*** Prof Jeremy Jackson, Smithsonian Institution and Scripps Institution of Oceanography	
10:10	**Q&A**	
10:30-11:00		Coffee Break
Session 1: Global and Regional Issues — Chair: James Crabbe		
11:00	Sandeman, I.	Using a torsion microbalance in a closed system, weight changes of *Agaricia agaricites* and concomitant changes of pH confirm that carbon dioxide is the substrate for calcification in living corals and points to problems with the alkalinity anomaly technique. *Ian Sandeman*
11:20	Pratte, Z.	The potential impact of global climate change on an essential component of coral innate immunity. *Zoe A. Pratte, Laurie L. Richardson*
11:40	Wieters, E.	Temperature anomaly trends correlate with coral reef trajectory. *E. Wieters, B. Riegl, A. Bruckner, S. Purkis*
12:00	Vardi, T.	Regional analysis of *Acropora palmata* population dynamics using Matrix Modeling with stochasticity. *Tali Vardi, Dana Williams, Stuart Sandin*
12:20		Announcements and Housekeeping
12:30-1:30		Lunch
Session 2: Oceanography and Coastal Processes (1) — Chair: Jorge Cortés Núñez		
1:30	Sherman, C.	Terrigenous sedimentation patterns at reefs adjacent to the Guanica Bay Watershed, Southwest Puerto Rico. *Clark Sherman, Yahaira Hutchinson, Raquel Hernández*
1:50	Small, H.	The planktonic communities of the Jamaican south eastern coastal shelf; a comparison of harbor, coastal shelf and offshore oceanic bank areas. *Hugh Small, Kristoffer Lue, Dale Webber, Mona Webber*
2:10	Chamberland, V.	Direct and indirect effects of nutrients on pre- and post-settlement performance of Caribbean corals. *Valérie F. Chamberland, Mark J. A. Vermeij*
2:30	Mitchell, A.	Sampling and analysis of ballast water in the Jamaican scenario. *Achsah A. Mitchell, Mona Webber, Dayne Buddo, Dale Webber*
2:50	Hutchinson, Y.	Composition of lithic substrates from mesophotic habitats in Puerto Rico and US Virgin Islands. *Yahaira Hutchinson, Clark Sherman*
Session 3: Oceanography and Coastal Processes (2) — Chair: Chris Corbin		
3:30	Tussenbroek, B.	CARICOMP seagrass monitoring: stability and change of seagrass communities throughout the Greater Caribbean. *Brigitta I. van Tussenbroek, Jorge Cortés, Ana C. Fonseca , Peter Gayle, Hector M. Guzmán, Gabriel E. Jácome, Rahanna Juman , Karen H. Koltes, Hazel A. Oxenford, Alberto Rodríguez Ramirez, Jimena Samper-Villarreal, Struan R. Smith, John J. Tschirky, Ernesto Weil*
3:50	Soler Figueroa, B.	Bioluminescent levels at Bahia Fosforescente: myth vs reality. *Brenda M. Soler Figueroa, Ernesto Otero*
4:10	Aldana Moreno, A.	Variación espacio-temporal de la estructura comunitaria de peces en el Parque Ecoturístico Xel-Há. *Alejandro Aldana Moreno, Jorge Montero Muñoz, Dalila Aldana Aranda*
4:30	Collado-Vides, L.	Halimeda dynamics relative to nutrients availability in the Florida Keys and Florida Bay: a good indicator of C production. *Ligia Collado-Vides, Alex Perez, James Fourqurean*
4:50	Announcements and Housekeeping	
5:00	Set up Poster Session 1	
5:30-7:30	Presentation and Judging of Posters	

Day 2: Tuesday June 18, 2013

Time	Presenters	Author & Title
Session 4: Coral Reef Ecology and Biology (Macroalgae, Gastropod) — Chair: Tyler Smith		
8:30	Larson, E.	Characterization of acropora palmata populations within the Veracruz reef system, Gulf of Mexico. *Elizabeth A. Larson, David S. Gilliam, Brian K. Walker , Jacobo Santander Monsalvo, Israel López Huerta*
8:50	Dou, N.	Evaluation of bioactive metabolites from *Anadyomene linkiana*, a bloom-forming green macroalgae in Biscayne Bay, Florida. *Natalie Dou, John Berry, Ligia Collado, Asha Jaja-Chimedza*
9:10	Duran, A.	Magnitude effect of major ecological drivers on succession of a coral reef macroalgal community. *Alain Duran, Ligia Collado-Vides, Deron Burkepile*
9:30	Narváez, M.	Evaluacion espacio temporal de los principales grupos funcionales de algas en un arrecife del Parque Nacional Archipielago de Los Roques, Venezuela. *Narváez Mariju, Villamizar Estrella, Moreno Maria G.*
9:50	Noguez Núñez, M.	Ecoetología del caracol rosa *Strombus gigas* (Linnaeus, 1758) en un ciclo anual en la Caleta de Xel-Há, Mexico. *Mariana Noguez Núñez, Manuel Sánchez Crespo, Francisco Gameros Escoto, Luis Alfonso Ascencio Aguirre, José Francisco Chávez Villegas, Nuria Estrada Saldívar, Irma Pérez García, Wendy González López, Alejandro Aldana Moreno, Dalila Aldana Aranda*
10:10	Aranda, D.	Queen conch, *Strombus gigas* a species with allele effect? *Dalila Aldana Aranda, Javier Bello, Manuel Sánchez Crespo, José Francisco Chávez, Jorge Monter*
10:30-11:00		Coffee Break
Session 5: Coral Reef Ecology and Biology (Reproduction) — Chair: James Crabbe		
11:00	D'Antonio, N.	Phenotypic plasticity in *Acropora cervicornis* on two southeast Florida near-shore substrate types. *Nicole L. D'Antonio, David S. Gilliam*
11:20	Vermeij, M.	Counterintuitive responses of brooding and spawning coral species to environmental stress. *Mark J. A. Vermeij*
11:40	Marhaver, K.	Cultured microbial isolates, antibiotics, and parental identity affect movement and settlement behavior of coral larvae. *Kristen L. Marhaver, Aaron C. Hartmann, Mark J.A. Vermeij, Valerie F. Chamberland, Stuart A. Sandin, Monica M. Medina*
12:00	Villegas, J.	Abundancia y composición de larvas de gasterópodos en el Caribe Mexicano. *José Francisco Chávez Villegas, Martha Enríquez Díaz, Dalila Aldana Aranda*
12:20		Announcements and Housekeeping
12:30-1:30		Lunch
Session 6: Coral Reef Ecology and Biology (Fisheries) — Chair: Bob Anderson		
1:30	Herrera-Reveles, A.	Population connectivity in *Abudefduf saxatilis* (Pomacentridae) using otolith natal elements as natural fingerprints in some Venezuelan coral reefs, South Caribbean. *Ana Teresa Herrera-Reveles, Baumar Marín, Mairin Lemus, Maria-Josefina Hernandez*
1:50	Alemu, J.	Fish assemblages on fringe coral reefs of Tobago. *Jahson B. Alemu I, Sherron Barker*
2:10	Aiken, K.	The spearfishing sub-sector in Jamaica: a large and growing threat. *Zahra Ennis, Karl Aiken*
2:30	López-Ordaz, A.	Variación espacio-temporal de la estructura comunitaria de peces arrecifales en zonas de la región oriental de Venezuela, Caribe sur. *Adriana López-Ordaz, Ana Teresa Herrera-Reveles, Maria Fernanda González-Rivero, Jose Gregorio Núñez, Luis Ariza, Alan Martínez*
2:50	Bolda, E., Musser, K.	Reef composition and fish population trends inside and outside Grenada's recently established marine protected area. *Emily Bolda, Katie Musser, Clare Morrall, Jon Jossart, Robert Anderson*
3:10-3:30		Coffee Break
Session 7: Coral Reef Ecology and Biology (Crinoids, Sponges, Birds, Turtles) — Chair: Heidi Hertler		
3:30	Meyer, D.	Changes in population density of shallow-water Crinoids on coral reefs of the Caribbean and Bahamas since the late 1960s. *David L. Meyer*
3:50	Halperin, A.	Comparing excavating sponge, *Cliona delitrix*, growth rates across three different reef habitats offshore southeast Florida. *Ariel A. Halperin, Andia Chaves-Fonnegra, David S. Gilliam*
4:10	Ainsworth, P.	The determination of the breeding success of the masked booby, *Sula dactylatra dactylatra* at Middle Cay, Pedro Bank, Jamaica. *Peter J. Ainsworth, Dale Webber*
4:30	Thompson, N.	Sea turtles in US Atlantic waters. *Nancy B. Thompson*
4:50	Announcements and Housekeeping	
5:00	Set up Poster Session 2	
5:30-7:30	Presentation and Judging of Posters	

Day 3: Wednesday June 19, 2013

Field Trips
1. Diving at Discovery Bay Marine Laboratory
2. Rafting on the Martha Brae River
3. Tour of the Port Royal Biodiversity Centre & UWI Mona Campus

Day 4: Thursday June 20, 2013

Time	Presenters	Author & Title
8:30	**Plenary 2**	
	Chair: Prof Dale Webber, Director, Centre for Marine Sciences, UWI, Mona Campus ***Managing the resilience of coral reefs to reverse phase shifts.*** Prof. Terry Hughes, Director of ARC Centre of Excellence for Coral Reef Studies, Australia	
9:10	**Q&A**	
Session 8: Monitoring and Assessment — Chair: Nancy Thompson		
9:30	Lopez Padierna, M.	Trends in coral cover in the Veracruz reef system, Gulf of Mexico. *Mauricio López Padierna, David S. Gilliam, Brian K. Walker, Israel López Huerta, Jacobo Santander Monsalvo, Marcos A. Rangel Avalos*
9:50	Creary Ford, M.	Results of long term coral reef monitoring at three locations in Jamaica. *Marcia Creary Ford, Sean Green, Loureene Jones Smith*
10:10	McField, M.	Report cards and eco-audits track essential components of reef condition and management response. *Melanie Mcfield, Lorenzo Alvarez Filip, Ian Drysdale, Marisol Rueda, Roberto Pott, Ana Giro*
10:30	Chin, D.	Spatial variation of the coral reefs in Foul and Folly Bays, St. Thomas, Jamaica. *Denise Chin, Mona Webber, Dale Webber*
	Williams, D.	Regional Analysis of *Acropora palmate* population dynamics using matrix modeling with stochasticity *Tali Vardi, Dana Williams, Stuart Sandin*
10:50-11:10		Coffee Break
Session 9: Coral Reef Restoration — Chair: Hazel Oxenford		
11:10	Ross, A.	Genet and reef position effects in out-planting of nursery-grown *Acropora cervicornis*. Andrew *Ross*
11:30	Mercado-Molina, A.	A comparison of survivorship, growth, and branch production between stabilized and un-stabilized fragments of the branching coral *Acropora*. *Alex E. Mercado-Molina, Claudia P. Ruiz-Diaz, Alberto Sabat*
11:50	Suleiman, S.	Participación voluntaria como estrategia de manejo en el cultivo de corales para la restauración de habitat. *Samuel E. Suleiman-Ramos*
12:10	Bliss, C.	Translocation of *Acropora cervicornis* across geographic regions: investigating species recovery and restoration. *Bliss, Cody, Gilliam, David, Ken Nedimyer*
12:30		Announcements and Housekeeping
12:30-1:30		Lunch
Session 10: Coral Diseases — Chair: Marilyn Brandt		
1:30	Brownell, A.	Sulfate reducing bacteria as secondary and necessary pathogens in black band disease of coral. *Abigael Brownell, Laurie L. Richardson*
1:50	Walton, C.	Bacterial communities associated with rapid tissue loss in *Acropora cervicornis*. *Charles J. Walton, Jose V. Lopez, David S. Gilliam*
2:10	Richardson, L.	How does the black band disease microbial community organize itself? *Laurie L. Richardson, Beth Zimmer, Chinmayee Behdi*
2:30	Brandt, M.	Spatial and temporal variability of white plague disease in Caribbean reef systems. *Marilyn Brandt, Elizabeth Clemens, Tyler B. Smith*
2:50-3:10		Coffee Break
Session 11: Reef Resilience — Chair: Brian Beck		
3:10	Brown, D.	Long-term changes in the population dynamics of the Caribbean hydrocoral *Millepora spp*. *D. Brown, P.J. Edmunds*
3:30	Smith, T.	Recent trends in mesophotic ecosystems of the US Virgin Islands. *Smith, Tyler B., Brandt, Marilyn E., Gyory, Joanna*
3:50	Henderson, L.	Sedimentation patterns and coral health across large gradients of human pressure in the US Virgin Islands. *Leslie M. Henderson, Tyler B. Smith, Marcia Taylor, Richard S. Nemeth*
4:10	Williams, S.	Spatial heterogeneity of species richness and composition of sponges, octocorals, and corals on shallow-water reefs in the Greater Caribbean region. *Stacey M. Williams, Jorge Cortés*
4:30	Beck, B.	The health and resilience of Pedro Bank coral reefs. *Andrew Bruckner, Brian Beck, Phil Renaud*
5: 00	Living Oceans Foundation Film	

Day 5: Friday June 21, 2013

Time	Presenters	Author & Title
		Panel Discussion
8:30		***The challenge of translating scientific knowledge into effective management practices*** Chair: Mrs. Alessandra Vanzella-Khouri, Programme Officer (SPAW), United Nations Environment Programme Panelists: **Mr. Anthony McKenzie***,* Director, Environmental Management and Conservation, National Environment and Planning Agency, Jamaica. ***Dr. Leonard Nurse***, Senior Lecturer, Centre for Resource Management and Environmental Studies, University of the West Indies Cave Hill Campus, Barbados. ***Prof. Brian LaPointe***, Research Professor, Florida Atlantic University. ***Dr. Judith Lang***, Scientific Coordinator of AGRRA and Chief curator of "Our Reefs-The Caribbean Connection" Travelling Exhibit, USA. ***Dr. Peter Edwards***, Natural Resource Economist and Social Science Coordinator, Coral Reef Conservation Program, NOAA, USA. ***Prof. James Crabb***e, Dean, Faculty of Creative Arts, Technologies and Science, University of Bedfordshire, U.K.
10:00	**Q&A**	
10:30-11:30		Coffee Break
Session 12: Conservation, Policy, Socio Economics and Public Awareness (1) — Chair: Chris Corbin		
11:00	González, R.	Scientific research and enhancement permits for corals proposed as endangered under the U.S. Endangered Species Act. *González Marrero, Rosa L.*
11:20	Hernández, E.	Recent trajectories of coral reef communities in Puerto Rico: a call for novel participatory management approaches. *Edwin A. Hernández Delgado, Raisa Hernández Pacheco, Alberto M. Sabat*
11:40	Villamizar, E	Biodiversidad y estructura de las comunidades de sponjas en los fondos coralinos del refugio de fauna de Isla de Aves. *Estrella Villamizar, Anaurora Yranzo, Marco Romero, Hazael Boadas*
12:00	Grey, O.	Application of the soil and water assessment tool (SWAT MODEL) on a small tropical island state (Great River Watershed, Jamaica) as a tool in integrated watershed and coastal zone management. *Orville P. Grey, Dale Webber*
	Rodríguez-Barreras, R.	Food resources of the three litoral echinoids in Puerto Rico: a stable isotope approach *Ruber Rodríguez-Barreras, Elvira Cuevas, Nancy Cabanillas-Terán*
12:20		Announcements and Housekeeping
12:30-1:30		Lunch
Session 13: Conservation, Policy, Socio Economics and Public Awareness (2) — Chair: James Crabbe		
1:30	Crabbe, J.	Science, capacity building and policy development - a case for improved reef protection. *James Crabbe*
1:50	Lang, J.	Bahamian reefs: a case for conserving novel diversity of form and function. *Judith Lang*
2:10	Coyolxauhqui Pérez García, I.	Pesca del recurso caracol en Isla Arena, Campeche, México caracterización social y económica *Irma Coyolxauhqui Pérez García, Dalila Aldana Aranda*
2:30	Buddo, D.	The use of biology, oceanography and geographic information systems to manage the release of ballast water in Kingston Harbour, Jamaica. *Dayne Buddo, Ava Maxam*
2:50	Allen, R.	The fishers of the Pedro Bank, Jamaica: a livelihood analysis. *Rachel Allen, Dale Webber*
3:10-3:30		Coffee Break
Closing Ceremony		
3:30-5:00		Closing Ceremony and Presentation of Awards

POSTER SESSION

Session 1. Monday, June 17, 2013

Managing lionfish in the Florida Keys: evaluating effectiveness of removals for an invasive reef predator. *Adam Nardelli*, David Kestetter, Richard Spieler, Benjamin Ruttenberg & Stephanie Green

Endoparasite fauna of the invasive lionfish complex (*Pterois volitans* and *Pterois miles*) in the Western Atlantic and Caribbean. *Kayelyn Simmons,* Chris A. Blanar & David W. Kerstetter

Interactions between root-fouling epibionts and the abundance and richness of fish in the mangroves of Lac Bay Bonaire, Dutch Caribbean. *Rachael Vietheer* BS, Maria C. Uyarra PhD & Rita Peachey PhD

A preliminary assessment of the relationship between zooxanthellae density and coral growth. *Alex E. Mercado-Molina*, P. Ruiz-Dia & Alberto Sabat

Rapid reassessment of zooplankton communities for the resource management of Kingston Harbour, Jamaica. *Patrice A. Francis*, Stacy A. Maxam & Mona K. Webber

The fishy and untold stories of bomb-cratered coral reefs in Culebra Island, Puerto Rico: from massive destruction to community-based ecological rehabilitation. *Edwin A. Hernández-Delgado*, Julio Oms-Hernández, Mary Ann Lucking & Samuel E. Suleimán-Ramos

Ecosystem-level cascade impacts of low-tech community-based coral reef rehabilitation: a before-after-control-impact (BACI) approach. *Edwin A. Hernández-Delgado*, Nicole M. Resto, Laura Bimbela, Iván Olivo-Maldonado & Samuel E. Suleimán-Ramos

Effectiveness of different low-tech, low-cost staghorn coral nurseries. *Iván Olivo-Maldonado*, Edwin A. Hernández-Delgado, Alex Mercado-Molina, Jaime Fonseca-Miranda, Pedro Alejandro-Camis, Carmen González-Ramos, Samuel E. Suleimán-Ramos

Preliminary findings of low-tech staghorn coral outplanting efforts in Culebra Island, Puerto Rico. *Alfredo A. Montañez-Acuña*, Abimarie Otaño-Cruz, Lee Vaasjo-Muñoz, Alex Mercado-Molina, Samuel E. Suleimán-Ramos & Edwin A. Hernández-Delgado

Composición y variación estacional del ensamble larvas de gasterópodos en Xel-Há, Quintana Roo. *José Francisco Chávez Villegas*, Francisco José Gameros Escoto & Dalila Aldana Aranda

Branching dynamics of the staghorn coral *Acropora cervicornis*. *Jaime Fonseca-Miranda* & Alex E. Mercado-Molina

Population assessment of *Acropora palmata*: relationship between habitat and reef associated species. *Kimberly Martínez*, David Bone, Aldo Cróquer & Adriana López-Ordaz

Estrategias reproductivas de dos gasterópodos del Banco de Campeche: *Busycon perversum* y *Strombus pugilis*. *Martha Enriquez Diaz*, Josefina Santos Valencia & Dalila Aldana Aranda

Preliminary ecology study of *Millepora spp* under contrasting hydrodynamic regime: abundance and population size- structure. *Juan David Murcia Eslava*

Rackham's Cay cut face coral succession study. *Camilo Trench*, Hugh Small, Lydia Morrison, Dale Webber & Mona Webber

Comunidad de corales y octocorales de Los Fondos Coralinos del Refugio de Fauna Silvestre Isla de Aves, Venezuelan Letters. *Anaurora Yranzo Duque*, Estrella Villamizar, Marco Romero & Hazael Boadas

Large-scale coral recruitment patterns in Mona Island, Puerto Rico: evidence of shifting coral community trajectory after massive bleaching and mortality. *Carmen González-Ramos*, Pedro Alejandro-Camis & Edwin A. Hernández-Delgado

Elkhorn coral (*Acropora palmata*) rehabilitation under high wave energy conditions in Puerto Rico: a novel community-based coral reef conservation and management approach. Ricardo Laureano, *Pedro Alejandro-Camis*, Alberto Archilla, ErnestoVélez Joel Díaz, Salvador Laureano, Samuel E. Suleimán-Ramos & Edwin A. Hernández-Delgado

POSTER SESSION

Session 2. Tuesday, June 18, 2013

Spatial patterns in post-bleaching benthic biodiversity in Mona Island, Puerto Rico. *Abimarie Otaño* & Edwin A. Hernández-Delgado

Variación del ciclo gonádico del ostión americano, *Crassostrea virginica* (Gmelin, 1791) en función de la talla en la Laguna de Tamiahua, Veracruz, Mexico. *Luis Alfonso Ascencio Aguirre*, Martha Enríquez Díaz , Imelda Martínez Morales & Dalila Aldana Aranda

Estructura y composición de comunidades de peces en ecosistemas de praderas de *Thalassia testudinum* en las costas del nororiente Venezolano. *José Gregorio Núñez*, Luis Alejandro Ariza, Lilia Ruiz & Elizabeth Elguezabal

Distribución, densidad y biomasa del caracol Strombus pugilis, en aguas insulares del nororiente Venezolano. *Luis Alejandro Ariza*, Jeremy Mendoza, Luis Freites, Natividad García & Vásquez Abel

Fish communities on artificial reefs in the nearshore waters of St. Kitts, West Indies. *Emma K. Grigg*, Lewis B. Bogdanovic, Sarah Turner & Rachel E. Palis

Harvesting mangrove land crabs in Trinidad: how, where and by whom? *Marie Ella Maynard &* Hazel A. Oxenford

A participatory marine resource and space-use information system for the transboundary Grenadine Islands. Kimberly Baldwin, *Hazel Oxenford* & Robin Mahon

Actividad microbiana de sedimentos superficiales de Río Caribe, Sucre, Venezuela. *Mary Isabel Segnini de Bravo*, Irma Gómez, Leonor Brito & Vanessa Acosta

Field and laboratory approaches to ocean acidification and carbonate chemistry at the Smithsonian's Bocas del Toro Research Station. Remy Okazaki & *Rachel Collin*

From chaos to reef-friendly enjoyment: a multidisciplinary, participatory and sustainable management effort using self-guided snorkeling trails in Arrecifes La Cordillera Natural Reserve, Northeastern Puerto Rico. *Jeiger Medina-Muñiz*, Humberto Figueroa, Marcos Ramos & Edwin A. Hernández-Delgado

Variaciones temporales de la biomasa foliar de una pradera de *Thalassia testudinum* (Banks ex König, 1805) en los Cachicatos, Golfo de carCaco, Venezuela. *M.I. Segnini*

Macroinvertebrados asociados a comunidades coralinas frangeantes en el Golfo De Cariaco, Venezuela. *Luis Alejandro Ariza*, Sioliz Villafranca, Mayré Jiménez & José Gregorio Núñez

Efecto de la temperatura en el desarrollo larval de *Strombus gigas*. *José Francisco Chávez Villegas*, Martha Enríquez Díaz & Dalila Aldana Aranda

The role of colony size in the resistance and tolerance of Scleratinian corals to temperature-induced bleaching on Jamaica's north shore reefs. *Bernadette Charpentier* & Peter Gayle

Sediment PAH Contamination in Curaçao: Potential Impacts from the Isla Refinery. *Dana L. Wetzel* & Erin L. Pulster

A survey of phytoplankton and water quality of Kingston Harbour and the north east Hellshire coastline, Jamaica. Helen Liu, Sheree Broomfield, Anya Duncan, Leon Grant, *Dale Webber* & Mona Webber

Preliminary assessments of the sessile-benthic assemblages at a mesophotic reef, Lang Bank, St. Croix, USVI. *Stacey M. Williams*, Jorge R. Garcia-Sais, Jorge Sabater, Rene Esteves & Milton Carlo

Are our marine protected areas protecting our juvenile stocks? A three month survey of Icthyoplankton in Jamaican waters. *Nasheika Guyah*, Mona Webber, Gale Persad & Patrice Francis

Biodiversity, ecological structure, and change in the sponge community of different geomorphological zones of the barrier fore reef at Carrie Bow Cay, Belize. *Estrella Villamizar,* María Cristina Díaz, Klaus Rüetzler & Renato De Nóbrega

Abundance and distribution of lionfish (*Pterois volitans/miles)* along the Venezuelan coast. *Esteban Aguido*, Juan Jose Cruz-Motta & Eduardo Klein.

Sulfate reducing bacteria as secondary and necessary pathogens in black band disease of corals

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Received 02-XI-2013 Corrected 02-II-2014 Accepted 24-III-2014

Abstract: Black band disease (BBD) is a complex, polymicrobial disease that consists of cyanobacteria, sulfide-oxidizing and sulfate-reducing bacteria (SRB), and heterotrophic bacteria. The cyanobacterium *Roseofilum reptotaenium* has been implicated as the primary pathogen of BBD, but other consortium members may be secondary pathogens that are necessary to the development of the disease. It is known that populations of the sulfate-reducing bacterium *Desulfovibrio* are present in BBD and that these populations generate sulfide within the band as a byproduct of dissimilatory sulfate reduction. It is also known that exposure of healthy corals to sulfide leads to cell lysis and coral tissue death. Previous work showed that when freshly collected BBD, which easily infects healthy corals, is exposed to sodium molybdate, a specific inhibitor of sulfate reduction, infection does not occur. In this study we examined the effect of sodium molybdate on infection of corals by a unialgal culture of *R. reptotaenium*. Coral fragments of *Montastraea cavernosa* and *Siderastrea siderea* were transferred into two experimental aquaria, one a control with only artificial seawater (ASW) and the second containing ASW and 2mM sodium molybdate. Small mats of cultured *R. reptotaenium* were inoculated onto the surface of experimental coral fragments. Both *M. cavernosa* (n = 6) and *S. siderea* (n=4) became infected and developed BBD-like infections in the control tank, while there were temporary attachments to, but no successful infection of *M. cavernosa* (n=3) or *S. siderea* (n=2) in the experimental tank containing sodium molybdate. The results of this study reveal that a secondary pathogen is essential to the infection process and development of BBD in scleractinian corals. Specifically, SRB such as *Desulfovibrio* are required for the development of BBD on the coral host. This is the first step in understanding the roles of secondary pathogens in a complex, polymicrobial coral disease. Rev. Biol. Trop. 62 (Suppl. 3): 1-9. Epub 2014 September 01.

Key words: Black band disease, sulfate-reducing bacteria, coral.

Coral diseases were first reported in the 1970s on reefs of the Caribbean (Antonius, 1976; Garret & Ducklow, 1975; Dustan, 1977; Gladfelter, Gladfelter, Monahan, Ogden & Dill, 1977). Since then, the number of documented coral diseases has increased significantly both in the Caribbean and on reefs worldwide. Coral diseases are correlated with many anthropogenic factors including elevated sea surface-temperature, sewage pollution, eutrophication, and sedimentation (Rogers, 1990; Harvell et al., 2002; Voss & Richardson, 2006). Such anthropogenic factors have also been shown to increase pathogen virulence and disease severity. For example, Voss & Richardson (2006) found that *in situ* nutrient dosing increased the migration rate of the band in black band disease (BBD) infected corals and accelerated coral tissue loss. Although several drivers of coral disease have been identified, the causative agents of most coral diseases are unknown. Of the 27 coral diseases documented worldwide, pathogens of only seven have been proposed, and Koch's postulates have only been fulfilled for five –white plague type II, aspergillosis, white pox, and two cases of bacterial bleaching (Harvell et al., 2002; Weil, 2004; Harvell et al., 2007).

A wide range of diseases afflict corals on reefs in the wider Caribbean (Weil, 2004). Of these, BBD is of particular interest because it kills large, reef-building coral. BBD is comprised of by a polymicrobial consortium of cyanobacteria, sulfate-reducing and sulfide-oxidizing bacteria, and a diverse assemblage of heterotrophic bacteria that together form a dark, band-shaped microbial mat (Antonius, 1976; Garret & Ducklow, 1975; Ducklow & Mitchell, 1979; Cooney et al., 2002; Frias-Lopez, Zerkle, Bonheyo & Fouke, 2002; Frias-Lopez, Klaus, Bonheyo & Fouke, 2004; Sekar, Mills, Remily, Voss & Richardson, 2006; Sekar, Kaczmarsky & Richardson, 2008). The BBD mat migrates across the surface of infected scleractinian, as well as gorgonian, coral hosts, lysing coral tissue and leaving behind bare coral skeleton (Antonius, 1981). At rates of up to 1cm a day, BBD can denude an entire coral colony in as little as one summer season (Richardson, 1996). The pathogenicity of BBD is caused by a combination of factors: anoxia at the BBD mat-coral interface, high levels of the toxicant sulfide, the presence of the cyanotoxin microcystin, and a synergistic interaction between sulfide and microcystin (Richardson, Kuta, Schnell & Carlton, 1997; Gantar, Sekar & Richardson, 2009; Glas, Sato, Ulstrup & Bourne, 2012, Miller & Richardson, 2012).

BBD infection can be easily modeled in a laboratory setting due to the highly infectious nature of the disease. In the model system, infection can be initiated when an inoculum of naturally-occurring BBD mat from an infected coral is placed onto a healthy coral fragment (Antonius, 1985). The inoculum can be observed to attach to the coral surface, penetrate and invade tissue, and develop into a BBD lesion that migrates across the coral surface, lysing coral tissue and eventually killing the coral, leaving a bare coral skeleton. In this model the inoculum contains a fully developed BBD-consortium: cyanobacteria, sulfide-oxidizing and sulfate-reducing bacteria, as well as associated heterotrophic bacteria. While several different members of the consortium have been proposed to be the primary pathogen of BBD, Koch's postulates have yet to be fulfilled for any member. It may be that BBD requires the entire consortium to be pathogenic –in this case it would not be possible to identify a primary pathogen and fulfill Koch's postulates.

There has been a lot of interest in identifying a primary pathogen of BBD. The major target has been BBD cyanobacteria, since the biomass of the band is always dominated by filamentous cyanobacteria (Antonius, 1976). The other members of the consortium –sulfate reducing bacteria (SRB) and sulfide oxidizing bacteria (Ducklow & Mitchell, 1979), as well as heterotrophic bacteria (Cooney et al., 2002)– have also been implicated. However, to date investigations of potential BBD pathogens have mainly focused on BBD cyanobacteria.

A critical member of the BBD consortium is *Roseofilum reptotaenium* (Casamatta, Stanić, Gantar & Richardson, 2012). *Roseofilum reptotaenium* is a gliding, filamentous, phycoerythrin-rich cyanobacterium detected in BBD mats of tropical and sub-tropical coral reefs around the world (Miller & Richardson, 2011). This cyanobacterium forms the matrix of the mat and is adapted to the harsh BBD conditions because of its ability to conduct sulfide-insensitive oxygenic photosynthesis (Myers, Sekar & Richardson, 2007). The ability to conduct photosynthesis in the presence of sulfide is a rare trait among cyanobacteria since sulfide poisons electron flow in Photosystem II (Cohen, Jorgensen, Revsbech & Poplawski, 1986). However, this trait has been found in all BBD cyanobacterial strains tested to date (Myers & Richardson, 2009). *Roseofilum reptotaenium* can perform sulfide-insensitive oxygenic photosynthesis in the presence of 0.5mM sulfide (Myers & Richardson, 2009), comparable to sulfide levels measured in intact Caribbean BBD (Carlton & Richardson, 1995).

In 2009, samples of BBD were collected from BBD-infected *Diploria strigosa* and *Siderastrea siderea* on reefs in St. Croix, U.S. Virgin Islands. Two strains of *R. reptotaenium* were isolated from the mat, designated as strain 101-1 (isolated from *D. strigosa*) and 100-1 (isolated from *S. siderea*). Stanić (2010) found that exposure of apparently healthy *D. strigosa* and *S. siderea* coral fragments to both strains led to BBD-like lesions that ultimately killed the fragments. The inoculum of each strain attached to scleractinian coral tissue, caused an infection, and eventually developed into a BBD-like lesion.

Additional work on BBD pathogenicity has targeted SRB associated with the disease, since the population of SRB is the source of toxic sulfide present in the band (Carlton & Richardson, 1995; Glas et al., 2012). To investigate the role of SRB in BBD pathogenesis, Richardson et al. (2009) used the coral fragment model of BBD infection to assess the effect of sodium molybdate on infection. Na molybdate is a specific metabolic inhibitor of the energy yielding, anaerobic respiratory pathway of dissimilatory sulfate reduction, which produces sulfide as a byproduct of the reaction. Na molybdate effectively stops this physiological process at concentrations of 2mM. In a series of experiments in flow through aquaria containing natural, sand-filtered sea-water, Richardson et al. (2009) inoculated fragments of *Montastraea annularis* and *S. siderea* with freshly collected BBD from infected colonies on the reef. The inoculum consisted of the fully developed consortium of BBD microbes. Coral fragments that were inoculated with BBD that was exposed to 2mM of Na molybdate prior to inoculation did not develop BBD infections (Richardson et al., 2009). Conversely, coral fragments infected with inocula that were not exposed to Na molybdate all developed actively migrating BBD lesions. When these infected fragments were then exposed to 2mM Na molybdate there was no effect on disease progression. These results demonstrated that when the entire BBD community is present, SRB are required for infection but not continued disease activity. Thus, the overall implication is that SRB are directly involved in the first stages of BBD pathogenesis.

The specific role of SRB as potential primary and/or secondary pathogens of BBD infection and development remains unknown. It may be that SRB are acting together with other, as yet unidentified, BBD bacteria to initiate the disease. The goal of this study was to further assess the role of SRB in BBD infection using a laboratory culture of *R. reptotaenium* for the inoculum. We hypothesized that the biomass of *R. reptotaenium* creates an anaerobic environment on the coral surface; that this environment enriches for SRB; and that the development of an SRB population is required for BBD infection.

MATERIALS AND METHODS

Fragments of two Caribbean scleractinian coral species, *Montastraea cavernosa* and *S. siderea*, were collected from the Florida Keys National Marine Sanctuary in Key West (Permit number FKMNS-2012-153). After collection, fragments were maintained at ambient (reef water) temperature during transport to Florida International University where they were placed in a 340L flow-through holding tank. After acclimation in the large tank for eight weeks, fragments approximately 4 to 7cm in diameter were then transferred to two 21L experimental aquaria for further acclimation (seven days) prior to beginning the experiment. One (control) aquarium contained only artificial seawater (ASW) at 34ppt salinity while the second (experimental) aquarium contained ASW (34ppt) as well as 2mM Na molybdate. Aquaria temperatures were kept between 27.5 and 29ºC on a 12/12 light-dark cycle using cool-white fluorescent light and metal halide bulbs. Light intensity, measured using a Biospherical Quantum Scalar Irradiance meter (model QSL100), was $1x10^{15}$quanta$\cdot s^{-1} \cdot cm^{-2}$. Experimental inoculations of the control fragments (ASW) and experimental fragments (ASW and Na molybdate) were run in parallel.

Two unialgal cultures of *R. reptotaenium* were used as inocula for the experiments. Strains were originally isolated using the gliding method (Castenholz, 1988) from BBD samples collected on a reef in Frederiksted, St. Croix, U.S. Virgin Islands (Stanić, 2010). The cultures were maintained in BG-11 and ASW at room temperature in filtered, natural light. Strains 101-1 and 100-1 were used to inoculate *M. cavernosa* and *S. siderea* respectively.

While strain 101-1 was not isolated from BBD on *M. cavernosa*, preliminary results proved it was infectious for this Caribbean coral species. To inoculate the experimental coral fragments, fragments were taken out of the water and a small amount of *R. reptotaenium* biomass was placed on the fragment surface between polyps. A sterile glass pipette was used to hold the biomass onto the coral surface. Coral fragments were then returned to the aquaria with the pipette in place. Once the biomass attached to the surface of the coral, 24-48 hours later, the pipette was removed. Following pipette removal, if the biomass was sloughed from the surface, a reinfection was attempted in the same area. Reinfections were attempted at least twice on coral fragments with failed inoculations. When infection occurred, progression of the lesion was documented by photographing the fragments a minimum of once a week.

The laboratory culture of *R. reptotaenium* strain 101-1 was photographed using a Leica Application Suite (version 2.8.1) imaging system with a Leica/Leitz DMRB light microscope. The image was analyzed using ImageJ processing.

RESULTS

In total, 21 experiments were conducted using 18 coral fragments. Six of eight *M. cavernosa* fragments and four of five *S. siderea* fragments from the control (ASW only) aquarium were successfully infected using *R. reptotaenium* strain 101-1 (Fig. 1) and 100-1 respectively. In infected coral fragments, the inoculum of *R. reptotaenium* filaments was observed to attach to the surface of the coral tissue within seven days (Fig. 2). The small amount of inoculum developed into a BBD-like lesion as the cyanobacterial biomass increased and began to spread (Fig. 2C-F). Thin tendrils of groups of cyanobacterial filaments could be observed to migrate between and into the coral polyps ahead of the advancing microbial mat (Fig. 2C). Over a period of several weeks, the infection grew into a BBD lesion that migrated across the coral surface (Fig. 2G), lysing tissue (Fig. 2H), and leaving a bare coral skeleton (Fig. 2I). Similar to naturally occurring BBD, the mat did not tightly attach to the surface of the coral and could be easily disturbed or dislodged from the coral surface.

In contrast to the controls, none of the experimental (ASW plus Na molybdate) fragments –three *M. cavernosa* fragments and two *S. siderea* fragments– became infected (Fig. 3). While the *R. reptotaenium* inoculum was observed to attach to the surface of the coral initially (Fig. 3A), within 72 hours following attachment the filaments were sloughed off of the surface of the coral (Fig. 3B). None of the five fragments exposed to *R. reptotaenium* in the presence of Na molybdate exhibited permanent attachment to the coral tissue or infection of the fragments, and there was no development of BBD lesions. Reinfection of each of the five coral fragments in the experimental tank containing Na molybdate was attempted at least twice, with parallel control (ASW only) reinfections of additional fragments to serve as controls. In the Na molybdate tanks, fresh clumps of *R. reptotaenium* were placed in the same area on the fragments as previous attempted infections. There were no successful reinfections of the coral fragments in the experimental tank. However, reinfection of coral fragments within the control tank was successful.

Fig. 1. Photomicrograph of the laboratory culture of *Roseofilum reptotaenium* strain 101-1.

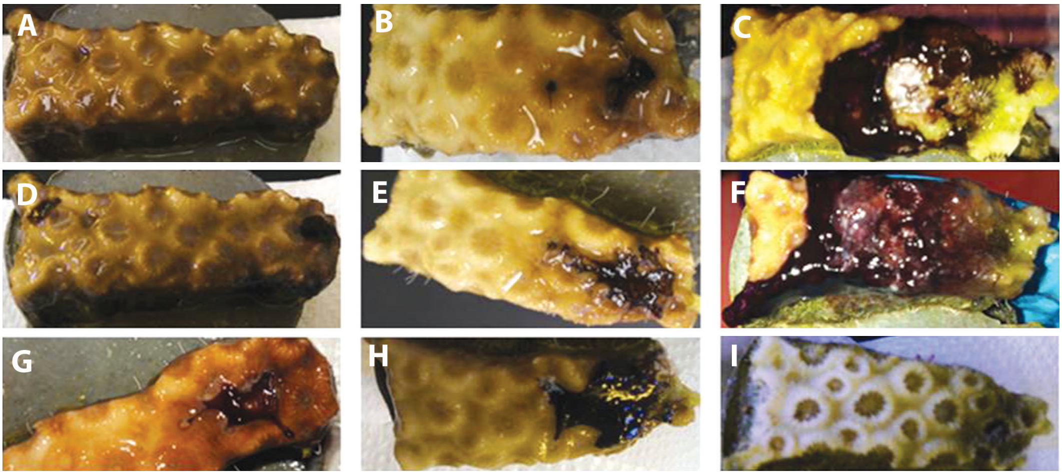

Fig. 2. Successful infection of a *Montastraea cavernosa* coral fragment after inoculation with *Roseofilum reptotaenium* in the control (artificial seawater only) tank. A) fragment before infection; B) t= 0, day of inoculation; C) t= 31 days; D) t= 53 days; E) t= 60 days; F) t= 66 days; G) t= 73 days, with formation of band apparent; H) t= 83 days, with band migration apparent; I) t= 115 days, bare coral skeleton due to complete tissue lysis. Arrow in plate B indicates inoculum.

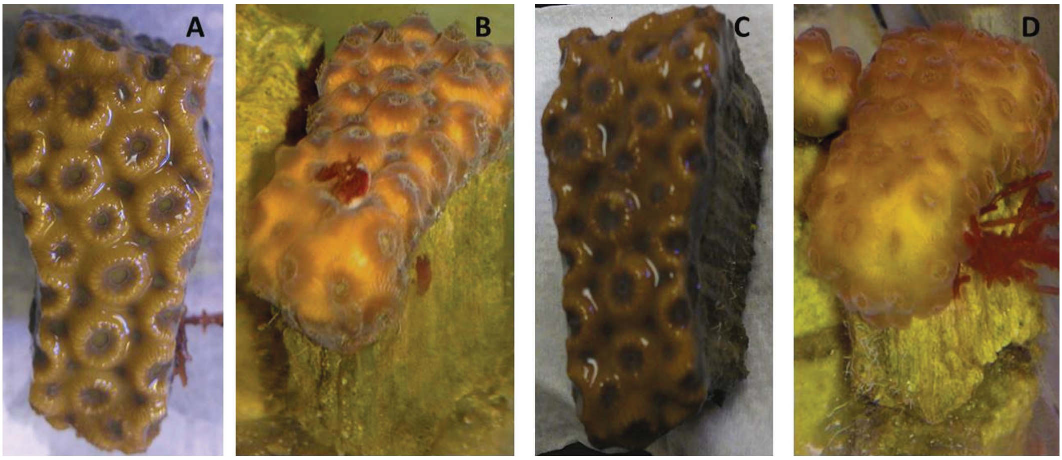

Fig. 3. Unsuccessful infection of a *Montastraea cavernosa* coral fragment after inoculation with *Roseofilum reptotaenium* in the experimental aquarium containing artificial seawater and sodium molybdate. A) t= 0, fragment before inoculation; B) t= 3 days, attachment of inoculum which was subsequently sloughed off; C) t= 31 days, prior to reinoculation; D) t= 115 days, healthy coral fragment after three unsuccessful attempts at infection. Arrows in plates A and C indicate areas of inoculation and reinoculation.

DISCUSSION

The results of this study revealed that blocking the growth of SRB using the metabolic inhibitor Na molybdate prevented the development of BBD when using unialgal cultures of the BBD cyanobacterium *R. reptotaenium* as the inoculum. Previous work showed that cultured *R. reptotaenium* can produce BBD in controlled laboratory settings and that populations of sulfur-cycle bacteria develop in the resulting BBD mat (Stanić, 2010). Additional previous work (Richardson et al., 2009) demonstrated that use of Na molybdate prevented BBD infection using freshly collected BBD from infected corals *in situ*. In those experiments the inoculum contained the intact polymicrobial BBD community which always includes active populations of SRB (Miller & Richardson, 2011; Glas et al., 2012).

The two strains of *R. reptotaenium* used in the experiments presented here are unialgal (each derived from a single cyanobacterial filament), however neither culture is axenic. In each case heterotrophic bacteria are growing in close association with the mucilaginous, polysaccharide-rich, filament sheaths. As is common with many cyanobacterial cultures, *R. reptotaenium* does not remain viable in an axenic culture for an extended period of time. Stanić (2010) was able to isolate strain 101-1 into axenic culture using the gliding method (Castenholz, 1988), however the culture died within six months. It is generally thought that bacteria associated with the mucilaginous sheath cyanobacteria may provide a necessary vitamin or co-factor for growth and survival. Whatever the underlying reason, the associated bacteria preclude fulfillment of Koch's postulates, which require infection using a pure (axenic) culture.

The bacterial contaminants in the *R. reptotaenium* cultures were isolated, their 16S rRNA genes sequenced, and it was found that no SRB were present (Stanić, 2010). Therefore, we can conclude that SRB must be recruited from the environment into the BBD consortium. In any oxygenated environment with the presence of organic carbon, the dominant microbial metabolic mode is aerobic respiration, since oxygen is the most preferred (highest energy yielding) electron acceptor. When such environments become anaerobic, any bacterium that is capable of anaerobic energy-yielding metabolic pathways has a competitive advantage for growth. For metabolically flexible SRB, a variety of conditions present in freshwater and marine mats and sediments provide an optimal microenvironment for anaerobic respiration using sulfate as the electron acceptor, specifically anoxia and the availability of sulfate (Plugge, Zhang, Scholten & Stams, 2011). In the case of marine environments, high concentrations (28 mM) of sulfate are present in seawater, providing SRB with an immediate alternate electron acceptor (Stal, 2002). It has been shown that a transition to anaerobic conditions in the marine environment, in the presence of organic carbon released by photosynthetic cyanobacteria, always enriches for SRB (Frund & Cohen, 1992).

In our experiments, no SRB were added to the artificial sea water of the control and experimental aquaria. Two potential reservoirs for SRB, however, were the coral fragments and the live-rock used to establish the tank for two weeks prior to the experiment. We theorize that as the cyanobacterial biomass increased at the site of infection on the coral surface, it created an anaerobic environment at the mat-coral interface. The anaerobic environment then enriched for SRB from the reservoirs in the tank, allowing them to proliferate in the anaerobic environment by using sulfate as a terminal electron acceptor and releasing toxic sulfide as a byproduct. Because prevention of sulfate reduction effectively blocked BBD initiation in the aquarium with Na molybdate, the presence of SRB –thus sulfide production– appears to be crucial for the development of the band.

The presence of high levels of sulfide in BBD has proven to be critical for the pathogenicity of the disease. Using microelectrodes, sulfide levels within BBD have been measured at >800µM on the Caribbean reefs and ~5mM on the Great Barrier Reef (Carlton & Richardson, 1995; Glas et al., 2012). Sulfide is highly toxic to eukaryotes and most photosynthetic cyanobacteria at levels lower than 0.5mM (Padan, 1979), making conditions within BBD harmful to coral tissue. According to a tissue degradation rating, developed by Miller & Richardson (2012), coral fragments exposed to 0.5mM sulfide for 22 hours rated as 2.80 out of 5.0; a rating two-fold higher than the control. In the presence of sulfide the coral epidermis visibly thinned and zooxanthellae were only loosely held in the gastrodermis (Miller & Richardson, 2012), leading to disintegration of coral tissue integrity as the band travels across the surface.

In a series of experiments aimed at studying BBD pathogenesis on the Great Barrier Reef, researchers documented an increase in populations of SRB during a transition of cyanobacterial patches, shown to be precursors of BBD, to fully developed BBD infections (Sato, Willis & Bourne, 2010). In cyanobacterial patches, SRB accounted for less than 1% of the total population but that number increased beyond 7% in BBD lesions (Bourne, Muirhead & Sato, 2011). The changes in the microbial community, specifically increasing SRB, lead to enhanced production of sulfide, and sulfide concentrations within the mat increased as the cyanobacterial patch transitioned into a BBD lesion (Bourne et al., 2011). Five-fold faster migration rates were observed with increased numbers of SRB in BBD-mats as opposed to the cyanobacterial patches (Sato et al., 2010); likely due to greater sulfide production in BBD.

While different genera of SRB have been identified by sequencing the BBD microbial community, members of the genus *Desulfovibrio* have been most consistently documented in BBD samples worldwide (Frias-Lopez et al., 2002; Viehman, Mills, Meichel & Richardson, 2006; Sekar et al., 2006; Sekar et al., 2008; Sato et al., 2010). Viehman et al. (2006) cultured and sequenced eight strains of *Desulfovibrio* from BBD collected from six coral colonies of four species in the Florida Keys. *Desulfovibrio* was also detected by Sato et al. (2010) as the SRB in BBD lesions rather than cyanobacterial patches. The presence of *Desulfovibrio* and other SRB in BBD on different species of coral worldwide strengthens the proposal that SRB are required for all BBD infections.

When comparing our laboratory results using *R. reptotaenium* as the BBD inoculum with the results of Richardson et al. (2009) using the fully developed BBD community, marked differences in infection rate between the cyanobacterial culture and the fully developed BBD inoculum are apparent. While infection of scleractinia coral using naturally occurring BBD occurred within two days, with formation of an actively migrating band within two to three additional days (Richardson et al., 2009), infection using *R. reptotaenium* took place over a period of weeks. This time lag may be due to the need to recruit SRB from the aquarium environment. These results are in agreement with the results of Sato et al. (2010), who determined that the transition from a cyanobacterial patch to a BBD lesion *in situ* on the Great Barrier Reef (GBR) occurred over a period of 62±5 days. This time period may similarly be based on the need to recruit SRB from the environment. Alternatively, the much longer time required for BBD to fully develop from inoculation with *R. reptotaenium* in the aquarium experiments, or from cyanobacterial patches on the GBR, may be based on the necessity to recruit additional BBD bacteria in addition to the BBD cyanobacterium and SRB.

The work presented here, together with the body of research to date on the pathogenesis of BBD, strongly suggests that BBD is induced by a sequential community of pathogens, beginning with the cyanobacterium *R. reptotaenium*, followed by recruitment of SRB, and perhaps involving incorporation of additional BBD bacteria. Based on these findings we propose that SRB are secondary and necessary pathogens of black band disease. This is the first step in understanding the role of a secondary pathogen in a complex, polymicrobial coral disease.

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation (NSF grant no. 1208784) and Florida International University.

RESUMEN

Bacterias reductoras de sulfato como patógenos secundarios y necesarios en la enfermedad de la banda negra de coral. La enfermedad de la Banda Negra (BBD) es una enfermedad polimicrobiana compleja, que consiste en las cianobacterias, sulfuro oxidante y bacterias reductoras de sulfato (SRB) y bacterias heterotróficas. La cianobacteria *Roseofilum reptotaenium* se considera como el principal patógeno de BBD, pero otros miembros del consorcio pueden ser patógenos secundarios que son necesarios para el desarrollo de la enfermedad. Se conoce que las poblaciones de la bacteria reductora de sulfato *Desulfovibrio* están presentes en BBD y que estas poblaciones generan sulfuro dentro de la banda como un subproducto de la reducción del sulfato. También se conoce que la exposición de los corales sanos a sulfuro conduce a la lisis celular y la muerte del tejido de coral. Trabajos previos muestran que cuando recién colectado el tejido con BBD, que infecta fácilmente corales sanos, se expone al molibdato de sodio, un inhibidor específico de la reducción del sulfato, la infección no se produce. En este estudio analizamos el efecto del molibdato de sodio sobre la infección de los corales en un cultivo unialgal de *R. reptotaenium*. Fragmentos de coral de *Montastraea cavernosa* y *Siderastrea siderea* se transfirieron a dos acuarios experimentales, uno control con solo agua de mar artificial (ASW) y el segundo que contenía ASW y molibdato de sodio 2mM. Pequeñas esteras de cultivo *R. reptotaenium* se inocularon en la superficie de fragmentos experimentales de coral. Tanto *M. cavernosa* (n=6) y *S. siderea* (n=4) se infectaron y desarrollaron infecciones BBD- como en el tanque de control, mientras que había adjuntos temporales, sin infección exitosa en *M. cavernosa* (n=3) o *S. siderea* (n=2) en el tanque experimental con molibdato de sodio. Los resultados de este estudio revelan que un patógeno secundario es esencial para el proceso de infección y el desarrollo de BBD en corales escleractíneos. Específicamente, SRB como *Desulfovibrio* son necesarios para el desarrollo de BBD en el coral hospedero. Este es el primer paso en la comprensión de las funciones de los patógenos secundarios en una enfermedad polimicrobiana compleja de coral.

Palabras clave: Enfermedad de banda, sulfato reductor de bacterias, coral.

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The status of coral reefs and associated fishes and invertebrates of commercial importance in Pedro Bank, Jamaica

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Received 04-IX-2013   Corrected 02-I-2014   Accepted 24-III-2014

Abstract: The coral reefs located off the north coast of the Jamaican mainland are some of the best and most studied reefs in the world. Coral reefs of Pedro Bank, Jamaica were assessed in March, 2012 as part of the KSLOF Global Reef Expedition using a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol. The main objectives were to: 1) characterize the distribution, structure and health of coral reefs; and 2) evaluate the population status of commercially important reef fishes and invertebrates. This work was conducted to assist in characterizing coral reef habitats within and outside a proposed fishery reserve, and identify other possible conservation zones. Within 20 reefs, live coral cover ranged from 4.9% to 19.2%. Coral communities were dominated by small corals (esp. *Agaricia*, *Porites* and *Siderastrea*) although many sites had high abundances of large colonies of *Montastraea annularis* and *M. faveolata*, and these were generally in good condition. A single area, within the proposed fishery reserve, had extensive *Acropora cervicornis* thickets, and several shallow locations had small, but recovering *A. palmata* stands. Macroalgal cover at all sites was relatively low, with only three sites having greater than 30% cover; crustose coralline algae (CCA) was high, with eight sites exceeding 20% cover. Fish biomass at all sites near the Cays was low, with a dominance of herbivores (parrotfish and surgeonfish) and a near absence of groupers, snappers and other commercially important species. While parrotfish were the most abundant fish, these were all extremely small (mean size= 12cm; <4% over 29cm), and they were dominated by red band parrotfish (*Sparisoma aurofrenatum*) followed by striped parrotfish (*Scarus iseri*). While coral communities remain in better condition than most coastal reefs in Jamaica, intense fishing pressure using fish traps (main target species: surgeonfish) and hookah/spear fishing (main target: parrotfish) is of grave concern to the future persistence of these reefs. The proposed fishery reserve encompasses some of the best coral reef habitat near the Cays, but this MPA should be expanded to encompass other habitats and MPAs should be considered for bank reefs at the northwestern end, as well as Banner Reef and Blowers Rock. Rev. Biol. Trop. 62 (Suppl. 3): 11-24. Epub 2014 September 01.

Key words: Pedro Bank, Jamaica, coral reef health, fish community structure, marine protected areas.

The coral reefs located off the north coast of the Jamaican mainland are some of the best and most studied reefs in the world (Hughes, 1994). In contrast, very few studies have been conducted on the banks located off the south coast of Jamaica. The first and only comprehensive coral reef assessment was conducted on a portion of Pedro Bank in 2005 (Kramer, 2006). Other studies have focused on fisheries, socioeconomics and terrestrial assessments (Nicholson & Hartsuijter, 1982; Munro, 1983; Koslow, Hanley & Wicklund, 1988; Espuet, 2006; Hay, 2006; Kramer, 2006). These studies have documented the progressive expansion of human populations on the Cays during the 1990s, and their effects on the reefs and associated resources. The importance of the Pedro Bank as a base for fishing has steadily increased as Jamaica's nearshore fisheries continue to decline. The influx of fishermen, together with the adoption of more efficient and destructive fishing techniques such as Antillean Z-traps and hookah spearfishing is leading to the overexploitation of lobster, conch, and finfish throughout Pedro Bank (Aiken & Kong, 2000; Koslow et al., 1988; Munro, 1983; Nicholson & Hartsuijker, 1982). Further, the increase in permanent inhabitants on Pedro Cays has resulted in destruction of coastal vegetation, excessive trash and marine debris, discharge of untreated sewage into surrounding waters, and diminished habitat for nesting turtles and seabirds (Espeut, 2006; Hay, 2006).

Since the mid-2000s, conservation agencies in Jamaica have been working to implement the Pedro Bank Coral Reef Management Project. This project has included biological and socioeconomic assessments, feasibility studies, and efforts to control and minimize overfishing and degradation of coral reefs and coral cays due to unsustainable human settlement. A primary goal has involved the development of a zoning strategy, including the adoption of a fishery reserve off southwest Cay. To help inform constituents of the value of these resources and the benefits that would ensue through establishment of networks of marine protected areas (MPAs), KSLOF and partners conducted an extensive survey of coral reef habitats within Pedro Bank. The current research used the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol, which is the same methodology applied in 2005 (Kramer, 2006). The areas assessed in 2005 were reevaluated during this study, and we expanded the surveys to new locations. Here we present data on the status of coral reefs and changes that have occurred since 2005, and provide recommendations on potential sites that would benefit from protection as MPAs.

MATERIALS AND METHODS

Study sites: Pedro Bank is a submerged bank rising abruptly from about 500m depth. It is located about 58km off Jamaica at its closest point (Portland Point), and roughly 98km from Kingston, Jamaica. It extends over an area of 8 040km^2 and has a circumference of roughly 590km. Much of the bank is relatively shallow (about 10-24m depth) with extensive seagrass beds, rubble and sandy habitats, and scattered patch reefs. The bank gradually deepens in a NW direction. The south and southeast sides of the bank face into the Caribbean current and have the best developed reefs. The coral reef community structure was assessed at 20 sites along the S/SE sides, within 18 fore reef locations and two patch reefs (Table 1). At each site, data were collected on benthic community structure, corals, fishes and motile invertebrates using the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol.

Benthic cover: Cover of benthic organisms was estimated using a minimum of six 10m long transects per site (158 transects total) and one to three 10m x 1m photo-transects. The organism and substrate type were recorded every 10cm for a total of 100 points per transect. Substrates were categorized as hard-ground, rubble, sand/silt, live coral, and dead coral. All corals were identified to species and recorded as live, bleached, recently dead or long dead. Other invertebrates were identified to the lowest taxonomic level possible. Algae were divided into five functional groups (fleshy macroalgae, erect coralline algae, crustose coralline algae, turf algae, cyanobacteria). Additional measurements of algal height were recorded for macroalgae.

Coral: Coral species diversity, abundance, size structure and health were assessed with 74 belt transects, each 1 x 10m in length. Each coral within the 10m^2 area, 4cm or larger in diameter, was identified, measured (length, width and height) and assessed. Visual estimates of tissue loss were recorded for each colony using a 1m bar marked in 1cm increments for scale. If the coral exhibited tissue loss, estimates of the amount of remaining tissue and percent that died were made based on the entire colony surface. Tissue loss was categorized as recent mortality (white skeleton, occurring within the last 1-5 days), transitional mortality (exposed skeleton with filamentous green algae and diatom colonization, 6-30

TABLE 1
Coordinates, depth and location of each site examined using SCUBA

Site #	Coordinates		Name	Depth (m)
	Long	Lat		
PB-01	77.8135	17.0064	Northern leeward side of SW Cay	10.9
PB-02	77.8396	16.9388	Bank edge, southwest of South Cay	13.9
PB-03	77.7970	16.9319	Bank edge, S-SE of South Cay	23
PB-04	77.7607	17.0451	Between NE and Middle Cay	10.4
PB-05	77.7972	16.9861	S-SE of SW Cay	11.5
PB-06	77.6861	17.0398	NW of Shannon Rock on edge	14
PB-07	77.7206	17.0492	SE of NE Cay on edge	11
PB-08	77.7907	16.9717	Bank edge, south of SW Cay	17
PB-09	77.7874	17.0026	Bank edge, north of SW Cay	15
PB-10	77.9198	16.9308	S-SW of D (2nd) Shoal	14
PB-11	78.0871	16.8395	Banner Reef	20
PB-12	78.1001	16.8435	Banner Reef	11
PB-13	77.9926	16.8898	South of C Shoal	14
PB-14	77.5301	17.0327	Blower's Rock	8
PB-15	77.5146	17.0474	Blower's Rock	17
PB-16	77.5746	16.9398	Beth Rock	15
PB-17	78.6633	16.9535	NW Ridge	19
PB-18	78.1025	16.8697	Banner Reef on western edge	12
PB-19	77.7960	16.9812	Bank edge, south of SW Cay	20
PB-20	77.8296	16.9389	Bank edge, southwest of South Cay	19

days) and old mortality (>30 days). For each coral with partial or whole colony mortality, the cause of mortality was identified if possible. The diagnosis included an assessment of the type of disease, extent of bleaching, predation, competition, overgrowth or other causes of mortality. Each coral was first carefully examined to identify cryptic predators. Lesions were diagnosed into four categories: recent tissue loss, skeletal damage, color change, and unusual growth patterns; an individual colony could have multiple characteristics (e.g. color change and recent tissue loss). The location (apical, basal, medial) and pattern of tissue loss (linear, annular, focal, multifocal, and coalescing) were recorded, and a field name (e.g. black band disease, yellow band disease, dark spots disease) was assigned.

The abundance of recruits (corals smaller than 4cm) was assessed using a minimum of five 0.25m^2 quadrats per transect, with each quadrat located at fixed, predetermined intervals (2, 4, 6, 8, 10m, alternating between right and left side of the transect line). Recruits were identified in both benthic and coral transects. Recruits were divided into two categories: <2cm diameter and 2-3.9cm diameter.

Motile invertebrates: The abundance of large motile invertebrates (crustaceans, molluscs and echinoderms) was quantified using random circular plots, each 10m diameter (total area = 314m^2), with 1-4 plots assessed per reef. One diver would extend a 10m line from a central point and then swim slowly in a circle while a second diver would record the numbers of each species of invertebrate seen within the plot. Additional roving surveys were undertaken to assess presence of invertebrates in cryptic areas, including ledges and caves. Invertebrates were also counted and recorded within coral belt transects.

Reef fish: The reef fish assemblage (approximately 70 species) was quantified within a minimum of six 30 x 2m belt transects per site (187 transects total). All species were identified and their size was estimated to the nearest 5cm using a T-bar marked in 5cm increments for scale. The assessment focused on species that are ecologically relevant to the health of reefs and also important for commercial or recreational fisheries, with emphasis on herbivores, invertivores and larger piscivores. Roving surveys were also undertaken to characterize species diversity.

Data analysis: All data were initially entered into Microsoft Excel spreadsheets with PRIMER software used for graphical and comparative analysis. Species diversity, richness and evenness was calculated using the Shannon – Weiner index (H`): [H` = - Σi pi (log pi)]; Margalef's species richness (d): d = (S - 1)/ log (N), where S= number of species; N = number of individuals; and Pielou's evenness (J`): J` = H`/ log (S) to determine how evenly individuals were distributed among different species.

Clustering of benthic data, coral composition and fish biomass/abundance by site was examined using multi-dimensional scaling (MDS) followed by similarity profiles (SIMPROF) analysis to determine the factors that contribute most to a particular grouping. Individual contribution (e.g. fish taxa, fish functional groups, coral species) to the similarity of resulting groups was estimated using the similarity percentage (SIMPER) analysis of untransformed datasets. SIMPER analysis results were visually inspected and biotopes were determined based on similarities, dissimilarities, taxa distribution and relative abundance (semi-quantitative data). Analysis of Similarity (ANOSIM) testing was also employed to evaluate relationships between benthic and fish attributes. These tests compare sites based upon ranked, species similarity measures. Coral species abundances were log transformed to create a Bray-Curtis dissimilarity matrix (d). ANOSIM results were graphically interpreted using non-metric, multi-dimensional scaling (MDS) (Clarke & Warwick, 2001; Clarke & Gorley, 2006).

A ***Reef Health Index*** (RHI) was calculated for each dive site using seven specific biological indicators assessed during the field surveys. The grades were calculated by converting the mean for each indicator into a rank of 1 (critical) to 5 (very good). Seven parameters, grouped into two categories, were used: a *Coral Index*, comprised of coral cover, coral disease prevalence and coral recruitment; and a *Reef Biota Index*, comprised of a macroalgal index, herbivorous fish abundance (parrotfish and surgeon fish only), commercial fish abundance (grouper and snapper only), and *Diadema* abundance. The ranked scores of the three *Coral* measures and the four *Reef Biota* measures and these two sub-indices were then averaged to calculate an integrated reef health index. Threshold values for each rank were based on data ranges presented in the Healthy Reef Initiative report (HRI, 2008).

RESULTS

Benthic community structure: Within coral reef habitats, over 60% of the bottom was covered by algae, most of which was fleshy and erect coralline macroalgae (31%) and crustose coralline algae (18%). Live coral cover ranged from 4.9% (PB-01) to 19.2% (PB-20). Mean cover of other invertebrates was 14.5%, while 12.3% of the bottom consisted of uncolonized substrate (sand, rubble or hardground); 1% was dead coral (Fig. 1). Sites contained a total of 33 species of scleractinian corals. The most abundant corals were *Agaricia*, *Siderastrea, Porites* and the *Montastraea annularis* complex, respectively (Fig. 2). Most corals were small (mean diameter= 20cm), with 30% of all colonies 21cm or larger and 2% of the corals 100cm or larger (Fig. 3). The only corals with a mean diameter that exceeded 20cm were the *M. annularis* complex, *M. cavernosa*, *Colpophyllia natans*, *Dendrogyra cylindricus*, *Acropora palmata* and *A. cervicornis* (Fig. 4). A single taxon, *M. faveolata*, was dominated by colonies that exceeded 50cm. All corals exhibited a very low percent partial mortality (mean= 10%) and virtually no recent or transitional

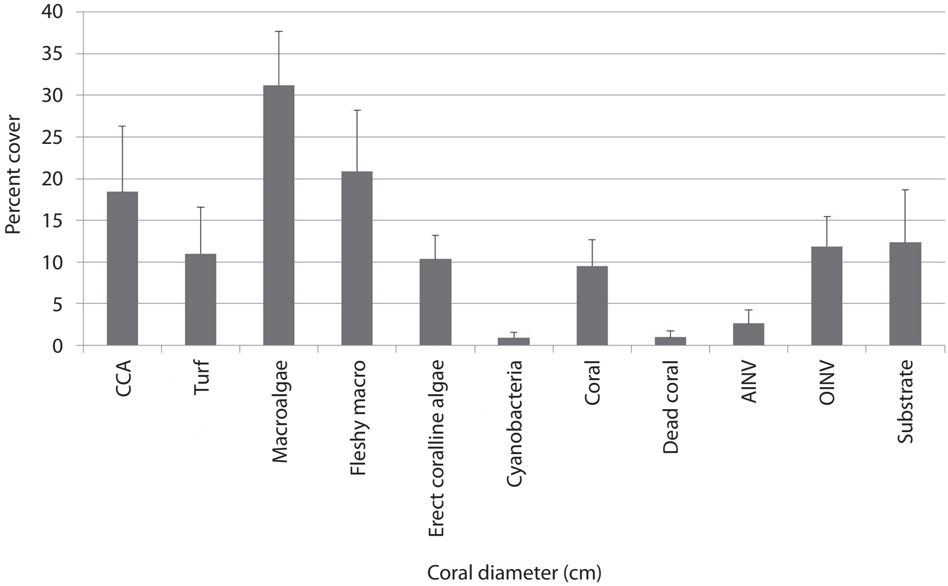

Fig. 1. Percent cover of benthic attributes examined within coral reefs on Pedro Bank. Data are presented as mean and standard deviation, pooled for all sites. Crustose coralline algae (CCA), turf algae (turf), macroalgae (fleshy macroalgae and erect coralline algae), fleshy macroalgae (fleshy macro), erect coralline algae, cyanobacterial mats, live coral (coral), dead coral, aggressive invertebrates (AINV), other invertebrates (OINV) and substrate (sand, hardground or rubble) are shown.

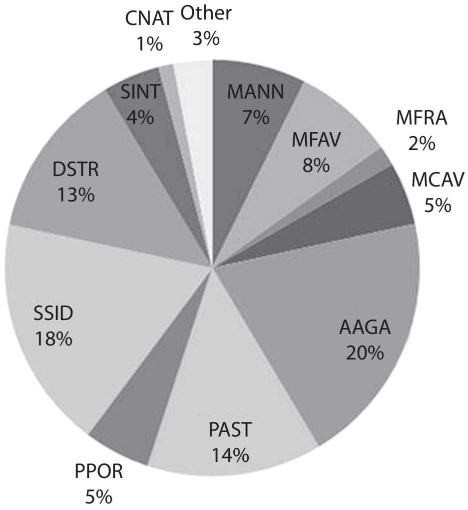

Fig. 2. Relative abundance (percent of the total population of corals) of the scleractinian corals pooled for all sites. "Other" includes 22 species of scleractinian corals.

mortality (<1%). The greatest amount of partial tissue loss was observed in the largest corals, including *C. natans* (20%), *M. annularis* (22%) and *M. faveolata* (27%) (Fig. 5). Coral recruits were dominated by *S. siderea* (27%), *P. astreoides* (19%), *A. agaricites* (14%), *M. cavernosa* (7%), *Favia fragum* (6.5%) and *Meandrina meandrites* (5.8%), with all species (pooled) occurring at a density of 3.3/m^2 (Fig. 6).

Reef fish communities: Reef fish populations exhibited a fairly low diversity (116 species), abundance (65 fish/100m^2), size (mean=13cm) and biomass (9 430g/100m^2). Populations were dominated by herbivores, with parrotfish occurring at the highest density (25fish/100m^2). *Sparisoma aurofrenatum* (redband parrotfish) and *Scarus iseri* (striped parrotfish) were most abundant, but all parrotfish were exceptionally small (mean=12cm total length) including terminal phase fish (18% were 21-29cm and 3% were 31-40cm). Other abundant species were surgeonfish (11fish/100m^2), wrasses (9fish/100m^2), and grunts (6fish/100m^2); most other functional groups had a density of <1 fish/100m^2.

All species of fish were small; over 78% were less than 20cm and only 3.5% were

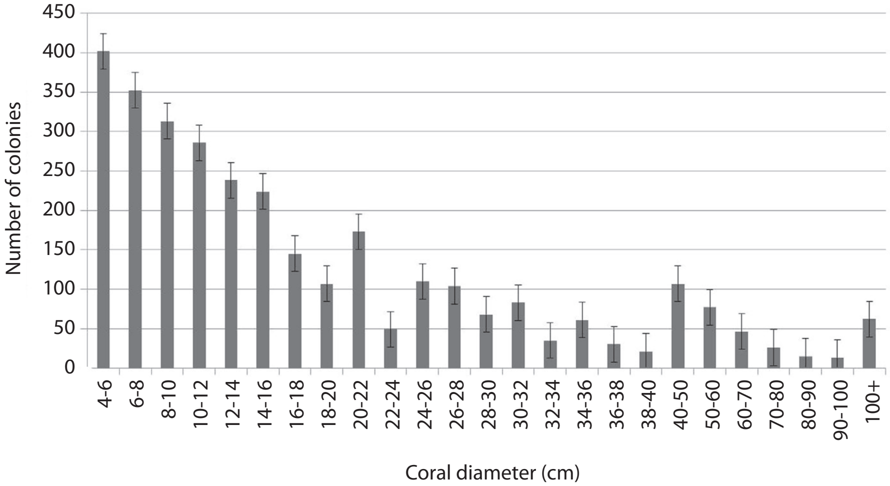

Fig. 3. The size frequency distribution for 3121 corals surveyed on Pedro Bank (pooled species and reefs).

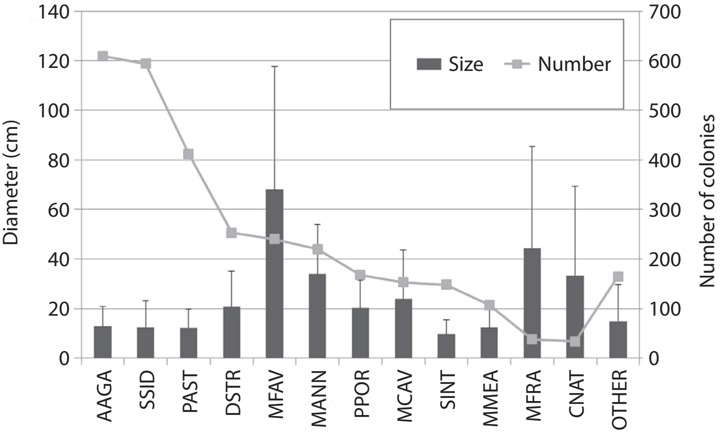

Fig. 4. Diameter of the dominant species of corals observed within belt transects (pooled for all reefs).

over 30cm. Overall biomass of reef fishes was low; herbivores had the greatest biomass, at 5 500g/100m^2 followed by invertivores (2 965g/100m^2). Triggerfish contributed most to the biomass of invertivores, with the abundance of these species increasing with distance from the Cays. Many functional groups of fishes were rare or absent including all snappers, large serranids (populations consisted only of hinds and graysby), barracuda, morays, grunts, and angelfish. Commercially significant species showed the lowest numbers and biomass overall, emphasizing the heavy fishing pressure occurring on Pedro Bank.

Although fish populations remain healthier on Pedro Bank than that observed off mainland Jamaica, fish community structure has shown substantial changes since 2 005 surveys (Fig. 7). Most importantly, the abundance and biomass of surgeonfishes has declined quite substantially. Parrotfish abundances are slightly higher than that recorded in 2005, but the

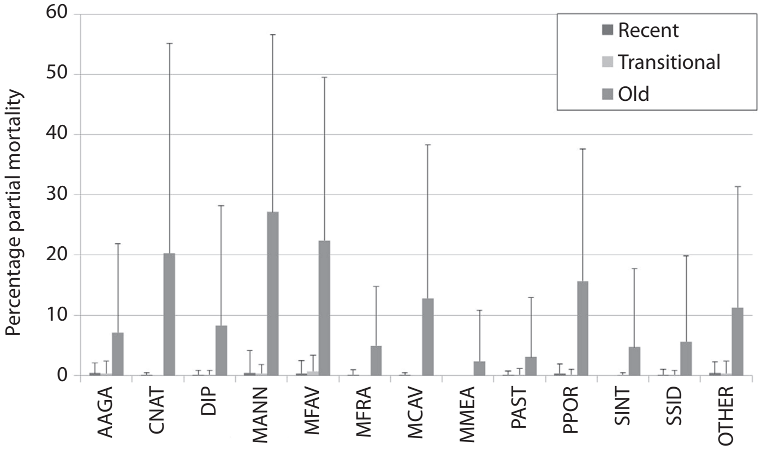

Fig. 5. Amount of partial tissue loss in scleractinian corals found on Pedro Bank. Data are pooled by species from all reefs. DIP includes *D. clivosa, D. strigosa* and *D. labyrinthiformis*; Ppor includes *P. porites, P. divaricata* and *P. furcata*. Other includes *A. cervicornis, D. cylindricus, D. stokesi, E. fastigiata, M. mirabilis, M. decactis, M. ferox, I. rigida, I sinuosa, Leptoseris cucullata*.

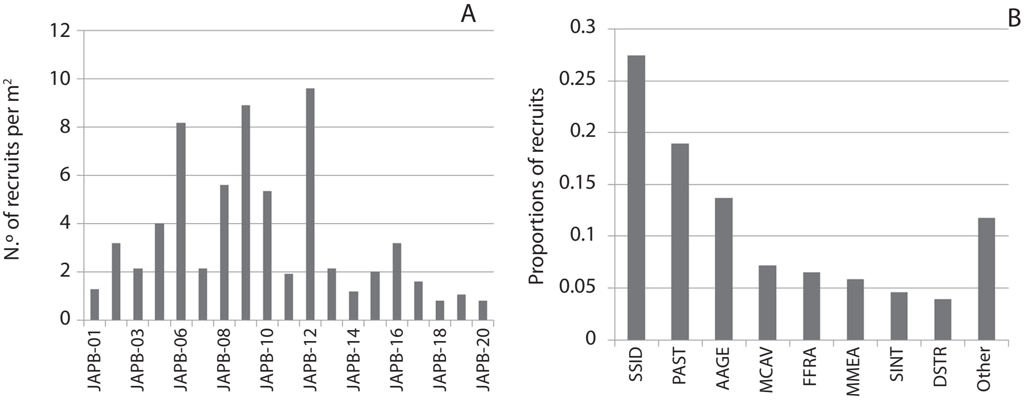

Fig. 6. Coral recruitment. A. Density of recruits by reef, pooled species. B. Proportion of recruits for each coral taxon pooled for all sites examined on Pedro Bank.

biomass for the two time periods is virtually the same, suggesting the average size of individual fish has declined over this period. In sites closest to the fishing village (0 to 10mi) the total biomass declined by 36% and the biomass of herbivores declined by 46% between 2005 and 2012. The biomass also markedly increased at a distance of 10mi from the fishing village in 2005, while the biomass in 2012 showed no increase except at distances of 20mi or more from the Cays.

Motile invertebrates: Commercially important (*Panulirus, Strombus*) and ecologically important motile invertebrates (*Diadema*, sea cucumbers, large crabs, octopus) were present in extremely low abundances. Queen conch were observed on 9 reefs at a very low density, with slightly higher abundances in six locations (0.1animal/m^2). This is not necessarily indicative of the population size on Pedro Bank, however, as key *Strombus* habitats were not examined. Lobsters were rarely observed

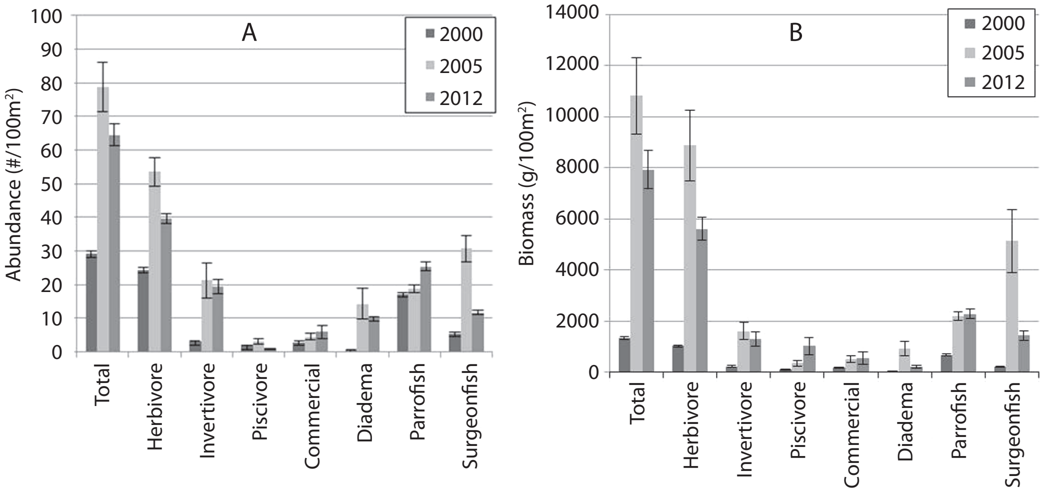

Fig. 7. Fish community structure for mainland Jamaica reefs (2000) and Pedro Bank (2005, 2012). A. Abundance by functional group. B. Biomass by functional groups. Mean and standard error are shown. Herbivore, Invertivore, Piscivore and *Diadema* predators include species defined in FishBase.

on reefs, occurring at 12 sites at densities of 2lobster/100m^2); much higher numbers were seen in landings examined on shore. Prominent *Diadema* populations occurred in two locations (12-20/100m^2); low densities (<0.5/100m^2) in other sites suggests they have shown limited recovery since the die-off in the 1980s.

Drivers of community structure: With exception of a few sites, dominant taxa were similar in size structure and abundance, and the condition of the substrate and health of corals showed minimal differences. Sites could be delineated into three groups based on benthic attributes, with macroalgae, crustose coralline algae (CCA) and non-living substrate contributing most to the differences (Fig. 8). Sites also subdivided into eight groups based on the contribution of different fish taxa to biomass, with groupings differentiated mostly due to relative amounts of parrotfish, surgeonfish and/or triggerfish. Most other variables were fairly homogeneous between locations. For instance, coral cover, fish abundance and biomass, and *Diadema* abundance were uniformly low among all sites. Analysis of Similarity (ANOSIM) testing did not reveal any significant relationships between coral abundance and macroalgal cover (R^2=0.155, p=0.161); coral abundance was related to fish biomass (all species pooled), but the R-value was very low (R^2=0.249; p=0.006). Fish abundance (all species pooled) was not related to coral cover (R^2=0.011; p=0.444) or vertical relief (height between the substrate and the tops of the corals; R^2=0.059; p=0.778), but it was related to macroalgal cover, although the R value again was low (R^2=0.428; p=0.013). Herbivorous fish populations (biomass and abundance of pooled species, parrotfish and surgeonfish) did not appear to be related to algae (CCA, fleshy macroalgae or turf algae) or coral (cover or abundance) populations. The lack of identifiable drivers of community structure may be due to the fact that all sites were overfished, coral cover was uniformly low, and algal communities were fairly homogeneous.

Resilience and health of reefs: The sites examined in this study exhibited Reef Health Index (RHI) scores that varied from 1-3 (critical to fair condition) for seven parameters (coral cover, coral recruitment, coral disease, fleshy algae biomass, herbivore abundance (*Diadema*, parrotfishes and surgeonfishes), and

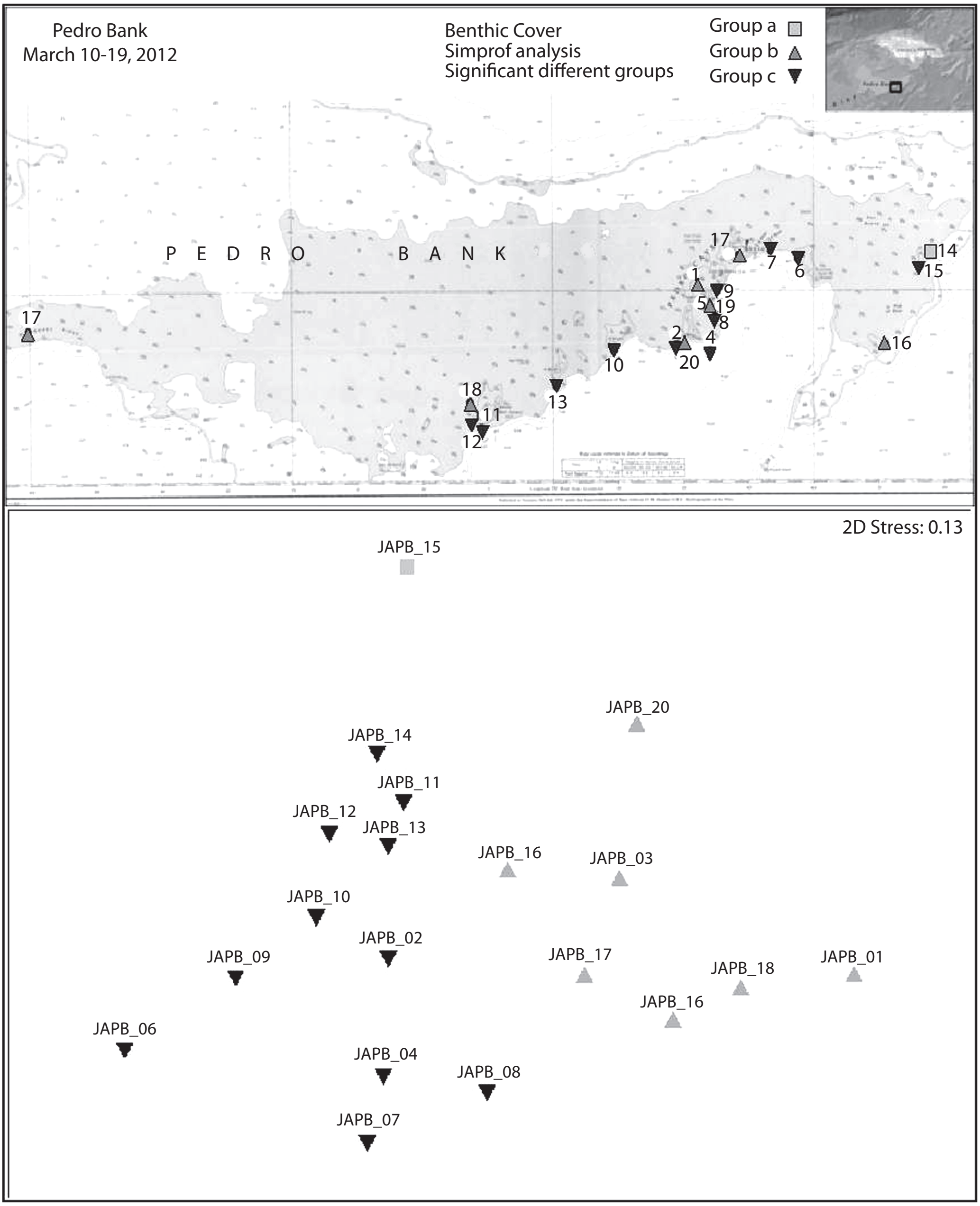

Fig. 8. Similarity of site-averaged benthic data plotted over the Jamaica site map (top) and two dimensional nonmetric multidimensional scaling (nmMDS) plot (bottom). Three distinct groupings were identified.

commercially important reef fish) and a cumulative RHI of 2 to 3.5 (Fig. 9).

DISCUSSION

Pedro Bank is a unique area that supports a wide variety of shallow marine habitats including seagrass beds, gorgonian hardgrounds, rubble fields, deep algal meadows, sand flats and coral reefs. Coral reef habitats occupied only a small percentage of the bank overall, and were mostly concentrated at the eastern and southeastern edge of the bank, adjacent to the dropoff. The new fishery reserve contains some of the healthiest coral reefs, including extensive shallow *Acropora palmata* framework and the largest healthy stand of *A. cervicornis* found on Pedro Bank. Other important high relief coral habitats and seagrass beds were adjacent but outside of the reserve boundaries and around Banner Rock, Blowers Rock and D and C shoal.

In all locations, coral cover was fairly low (<20%) and dominated by small corals, especially early colonizing species (*Agaricia* and *Porites*) as well as *Siderastrea*, *Diploria*, and *Meandrina.* Of note were several populations of larger massive framework corals such as *Montastraea annularis* (complex), as well as stands of *Madracis mirabilis*, and numerous large *Dendrogyra* colonies. *Montastraea*

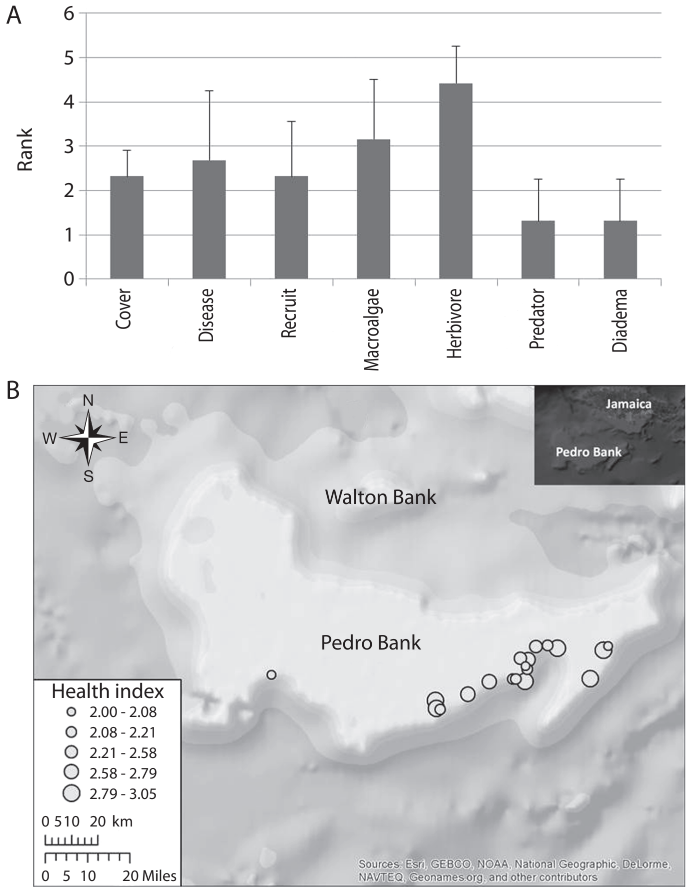

Fig. 9. Reef Health Index (RHI) A. Mean rank (and standard deviation) for each of the seven parameters that make up the RHI, pooled for all sites examined on Pedro Bank. B. The Reef Health Index for each of the 19 sites examined on Pedro Bank. Larger circles refer to more resilient sites.

annularis (complex), once the most important frame builders in the Western Atlantic, has declined throughout its range since the mid-1990s, primarily from recent bleaching events and disease (white plague and yellow band disease) (Miller, Atkinson & Witcher, 2009; Bruckner, 2012a). These corals formerly made up 50-80% of the live coral cover, but recently have been reduced to 2-5% cover; what were once large (several meter) colonies are now skeletons colonized by other corals, algae and invertebrates, with small *M. annularis* tissue remnants. On Pedro Bank, most of the larger *M. annularis* and *M. faveolata* colonies were completely 'live". Very little disease, bleaching and recent mortality was noted on these species. Extensive *Acropora* framework with scattered live colonies surrounded many of the cays and emergent shoals, and small patches of *A. cervicornis* were found on many of the deeper reefs (10-30m depth). Acroporid corals have become rare in most Caribbean locations as a result of white band disease outbreaks in the 1980s, recent bleaching events, storm damage and a host of other factors and were recently listed on the U.S. Endangered Species Act (Bruckner, 2003). The lack of disease, few corallivores and presence of small colonies with little mortality on Pedro Bank is indicative of ongoing recovery of these species.

One of the most positive findings among the stony corals examined on Pedro Bank was the low level of partial mortality. AGRRA surveys that have been conducted throughout the Caribbean over the last 15 years (Lang, 2003; Bruckner & Hill, 2009; Bruckner, 2012b), as well as the Caribbean surveys completed during the Global Reef Expedition, have recorded a mean of about 20-30% partial mortality on all species pooled and upwards of 50-80% partial mortality in *M. annularis* complex and other larger massive corals. On Pedro Bank most colonies were intact; partial mortality was usually less than 10% and colonies of *M. annularis* (complex) showed about 20% partial mortality. The presence of healthy, undamaged colonies may be an indication of higher resilience, better environmental conditions and a greater potential for successful reproduction, as corals have not been reduced below the minimal size threshold necessary for gametogenesis (Szmant-Froelich, 1985; Szmant, 1991).

The benthos also appeared to be in fairly good condition. Even though *Diadema* were rare in most locations, and cover of macroalgae exceeded the cover of living coral, there was a general impression that fleshy macroalgae was less abundant than that reported from many other Caribbean localities (Lang 2003). The substrate had a prominent cover of crustose coralline algae, with small patches of erect coralline algae and some macroalgae, most of which were concentrated at the margins of corals and not on open reef substrates. Unlike other areas in the Caribbean, the reef was not being smothered by thick mats of *Dictyota, Microdictyon* (completely absent) and *Lobophora* (occurred in low abundances), only on a few corals showed partial mortality, and cyanobacterial mats were rare.

The largest concern to Pedro Bank reefs is overexploitation of the fishery resources. Exploitation of Pedro Bank began in the 1960s, but has progressively increased as the densities of humans on the cays increased (Munro, 1983). Most fishing effort is concentrated on the southeast (SE) portions of the bank, near the cays, which is also the location of some of the best developed coral reefs. As a result, the biomass of reef fish was lowest surrounding the fishing village with higher biomass (mainly invertivores) seen at distances of 20mi or further from the village. This is probably related to the distance that a fisherman can realistically travel from the fishing village. Fishers tend to go to their farthest point (under ten miles in one day) and then work their way back, fishing at different spots as they return (Meggs pers. comm.).

Intensive fishing pressure appears to have affected most species as all reefs had a fairly low biomass of fishes and many key species were extremely rare or absent. The current targets of the fishery appeared to be two families of herbivores which made up the bulk of the catch, scaridae and acanthuridae. Very few schools of surgeonfish were documented and individuals were small (5-15cm) and large-bodied scarids were infrequently seen. In addition, the dominant parrotfish on these reefs (and in the catch) was the red band parrotfish followed by stoplight parrotfish. While parrotfish were still fairly abundant, both species were very small (most <15cm). These species were changing sex from initial phase (females) to terminal phase (males) at a much smaller size than that seen historically (TP fish of 10cm were fairly common). The smaller than average size in sex change may be a survival mechanism that is a direct outcome of high fishing pressure (Hawkins & Roberts, 2003). However, the decline in the average size of the population will cause a disproportionate decline in the reproductive output, because there is an exponential relationship between body length and egg production (Bohnsack, 1990), which may have negative consequences on the long term persistence of these fish.

Two main fishery approaches are now undertaken on Pedro Bank, trap (pot) fishing and spearfishing using hookah (Aiken & Kong, 2000; Gustavson, 2002). The Antillean z-traps were observed on or adjacent (in sand) to coral reef habitats in many of the sites we surveyed. Traps typically contained a very low biomass of fish, but the fish consisted of a broad spectrum including piscivores (small serranids, lutjanids, grunts, balistids, pomacanthids), as well as herbivores (scarids), but surgeonfish were the dominant species noted. These traps seemed to favor smaller species and individuals (partially because no large fish remain), which may contribute to growth overfishing. Further, the depletion of large predatory fishes has triggered a shift from high value species to a high diversity of lower value species, especially species that formerly were considered non-target species and are important indicators of a healthy reef system (e.g. butterflyfish, angelfish); this is suggestive of ecosystem overfishing (Pauly, 1979). As traps have become less economical, there has been expanded use of hookah, primarily targeting parrotfish with incidental catch of other "large" fish and lobsters, which may lead to Malthusian overfishing (Pauly, 1990). A continued decline of herbivores will also cause ancillary damage as reef substrates become monopolized by increasing amounts of fleshy algae, reducing the area available for encrusting coralline algae, and inhibiting coral settlement. Over the longer term, the reefs will be less likely to resist future disturbances and their potential to rebound may be reduced.

At this time, the overall condition of Pedro Bank's coral reefs remains far better than most reefs off mainland Jamaica, but these reefs are at a tipping point. The establishment of the South West Cay Special Fishery Conservation Area is a key step forward in conservation of Pedro Bank's coral reef resources, as it will allow fish to grow larger, potentially producing more offspring and spill over into adjacent fished areas. In particular it can help increase the abundance and size of parrotfish which represent the primary target of fishermen and concurrently species responsible for one of the most important processed in maintaining ecological balance, herbivory. The newly established, measuring 16.3 km^2, is far too small to adequately protect fishery resources as this represents <0.1% of the total area (9247km^2; Zenny, 2006) of Pedro Bank. Furthermore, the increasing fishing effort and destructive types of fishing are unsustainable and are likely to trigger deleterious changes to the reefs. Additional conservation measures that emphasize an expanded network of protected areas may help maintain and restore Pedro banks precious coral reefs.

RECOMMENDATIONS

Significant benefits could be achieved by expanding the boundaries of the newly established Fishery Reserve such that it encompasses extensive and healthiest high relief *Montastraea* dominated coral habitat found to the south and west, and it includes an adjacent large seagrass bed. Banner reef should be considered a candidate site for an MPA as it contained the largest number of different marine habitats including a very diverse shallow water reef dominated by large *Montastraea faveolata* and *M. annularis* colonies intermixed with extensive stands of *Porites porites*, *A. cervicornis* patches, large colonies of *Dendrogyra cylindricus* and high relief coral bommies in deeper sandy areas, extensive *Acropora* framework, and an elongate ridge with steeply sloping sides, caves, and ledges that provided considerable habitat for large crabs, lobsters, octopus, groupers and other high value species. Banner reef also had the largest population of *Diadema* seen on Pedro Bank, the highest diversity of fish families, and a high biomass of fish composed of schools of grunts, parrotfishes and surgeonfishes. Blowers Rock is also another candidate MPA site. It had the largest high-relief *Acropora palmata* framework seen on Pedro Bank with extensive patches of live *A. palmata.* A very unusual *Montastraea* dominated reef was also identified in 15-20m depth. This reef had unusually large (2-4m diameter/height) and old *Montastraea faveolata* colonies, the largest seen on the bank. Because these areas are east (and upcurrent) of the inhabited Cays and the Fish Sanctuary, the endangered corals that occur on these reefs (*Montastraea* and *Acropora*) could serve as seed stock for other areas on the bank to the west. They also provide considerable habitat for other species as a result of their high relief. Finally, C Shoal and D Shoal are additional candidates for inclusion in an MPA network. It had extensive *Acropora palmata* framework with small stands of living *A. palmata* in shallow (2-5m depth) areas and extensive diverse deeper coral habitats composed of large *Montastraea*-dominated communities, patches of *Acropora cervicornis* and the only large stands of *Madracis mirabilis* and *Porites porites* seen in the region.

ACKNOWLEDGMENTS

The data presented in this manuscript were collected during the fifth coral reef research mission completed during the Global Reef Expedition (GRE). All research was performed under a permit obtained from the National Environment and Planning Agency (NEPA) (ref #18/27, 8 December, 2011). Financial support for the surveys and the research vessel, *M/Y Golden Shadow* was provided by His Royal Highness Prince Khaled bin Sultan. We are grateful for the involvement of the Nature Conservancy, Jamaica, the University of West Indies, the Ministry of Agriculture & Fisheries, the National Environment and Planning Agency; and Natural Resource Management and Environmental Planning Department (NRMEP), Nova Southeastern University, Atlantic and Gulf Rapid Reef Assessment, and Reef Environmental Education Foundation. Special thanks to Judy Lang, Ken Marks, David Grenda, Alex Dempsey, Llewyn Meggs, Nathalie Zenny and Rachel D'Silva for their assistance with the coral, algae, fish and invertebrate surveys.

RESUMEN

Estado de los arrecifes de coral y comunidades de peces e invertebrados con interés comercial asociadas al Banco de Pedro, Jamaica. Los arrecifes de coral ubicados en la costa norte de Jamaica son los mejores y mas estudiados corales del mundo. Los corales de arrecife del Banco de Pedro, Jamaica, fueron evaluados en marzo 2012 como parte de la expedición global KSLOF utilizando una modificación del protocolo de estimación rápida de arrecifes para el Atlántico y el Caribe (AGRRA). Los objetivos principales fueron: 1) caracterizar la distribución, estructura y salud de los arrecifes de coral; y 2) evaluar la condición de las poblaciones de peces arrecifales e invertebrados de interés comercial. Este trabajo fue realizado con el propósito de colaborar en la caracterización de hábitats arrecifales, tanto dentro como fuera de un área sugerida como reserva marina, e identificar otras áreas de conservación. Para los 20 arrecifes, la cobertura de coral vivo varió entre 4.9% y 19.2%. Las comunidades de corales son dominadas por corales pequeños (*Agaricia*, *Porites* y *Siderastrea*), aunque en varias localidades se presentó una mayor abundancia de colonias grandes de *M. annularis* y *M. faveolata,* y estos se encontraban por lo general en buenas condiciones. Dentro de la reserva pesquera propuesta, una sola área presentó fragmentos de *A. cervicornis*, y varias localidades someras presentaron pequeños fragmentos de *A. palmata*, pero en proceso de recuperación. La cobertura de macroalgas en todas las áreas fue relativamente baja, solo tres lugares presentaron más de un 30%; la cobertura de algas coralinas calcárea (CCA) fue alta, ocho lugares excedieron el 20%. La biomasa de peces fue baja en todos los sitios cercanos a los cayos, y hubo dominancia de herbívoros (pez loro y cirujanos), y en general ausencia de chernas, pargos y otras especies de peces de interés comercial. Aunque los peces loro fueron los más abundantes, estos presentaron tamaños extremadamente pequeños (tamaño promedio = 12cm; <4%

por encima de 29cm), y estuvieron dominados por el pez loro de banda roja (*Sparisoma aurofrenatum*), y por el pez loro de rayas (*Scarus iseri*). Mientras que las comunidades de coral permanecen en mejor condición que muchos de los arrecifes costeros de Jamaica, existe una intensa presión pesquera usando trampas de pesca (principal objetivo: cirujanos) y de compresores de aire (hookah)/ pesca con arpón (principal objetivo: pez loro) es preocupante, y compromete la persistencia y el futuro de estos arrecifes. La reserva marina (MPA) que se sugiere incluye algunos de los mejores hábitats de arrecife coralino cerca de los cayos, pero es recomendable que se amplíe para incluir otros hábitats y que se consideren áreas marinas protegidas en los bancos de arrecife del extremo noroeste, así como el arrecife Banner y Blowers Rock.

Palabras clave: Banco de Pedro, Jamaica, salud del arrecife de coral, estructura comunitaria de peces, áreas marinas protegidas.

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Unexpected results from direct measurement, with a torsion microbalance in a closed system, of calcification rates of the coral *Agaricia agaricites* (Scleractinia:Agariicidae) and concomitant changes in seawater pH

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Received 15-VIII-2013   Corrected 23-II-2014   Accepted 24-III-2014

Abstract: Ocean acidification is impacting the calcification of corals, but the mechanisms of calcification are still unclear. To explore the relationship between calcification and pH, small pieces of coral were suspended from a torsion microbalance in gently stirred, temperature controlled, seawater in a closed chamber. Net calcification rate and pH were continuously monitored while light, temperature or pH could be manipulated. The coral pieces were from the edges of thin plates of *Agaricia agaricites* and were studied alive and freshly collected. Unexpectedly, when calcification was taking place (n=9, 0.082 mg.hr^{-1}.cm^{-2}), as determined by weight increase, the pH of the surrounding seawater medium changed little (n=10, -0.0047 pH units.hr^{-1}.cm^{-2}). When calcification was not taking place the decrease of seawater pH was an order of magnitude higher, -0.013 pH units.hr^{-1}.cm^{-2}. This is the opposite of what is expected when calcium carbonate ($CaCO_3$) forms. Similarly, fresh skeleton initially showed no change of pH in the seawater medium although the rates of weight gain were high (upto 1.0 mg hr^{-1}.cm^{-2}). After 10 hours, as the rate of deposition decreased following a generalized Michaelis-Menten growth curve, the pH began to decrease dramatically indicating an increase of CO_2 in the seawater. These unexpected results can be explained if unstable calcium bicarbonate ($Ca(HCO^3)_2$) is formed in the organic matrix/carbonic anhydrase surface and slowly transforms later to $CaCO_3$. Pieces of living coral monitored in the chamber for 30 hours gained weight during the day and loss it at night. The loss would be consistent with the transformation of $Ca(HCO^3)_2$ to $CaCO_3$ with the release of CO_2. The mean calcification rate of live coral was greater (n=8, p=0.0027) in high light (120 µmol.s^{-1}.m^{-2}) at 0.098 mg.hr^{-1}.cm^{-2}, compared to 0.063 mg.hr^{-1}.cm^{-2} in low light (12 µmol.s^{-1}.m^{-2}). However, at the same time the mean rate of pH change was -0.0076 under low light compared to -0.0030 under high light (n=8, p=0.0001). The difference can be explained by CO_2 being used for photosynthesis by zooxanthellae. The deposition rate of live coral was not affected by the addition of phosphate but the rate of weight gain by the freshly collected skeleton was strongly enhanced by phosphate. These results indicate that care should be applied in the application of the alkalinity anomaly technique for the measurement of calcification in corals. Rev. Biol. Trop. 62 (Suppl. 3): 25-38. Epub 2014 September 01.

Key words: coral calcification, CO_2, pH, organic matrix, carbonic anhydrase, $Ca(HCO^3)_2$.

The processes involved in the production of an aragonite ($CaCO_3$) skeleton in corals are poorly known compared compared to calcification in other animals (Allemand, Tambutté, Zoccola & Tambutté, 2011). Seawater contains about 10.3mmol.Kg^{-1} of calcium ions (Ca^{2+}), dissolved inorganic carbon is present as carbon dioxide (CO^2), carbonic acid (H_2CO_3), bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}), with the equilibria between them described by their equilibrium constants and their relationships with pH , alkalinity and temperature. It seems to have been taken for granted that the formation of aragonite crystals would result from the combination of Ca^{2+} and CO_3^{2-} . However, Lee, Park, Kwak & Cho (2010) have reported crystalline aragonite deposition from a solution of $CaCl_2$ containing carbonic anhydrase using CO_2 directly from the atmosphere. The sources of calcium and carbon and how they reach the calcification site have been reviewed by Cohen and McConnaughey (2003), Furla, Galgani, Durand and Allemand (2000) and Allemand et al. (2004; 2011). Carbon dioxide which can move freely through cell membranes was proposed by McConnaughey (1989) as a substrate for calcification to account for ^{18}O and ^{13}C deficiencies in coral skeletons (McConnaughey, 2000). The response of corals to changes of CO_2 partial pressures and temperature was reviewed by Reynaud et al. (2003). While calcification and photosynthesis may compete for the same DIC pool they are sometimes regarded as complementary (Gattuso, Allemand & Frankignoulle, 1999) rather than in competition (Langdon & Atkinson, 2005). With a focus on ocean acidification as the result of increased anthropogenic carbon dioxide in the atmosphere, calcification has been increasingly linked to the calcium-carbonate saturation state (ω) which is the ratio of the ion concentration product ($[Ca^{2+}] \times [CO_3^{2-}]$) to the solubility product of the mineral deposited, in this case aragonite (Allemande *et al*. 2004). As acidity increases the relative concentration of carbonate in seawater is reduced and has been used to predict decreased calcification at the organism and community levels (Kleypas et al., 1999; Gattuso et al., 1999; Marubini & Thake, 1999; Langdon, 2000; Langdon et al., 2000; Langdon, Broecker & Hammond, 2003; Erez et al., 2011).

The mechanisms of calcification have been fully reviewed by Allemand et al. (2011). Active calcification by the coral involves secretion of a layer of organic matrix (reviewed by Allemand, Tambutté, Girard & Jaubert, 1998 and Allemand et al., 2011). Sandeman (2012) presented evidence that carbon dioxide is the probable substrate for calcification and that carbonic anhydrase present in organic matrix is the basis for calcification that takes place on the surface exposed after removal of living tissue by waterpiking. Deposition of calcium carbonate crystallized in the form of aragonite takes place from the extracellular calcifying fluid (ECF) or hydrogel-like medium (ECM) (Bryan & Hill, 1941) on an organic matrix framework on the surface of the skeleton underlying the calicoblastic layers. What is still not clear is in what form dissolved inorganic carbon (DIC) reaches the site of calcification, and to what extent, if at all, the calcifying surface is in direct contact with seawater. Charged ions such as Ca^{2+}, HCO_3^- and CO_3^{2-} cannot move passively through cell membranes so either active transport via a transcellular route or passive diffusion of ions or seawater using a paracellular route at the boundaries of cells or some combination of these routes may be involved (Allemand et al., 2011). The median value of enhanced calcification in light (LEC) is around 3 (Gattuso et al., 1999). The range of ratios observed is large and Allemand et al. (2011) reviewed the possible mechanisms by which calcification is enhanced. The answers to these questions are complicated by the fact that zooxanthellae in the tissues take up CO_2 for photosynthesis and CO_2 is released as the result of respiration by coral tissue and their symbionts. Sandeman (2012) presented evidence that CO_2 is the substrate for calcification by living and freshly waterpiked coral skeleton and that the enzyme carbonic anhydrase appears to be incorporated in the organic matrix secreted by the calicoblastic layers. It was also shown that for dead coral skeleton in sea water CO_3^{2-} is the substrate and at $pH> 7.4$ the skeleton gained weight and at $ph<7.4$ dissolved.

Calcification rates of corals are commonly derived by buoyant weighing techniques (Davies, 1989), uptake of the radioactive isotope ^{45}Ca (e.g. Moya et al., 2006; Al-Horani, Tambutté & Allemand, 2007), the alkalinity anomaly technique (Smith & Key, 1975) or using a sclero-chronological technique (e.g. by Gischler & Oschmann, 2005). Each of these methods has its advantages and disadvantages, with some requiring destruction of the coral. The buoyant weighing technique used by Franzisket (1964) and developed by Davies (1989) for nubbins of *Porites porites* has been used to measure calcification rates over time periods of less than a day but a disadvantage in physiological studies is that the coral or a coral 'nubbins' has to be transferred to and from a balance for weighing. For physiological experiments over shorter time periods it is desirable to minimise any physical disturbance and provide stable conditions while still being able to change experimental parameters such as light, temperature or pH. Sensitive balances are expensive, sensitive to sea air and because they tend to drift they may require re-zeroing regularly which requires disturbing the organism. Davies (1989) established with his buoyant weighing technique that for corals changes in the tissue weight over the time span of an experiment were small and could be corrected for, and for imperforate corals such as thin plates of *Agaricia* could be ignored.

In an earlier paper Sandeman (2012) reported on a torsion balance developed to investigate calcification in small pieces of the coral *Agaricia agaricites*. A major disadvantage of the technique was that in an open system, the seawater medium could exchange CO_2 with the air, changing the pH and bringing uncertainty to the carbon chemistry. In this study the torsion balance has been completely enclosed in a sealed chamber to avoid the exchange of CO_2 with the air. The pH electrodes and their associated temperature sensors have been incorporated so that pH can be continuously monitored while calcification takes place. In order to seal off the system from the air some modifications were made to the balance. The torsion wire was of tungsten and shortened considerably. The beam also had to be shorter in order to fit the container and, to regain some of the lost sensitivity, thinner (0.025mm) wire was used. The lighter the beam of a balance the higher is the sensitivity (Vogel, 1961) and it was found that a hollow, sealed, carbon fibre beam, sealed at its ends, provided buoyancy making the beam assembly lighter under water and greatly increasing the sensitivity of the balance.

Seawater contains about 10.3mmol.kg^{-1} of calcium ions (Ca^{2+}), dissolved inorganic carbon is present in seawater as carbon dioxide (CO^2), carbonic acid (H_2CO_3), bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}), the equilibria between the species of carbon can be represented as follows:

$$\begin{array}{ccccccc} CO_2(Aq) & \leftrightarrow & HCO_3^- & \leftrightarrow & CO_3^{2-} & & \text{(Eq. 1.)} \\ +H_2O & & +H^+ & & +H^+ & & \end{array}$$

The equilibria between the species of carbon are governed by their equilibrium constants and their relationships with pH, alkalinity and temperature. These relationships can be seen in Fig. 1 which is similar to Fig. 1. 1. 3 in Zeebe and Wolf-Gladrow (2000) but is for seawater (S= 35.5 and T= 28°C) used in this study. In general, at normal seawater pH (8-8.2), the bulk of the carbon is present as HCO_3^- with a small quantity as CO_3^{2-} and even smaller quantity as CO_2. If, as in the acidification of sea as the result of increased atmospheric carbon dioxide, there is an increase in dissolved CO_2, the total dissolved organic carbon (DIC) increases but total alkalinity (TA) does not change and a decrease in pH results (Fig. 1). If CO_2 in the system decreases the opposite happens, DIC decreases and TA remains the same and there is a consequent increase in pH. If

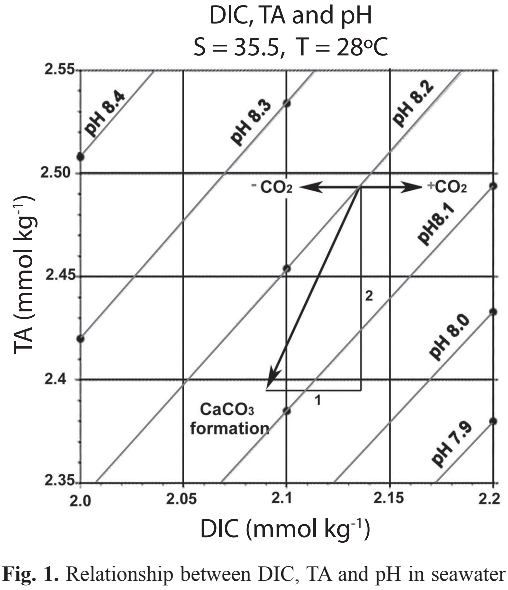

Fig. 1. Relationship between DIC, TA and pH in seawater (S=35.5, T= 28°C) showing the effect of $CaCO_3$ formation and of taking up or losing CO_2. Calculated with CO@SYS program.

calcification takes place with the formation of calcium carbonate as a result of the following reaction (Zeebe & Wolf-Gladrow, 2000):

$$Ca^{2+} + CO_3^{2-} \rightarrow CaCO_3 \qquad \text{(Eq. 2.)}$$

DIC decreases by 1 unit and TA decreases by two units, (as calcium ions have a double positive charge). The new equilibrium position, as seen in Fig. 1, results in a lower pH. If $CaCO_3$ dissolves the direction of the arrow is reversed and there is an increase of 1 unit in DIC and two units of TA and the pH increases. The change in equilibrium point for $CaCO_3$ formation is the same whether the source of carbon is CO_3^{2-}, HCO_3^- or CO_2 (Zeebe & Wolf-Gladrow, 2000).

The aim in this study was use the improved torsion balance to follow up on the rather extraordinary findings related to freshly waterpiked *Agaricia* skeletons (Sandeman, 2012) and to further explore the indications that calcification in the living coral might involve CO_2 rather than CO_3^{2-}. Generally two of DIC, TA, pH and [CO_2] are required to calculate the components of the carbonate system in seawater. The experimental set-up used here permits continuous monitoring of pH change and weight change of the coral. If the weight change is mainly of skeleton formation or dissolution then this permits estimates of changes of both DIC and TA. The closed chamber, however, does not permit TA to be measured other than at the beginning and end of an experiment and was not attempted. It was also hoped that under different lighting conditions insight might be gained on the mechanism involved in the enhancement of calcification of corals by light.

MATERIALS AND METHODS

Small pieces of *Agaricia agaricites* were snipped from the edge of thin plates of young colonies growing near the reef crest opposite the Discovery Bay Marine Laboratory. The pieces were immediately transported to the seawater tables where they were trimmed to a suitable size (1-2cm^2) then suspended, in a horizontal orientation, by loops of thin (0.025mm diam.) polyester monofilament in gently flowing seawater in a seawater table. The pieces were used in experiments within an hour of collection. There is some indication that orthophosphate in low concentrations inhibits the deposition and dissolution of calcium carbonate (Pytkowicz, 1973; Morse, 1974; Burton & Walter, 1990) and for live corals and freshly waterpiked coral skeleton the seawater used in the experimental chambers was collected from at least a mile offshore. This proved to have the lowest phosphate levels as measured by the method for reactive phosphorus in Strickland and Parsons (1965). For experiments with dead corals "Instant Ocean" artificial seawater which has low (0.05μmol) phosphate concentration (Atkinson & Bingham, 1999) was used. All seawater was millepore filtered (0.45μ) immediately before use. Salinity was measured with a Pinpoint Salinity Monitor (American Marine Inc.). Total Alkalinity of the seawater was estimated using the method of Smith and Kinsey (1978). The relationships between DIC, TA and pH and [CO_2], [CO_3^{2-}] and ω for each batch of seawater (Table 1) were estimated using the CO@SYS program. From the initial salinity, temperature, total alkalinity (TA) and pH for each batch of seawater the total dissolved carbon (DIC) was obtained. The experimentally measured change of weight of the skeleton then permits calculation of the carbonate withdrawn from the seawater medium and estimation of DIC at the end of each experiment.

The balance (Fig. 2) chambers (volume ≈ 1lL) were filled with millepore filtered seawater brought to the temperature at which the experiment was to be conducted (27°C). Temperature sensing thermistors, control circuits, and insulated heater coils maintained a constant temperature within 0.2 °C. Small magnetic stirrers (1.0x0. cm) gently and continuously circulated the water in the chambers. The pH could be changed by exchanging some of the seawater in the chamber with seawater that had a high dissolved CO_2 content using a syringe through the hole in the centre of the

TABLE 1
Estimated carbon parameters for seawater used

Parameter (Salinity=35.5, Temp. 28°C)	Natural seawater (1km offshore, Discovery Bay)	Artificial seawater (Instant ocean)
Total Alkalinity (TA), μeq kg^{-1}	2 490	2 560
pH (NBS)	8.18	8.21
Total Carbon (DIC), μmol kg^{-1}	2 029	1 911
[CO$_2$] , μmol kg^{-1}	10.8	9.5
[HCO$_3^-$] , μmol kg^{-1}	1 781	1 665
[CO$_3$] , μmol kg^{-1}	236	237
Ω	5.7	5.7

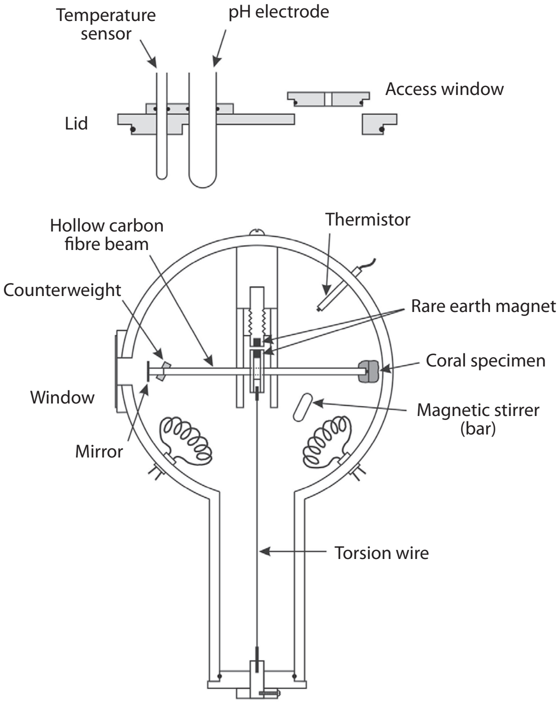

Fig. 2. The torsion balance. The ends of a 15cm length of torsion wire (tungsten, diam. 0.05-0.11mm) are embedded in short pieces of stainless steel tubing (0.5mm OD) with cyanoacrylate. One end is held by friction fit in a polyethylene cylinder which can be rotated in its mount (torsion wire adjustment). The other end of the torsion wire is inserted into a neoprene cylinder at one end of a 1.5cm tube (diam. 0.63cm) of plexiglass with a cylindrical rare earth magnet (0.31 x 0.31cm diam.) embedded in its other end. The wire is held under tension by a second similar magnet embedded in the end of a threaded 6.3mm diam. plexiglass rod. This rod can be turned to change the separation between the two magnets. Both magnets are covered by thin plastic so that they are not in contact with the seawater. The hollow carbon fibre tubular beam has both ends sealed and is inserted through a hole drilled through the plexiglass cylinder at right angles to the torsion wire. One end of the beam has a small tungsten wire hook to support the specimen the other end has a small (4x8mm) piece of thin cover glass cemented on the end, at right angles, which acts as a mirror. The other end of the beam supports a small weight that can be slid along the beam and acts as a counterbalance. The wall of the chamber has a thin glass window near the mirror. The beam from a laser pointer is directed through the window and is reflected by the mirror back through the window onto a scale at a distance of about 3 m. This enables small angles of rotation of the torsion wire to be detected and measured. The lid of the chamber has an O-ring seal, holes with O-ring seals for a pH electrode and temperature sensor and an access window above the specimen and closure also with o-ring seal. The centre of the closure has a hole through which seawater can be or air bubbles released.

access window. For higher pH levels water in the vessel was exchanged with seawater that had been bubbled with CO_2 free air. Two pH meters (Omega, PHB-212) with PHE-210 glass or PHE-1411 double junction electrodes, calibrated daily before experiments, using Omega PHA-4, PHA-7, and PHA-10 buffers, were used to monitor changes of pH in each balance chamber Although the NBS scale is not recommended for use with sea water (Zeebe & Wolf-Glarow, 2000) this study is only concerned with changes in pH rather than absolute pH levels. Room lighting was 12-15μmol.s^{-1}.m^{-2} and additional light was provided by a metal halide spotlight (Philips 25W, 10°) above the balance chamber. Irradiance levels were measured with a LI-COR Quantum/Radiometer (LI-250).

Pieces of coral were carefully inspected before each experiment and were rejected if there were signs of damage to the living tissue on the upper or lower surfaces or if mucus was present. A piece of coral was suspended by its monofilament loop from a hook at the end of the carbon fibre beam of the torsion balance (Fig. 2). The beam was balanced by sliding the counterweights along the other arm of the beam so that the reflected spot from the laser pointer was in the appropriate part of the scale. Further adjustment of the laser spot could be made with the torsion wire adjustment (Fig. 2). The lid with the pH and temperature probe was placed on the chamber and pressed into place so that its o-ring sealed the system, air bubbles were removed and sea water added through the access window. Finally the access window closure was put in place and its centre hole covered with a glass cover-slip and silicone grease seal. Change in weight as aragonite skeleton is deposited result in movement of the laser beam spot on the scale and readings were taken at intervals of about ten minutes. The course of an experiment was followed by plotting the readings on graph paper. Rates of weight gain or loss were calculated by regression analysis of series of 4-6 readings. Readings of pH were also taken at the same time. After a set of control reading a single experimental parameter (irradiance, temperature or pH) could be changed and after an hour for acclimation a new set of readings could be taken to give a new rate. When rates of change were very low, longer periods between reading and more readings were taken. When calcification rates were high, as in the experiments involving freshly waterpiked coral, thicker (0.11mm) tungsten wire was used in the balance.

A series of small solid aragonite cubes (1-3mg) were prepared beforehand, these were cut from *Agaricia* skeletons, and their dry weights were accurately known. Each cube was attached to a 20 cm length of extremely fine monofilament consisting of a single strand from dental floss. Attachment was by dipping the end of the filament into cyanoacrylate and touching it to the cube. An aragonite cube was used to calibrate the system at the end of each experiment by dropping it, suspended by its monofilament, through the access window, carefully onto the coral's surface. The position of the laser spot on the scale with and without the aragonite cube in position was recorded. This was repeated several times and the mean displacement for the cube was calculated. From this the equivalent dry wt. of aragonite per scale unit could be calculated. The aragonite cubes were also used to verify the linearity of the scale. A commercial dental waterpik that had been modified with a narrower jet and to work at higher pressure was used to blast away the living tissue with a jet of seawater (waterpiking). This exposes organic matrix and most recently deposited aragonite on the surface of the skeleton. Inspection with a dissecting microscope established that tissue was completely removed even from the deepest polyp cavities. Waterpiked skeletons that had been soaked in seawater for at least 72 hours were treated in experiments as "dead coral". Coral surface areas were estimated with aluminium foil (Marsh, 1970). NCSS statistical software (Number Crunching Statistical Systems, Dr Jerry Heintze, Kaysville, Utah) was used for obtaining a best fit for the growth curves.

RESULTS

Waterpiked coral: Freshly waterpiked corals showed the pattern of weight gain reported previously (Sandeman, 2012). In a typical example (Fig. 3A) the initial rate (first hour) of weight gain of 0.97 mg.h^{-1} decreased following the generalized Michaelis Menten growth curve (Lopez et al., 2000; Sandeman, 2012) for the first 15 hours then maintained a steady rate of increase of 0.072mg.hr^{-2}.cm^{-2} until the termination of the experiment ten hours later. During the initial phase the pH of the seawater remained contant while the deposition rate changed from an initial 0.99mg.hr^{-1} to a constant rate of 0.072mg hr^{-1}. However, as the changeover point was reached the seawater pH started to drop and eventually reached a steady rate of change of 0.0047 pH units.hr^{-1}.cm^{-2}. The mean initial calcification rate (n=4), over the first hour, was 0.84mg.hr^{-1}.cm^{-2} with the pH changing at -0.00041units.hr^{-1}.cm^{-2}. After reaching a steady rate of increase the mean calcification rate was 0.036mg.hr^{-1}.cm^{-2} and the pH rate of change increased by an order of magnitude to 0.0030 pH units.hr^{-1}.cm^{-2}.

Over the pH range of 6.9-8.6 aragonite growth rates have been shown to decrease with increasing PO_4^{3-} (Burton &Walton, 1990). Experiments to see how freshly waterpiked coral responded to 50µmol of orthophosphate gave the surprising result that rather than being inhibited the deposition rate on waterpiked coral (Fig. 3B) increased by over an order of magnitude from 0.04mg.h^{-1} to 0.88mg.h^{-1}. The experiment was repeated four times with similar results.

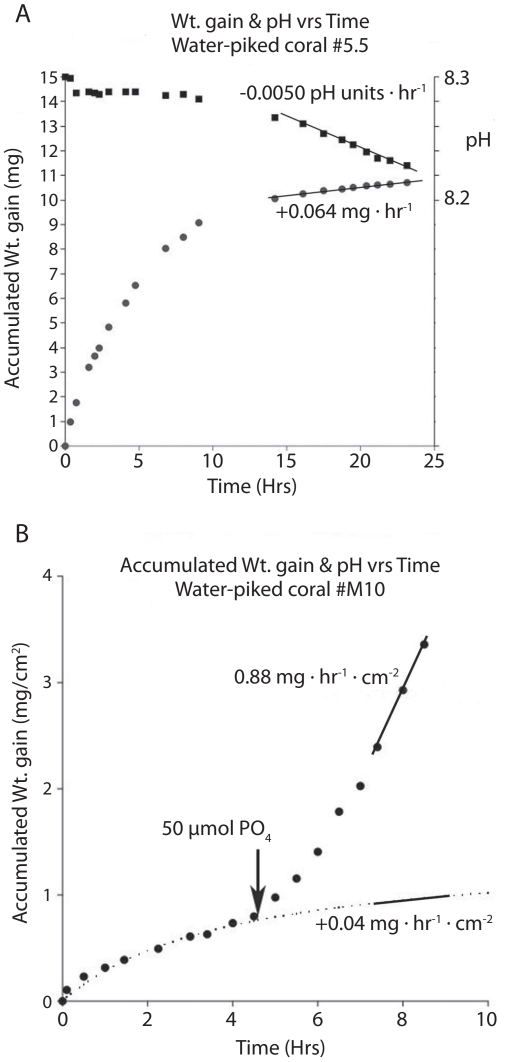

Fig. 3. Freshly water piked *Agaricia* skeleton, Slopes calculated by regression analysis. A: Accumulated weight and pH versus time. B: Accumulated weight gain versus time. Predicted weight gain from the best fit curve (Sandeman, 2012) for $W_t = (W_{max}.t)(K+t)$ compared to actual weight gain after spiking with orthophosphate.

Live coral: When placed in the sealed chamber live corals commonly showed no weight increase for the first few hours then started calcifying at a steady rate. During the period when no calcification was taking place the pH of the chamber decreased steadily. After calcification started, as indicated by weight increase gain and during calcification the pH in the chamber remained nearly constant. For example, for coral #8.2 (Fig. 4A) during the initial period with no calcification taking place the pH decreased by 0.0116 pH units.h^{-1}.cm^{-2}. After calcification started (0.058mg.hr^{-1}.cm^{-2}) the pH remained nearly constant, decreasing at the much lower rate of 0.0011 pH units.hr^{-1}.cm^{-2}. In seawater with a mean pH of 8.173 when no calcification was taking place the mean pH change (n=10) was -0.013 pH units.

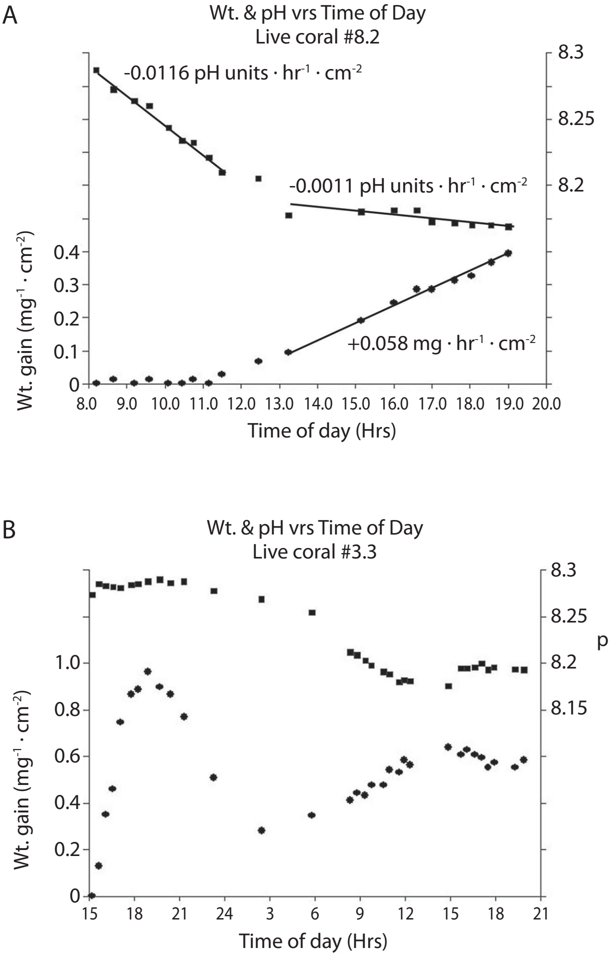

Fig. 4. Live *Agaricia*, A: Showing weight change and pH versus time. Rates calculated by regression analysis. B: Weight and pH change plotted against time of day over a period of 30 hrs.

hr^{-1}.cm^{-2}. After calcification started the mean calcification rate of the corals was 0.082mg. hr^{-1}.cm^{-2} and the pH rate of change decreased to a mean of -0.0047 pH units.hr^{-1}.cm^{-2}.

A piece of *Agaricia* placed in the balance chamber at 3pm and kept for 30 hours (Fig. 4B) showed calcification taking place (0.348mg.hr^{-1}.cm^{-2}) until 7 pm coupled with small changes in pH. Thereafter the coral lost weight (-0.94mg.hr^{-1}.cm^{-2}) and the pH decreased (-0.0019pH units.hr^{-1}.cm^{-2}) until about 3 am. Weight gain commenced again and continued until about 3pm, but this time the pH decreased at a higher rate. The weight after 24 hours did not reach its previous level. Similar results were obtained when the experiment was repeated.

Mean calcification rates obtained under low laboratory lighting (12µmol.s^{-1}.m^{-2}) were O.063 mg.hr^{-1}.cm^{-2} as compared to 0.098mg. hr^{-1}.cm^{-2} under higher light (n=8, p=0.0027). At the same time the pH change under low light was -0.0076 pH units .hr^{-1} while under higher light was lower at -0.0030 pH units.hr^{-1} (n=8, p=0.0001).

Dead coral: The relationship between calcification rate and pH was explored and the results presented in an earlier paper (Sandeman, 2012). When the experiments were repeated with pH monitoring the results obtained were exactly as expected from Zeebe and Wolf Gladrow (2000) and Fig. 1. When the rate of weight change was positive, i.e. when deposition of calcium carbonate was taking place, the concomitant pH change in the seawater medium was always, as expected (Fig. 1), in a negative direction and when dissolution of the coral skeleton took place the pH of the seawater medium always increased.

DISCUSSION

Waterpiked coral: Freshly waterpiked coral provides a simpler system than live coral in that calcification takes place directly on the surface of the organic matrix/skeleton which contains the enzyme carbonic anhydrase and which is in direct contact with the sea water medium (Sandeman, 2012) and is not separated by layers of tissue. The very high initial rate of calcification (mean, 0.84mg.hr^{-1}.cm^{-2}) was always accompanied by relatively small changes in pH of the seawater medium (mean 0.0004 pH units.hr^{-1}.cm^{-2}). During the first 10 hours the calcification rate dropped by an order of magnitude but the pH hardly changed. If $CaCO_3$ was formed, the pH of the seawater would have decreased rather than remain constant as the $CaCO_3$ arrow follows the reduction of DIC by one unit and TA by two units. Second, the rate of pH change would be proportional to the calcification, starting with a high rate and decreasing as the calcification rate decreases. The results obtained here cannot be reconciled with the conditions described in Zeebe and Wolf-Gladrow (2001) which are clearly set out "Precipitation of 1mol $CaCO_3$ reduces DIC by 1 mol and TA by 2mol independent of the carbon source (HCO_3^-, CO_3^{2-}, or even CO_2) used by the organisms for calcification". A possible resolution to the problem is that the "$CaCO_3$ formation" arrow (cf. Fig. 1) would follow the line for pH 8.2 if the DIC:TA ratio was 2:2. A possibility is that in the initial phase of exposure of the freshly waterpiked skeleton the following reaction takes place on the surface with carbonic anhydrase resulting in the formation of the unstable calcium bicarbonate:

$$2CO_2 + 2H_2O + Ca^{2+} \rightarrow Ca(HCO_3)_2 + 2H^+ \qquad \text{(Eq. 3)}$$

The reaction of two moles of carbon with one mole of Ca^{2+} would fulfill the requirement of a 2:2 ratio for DIC: TA to remain on the iso pH line (cf. Fig. 1).

After the initially very high rate of weight gain of the freshly waterpiked coral the rate decreases steadily but the pH remains the same indicating the same process is taking place during that period. In the second phase the pH begins to decrease and the weight gain reaches a steady rate. During this second phase the mean deposition rate was 0.036 mg.hr^{-1}.cm^{-2} and the mean rate of pH change was 0.003 pH units.hr^{-1}.cm^{-2} which is an order of magnitude greater than the expected rate of pH change. However if, during this second phase, the calcium bicarbonate was slowly converting to calcium carbonate following the reaction:

$$Ca(HCO_3)_2 \rightarrow CaCO_3 + H_2O + CO_2 \qquad \text{(Eq. 4)}$$

Then the resulting release of CO_2 into the seawater would help to explain its high rate of pH decrease. The conversion of $Ca(HCO_3)_2$ to $CaCO_3$ would mean a decrease in weight of the skeleton but this was not evident in the results and it seems likely that as earlier experiments showed (Sandeman, 2012) deposition of $CaCO_3$ is taking place from seawater at the same time following Eq. 2. Calcium bicarbonate is only known in solution and has not previously been suggested as a precursor to carbonate formation in corals. It appears quite commonly in the geological literature as a precursor to calcium carbonate deposition in nature and its formation when carbonate solutions are bubbled with CO_2 is widely used for the experimental deposition of calcium carbonate. For example it was used in crystallization studies (Reddy, Plummer & Busenberg, 1981) and in a study of the kinetics of aragonite formation

(Romanek, Morse & Grossman, 2011). It has also used in investigations of the conditions under which vaterite, calcite or aragonite are deposited and the effect of metallic ions on deposition (Tokuyama, Kitana & Kanamori, 1973; Kitano, Tokuyama & Arakaki, 1979). Of some interest is their finding that the presence of Mg^{2+} ions inhibits calcite formation and promotes aragonite formation. Calcium bicarbonate has also been used in the production of cooccolith-like hollow shells by Walsh and Mann (1995) and in the growth of crystals on chitosan by Zhang et al. (2006). While the suggested formation of calcium bicarbonate might explain some of the experimental results obtained in this study further work will clearly have to be carried to confirm any role it might have in coral calcification.

The finding that phosphate enhanced rather than inhibited the deposition rate on the freshly waterpiked aragonite skeleton was very surprising. It seems unlikely that the weight increase could be the result of deposition of the added phosphate because in some experiments the weight deposited (up to 10mg) on the coral exceeded the weight of the added phosphate (50μmols) and the deposition rates as shown by the slope of the curves showed no signs of depletion of phosphate in the medium. Phosphate has been found to enhance the catalytic activity of human carbonic anhydrase III (Paranawithana, Tu, Laipis & Silverman, 1991) so the rather unexpected finding that phosphate enhances calcification in a freshly waterpiked coral adds weight to the conclusion (Sandeman, 2012) that carbonic anhydrase is indeed incorporated in the organic matrix of *Agaricia*. There is also a possibility that, if present, phosphate could have a role in calcification by enhancing the activity of carbonic anhydrase and amplifying the formation of skeleton where the quantities of carbonic anhydrase are highest. The results seen in Fig. 4 also suggest the shape of the Michaelis-Menten curve reaching an asymptote may not be the result of a limitation set by the concentrations of the reactants.

Live coral. In early stages of experiments with living coral (Fig. 4A) the seawater pH decreased steadily (-0.0116 pH units.hr^{-1}.cm^{-2}) while the coral was not calcifying. When calcification was active the mean pH rate of change decreased by an order of magnitude to 0.0011 pH units.hr^{-1}.cm^{-2}. If carbonate is the substrate for calcification and the ratio of DIC:TA 1: 2 then the pH of the seawater should decrease during calcification and not change when the coral is not calcifying as indicated by weight changes taking place.

While calcification is taking place the pH of the medium remains nearly constant. This would suggest that DIC is being taken up and the TA is changing with a ratio of 2:2 and the same reaction could be taking place as was suggested for the freshly waterpiked skeleton surface. During periods when no calcification is taking place, there is no change in the calcium content of the sea water so the TA does not change. Following (Fig. 1) the decrease in pH must be the result of release by the coral of CO$_2$ into the seawater medium. Thus a possible explanation for the results obtained here is that calcium bicarbonate is deposited (Eq. 3) and that later the calcium bicarbonate is slowly converted to calcium carbonate (Eq. 4) accompanied by the release of CO$_2$.

The results from experiments in which corals were kept in the balance chamber, without the water being changed for 30 hours showed weight gain in the daylight hours followed by weight loss during the night. That the weight lost during the night was not recovered during the next day suggests that the corals were under stress and perhaps much weight should not be placed on this result. Decalcification in scleratinian corals is not common (Gattuso et al., 1999) but Kawaguti and Sakumoto (1948) reported output of Ca^{2+} in all corals exposed to dark. Tentori & Allemand (2006) reported decalcification and a daily cycle of sclerite formation in the soft coral *Cladiella*. While weight decrease took place (Fig. 4B) the pH of the medium decreased indicating a transfer of CO$_2$

from the coral into the seawater. This could be the CO_2 produced as the result of conversion of $Ca(HCO_3)_2$ to $CaCO_3$, in which case a loss of 38% in weight might be expected.

How the materials necessary for calcification to take place reach the ECF is suggested in Fig. 5. CO_2 is uncharged and can diffuse through the plasma membranes of the coral tissues and be assisted in moving into the ECF by the CO_2 gradient which results from the activity of the Ca^{2+} ATPase pump. Protons generated (Eq. 3) on the skeleton surface in the ECF (Fig. 5) probably enter the calicoblastic layer via the Ca^{2+} ATPase pump which moves calcium out of the tissues while moving protons in the other direction. Cohen and McConnaughey (2003) suggested that the calcium pump is light sensitive and there is some experimental evidence to support this (Sandeman, 2008a). There are several possibilities for what happen to protons thereafter. Although charged and existing in the form of hydronium ions (H_3O^+) in solution, in their hydrogen bonding, they have a unique conduction mechanism enabling them to hop from one water molecule to the next. They are able to move through membranes through water wires or specific protein channels of which voltage gated channels, regulated by pH and voltage are the most efficient (DeCoursey, 2003). The voltage gated channels are directional, transfer protons out of cells and may be the mechanism involved here. The organic matrix has been shown (Puveral et al., 2005) to contain proteins with 36.5% and 45.5% of the amino acids present as aspartic and glutamic acid respectively. One of two sequences of *P pistillata* included a long poly-aspartate domaine with 36 aspartic residues. While Puverel et al. (2005) suggested a calcium binding function it is also possible that these amphoteric amino acids may have a role in the sequestration of protons. If protons are sequestered for any length of time TA may be affected. How sufficient calcium ions get into the calicoblastic layer is not clear, but toxins produced by zooxanthellae may open Ca^{2+} channels (McConnaughey, 2012) or, as suggested by Sandeman (2008b) hydrogen peroxide generated during photosynthesis might make the plasma membrane leaky to calcium ions.

The experiments with low and increased illumination indicated that mean calcification rate increased from $0.063 mg.h^{-1}.cm^{-2}$ to

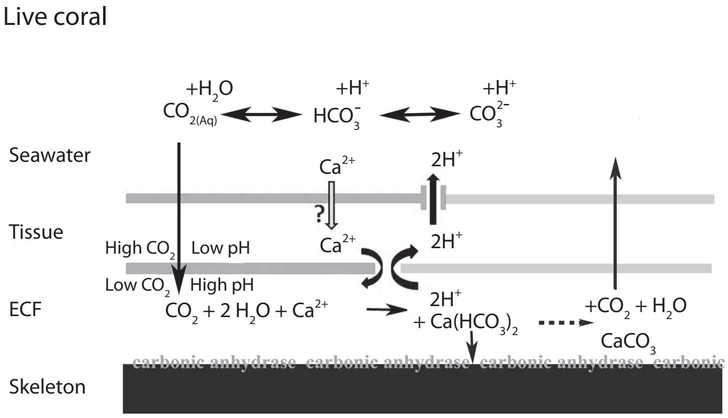

Fig. 5. Schematic model for calcification. CO_2 is uncharged and diffuses through the tissues to the ECF. Ca^{2+} is actively transported into the ECF by the Ca^{2+}ATPase pump and protons are transported in the opposite direction. The latter enhances diffusion of CO_2 into the ECF. Protons produced in the ECF are transported into tissue layers by the Ca^{2+}ATPase pump, from there the protons are probably transferred out of cells by voltage gated channels. The organic matrix has calcium binding properties and carbonic anhydrase which catalyses the reaction in which $Ca(HCO_3)_2$ is formed on the surfaces in the organic matrix. The $Ca(HCO_3)_2$ later slowly converts (dotted arrow) to $CaCO_3$ releasing CO_2 which can diffuse out or be re-combined with water to form more $Ca(HCO_3)_2$.

0.098mg.hr^{-1}.cm^{-2} with increased illumination which is as expected. The rate of change of pH in the seawater medium was from -0.0076 pH units.hr^{-1}.cm^{-2} to -0.0030 pH units.hr^{-1}.cm^{-2} in increased illumination. A reduction of pH in the medium is the result of transfer of CO_2 into it, and it has to be from the coral. It is to be expected that if CO_2 is being taken up by zooxanthellae and used for photosynthesis that the amount transferred would be less. A change of -0.0076 in pH of the seawater would result from an increase of 4.9µmol of CO_2 and -0.0030 from an increase of 1.92µmol of CO_2, so this would indicate an uptake of 3µmol of CO_2 by the algae.

Calcium bicarbonate is known to only exist in solution so it may seem an unlikely candidate for involvement in calcification. Experimentally, solutions of calcium bicarbonate (Ca^{2+}, 320-370 ppm) will precipitate $CaCO_3$ while slowly releasing CO_2. If magnesium ions are present calcite formation is inhibited and aragonite precipitation favoured (Kitano et al., 1979). It seems possible therefore that if the right ions are present, a fairly concentrated solution of calcium bicarbonate could build up in the spaces of the organic matrix and slowly convert to a deposit of aragonite on the surface present. The unusual results obtained in this study are explainable by an initial formation of calcium bicarbonate and its slow conversion to carbonate. The temporal separation between uptake of Ca^{2+} (change of TA) and movements in, then later out, of CO_2 (changes in DIC), means that care should be applied in the application of the alkalinity anomaly technique for the measurement of calcification in corals.

RESUMEN

Resultados inesperados de medición directa, con una microbalanza de torsión en un sistema cerrado, de las tasas de calcificación de los corales *Agaricia agaricites* **(Scleractinia:Agariicidae) y concomitantes cambios de pH en el medio del mar.** La acidificación del océano está impactando la calcificación de los corales, pero los mecanismos de la calcificación son aún inciertos. Para explorar la relación entre la calcificación y pH, pequeños trozos de coral fueron suspendidos en una microbalanza de torsión en agitado suave, temperatura controlada, y agua de mar en una cámara cerrada. La tasa de calcificación neta y el pH se monitorearon continuamente mientras que la luz, temperatura o pH podían ser manipulados. Las piezas de coral eran de los bordes de placas finas de *Agaricia agaricites* y se estudiaron vivos y recién colectados. Inesperadamente, cuando la calcificación (n= 9, 0.082 mg.hr^{-1}.cm^{-2}) se estaba dando, según lo determinado por el aumento de peso, el pH del agua de mar circundante cambió poco (n = 10,-0.0047 pH units.hr^{-1}.cm^{-2}). Durante los períodos cuando la calcificación no se estaba dando la disminución del pH del agua de mar era un orden de magnitud mayor, -0.013 pH units.hr^{-1}.cm^{-2}. Esto es exactamente lo contrario de lo que se espera cuando se forma carbonato de calcio ($CaCO_3$). Del mismo modo un esqueleto recién colectado al inicio no mostró cambios de pH en el agua de mar aunque eran muy altas las tasas de ganancia de peso (hasta 1.0 mg hr^{-1}.cm^{-2}). Después de 10 horas, la tasa de deposición disminuyó hasta seguir una curva de crecimiento generalizada de Michaelis-Menten, el pH comenzó a disminuir drásticamente, lo que indica un aumento de CO_2 en el agua de mar. Estos resultados inesperados pueden explicarse si el bicarbonato de calcio inestable ($Ca(HCO^3)_2$) se forma en la superficie de la anhidrasa carbónica/matriz orgánica y lentamente se transforma más tarde a $CaCO_3$. Piezas de coral vivo vigiladas en la cámara durante 30 horas demostraron un patrón de ganancia de peso durante el día y de pérdida en la noche. La pérdida sería coherente con la transformación de la Ca $(HCO^3)_2$ a $CaCO_3$ con el lanzamiento de CO_2. La tasa de calcificación media de coral vivo fue mayor (n= 8, p= 0.0027) en luz alta (120 μmol.s^{-1}.m^{-2}) a 0.098 mg.hr^{-1}.cm^{-2}, en comparación con 0.063 mg.hr^{-1}.cm^{-2} en condiciones de poca luz (12 μmol.s^{-1}.m^{-2}). Sin embargo, al mismo tiempo la tasa media de cambio de pH fue de -0.0076 bajo luz baja en comparación con -0.0030 bajo luz alta (n= 8, p= 0,0001). La diferencia puede explicarse porque el CO_2 está siendo utilizado para la fotosíntesis por zooxantelas. La tasa de deposición de coral vivo no fue afectada por la adición de fosfato pero la tasa de ganancia de peso de los esqueletos recién colectados era fuertemente reforzada por fosfato. Estos resultados indican que la atención debe aplicarse en la aplicación de la técnica de alcalinidad anormal para la medición de la calcificación de los corales.

Palabras clave: coral, calcificación, CO_2, pH, matriz orgánica, anhidrasa carbónica, Ca $(HCO^3)_2$.

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Status of the coral reefs in Foul and Folly Bays, Morant Wetlands, south-eastern Jamaica, with emphasis on corals and macroalgae

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Received 16-X-2013 Corrected 05-II-2014 Accepted 24-III-2014

Abstract: Foul and Folly Bays are located within the Morant Wetlands near the eastern tip of Jamaica. They have never been investigated but were believed to be important for larval productivity because of the extent of benthic habitats, absence of major coastal developments and remote location. The study was aimed at providing baseline data on the spatial distribution and status of corals and associated benthos. We investigated coral reefs and associated areas with phototransects at eight stations analysed with the Coral Point Count software. Most areas were dominated by algae, evidence of a phase shift from coral to algal reefs. Coral cover varied significantly across the bays (ANOVA, p= 0.0342) with a maximum of 27.03% at the deepest station and a mean of 5.6% at all other stations combined. Mean cover of macroalgae was 39% and varied significantly across stations (α= 0.05, F= 7.472, p= 0.005). The deepest station also had the highest percentage of calcareous algae and live coral while dead coral with algae (DCA) was a significant variable across all other stations (ANOVA, p<0.001). Gorgonians (ANOVA, p<0.001), sponges and urchins were also assessed. *Diadema antillarum* was not observed at any station. Overall the status of the reefs was poor, probably due to overfishing, absence of urchins and the resultant algal proliferation. Rev. Biol. Trop. 62 (Suppl. 3): 39-47. Epub 2014 September 01.

Key words: Coral Reefs, Spatial Variation, Foul Bay, Folly Bay, Jamaica.

Coral reefs are complex and diverse marine ecosystems (Woodley et al., 1981; Moberg & Folke, 1999). They offer many economic and environmental services including their natural beauty, recreation, food, jobs, chemicals, pharmaceuticals and shoreline protection (Moberg & Folke, 1999). Jamaica is the third largest island of the Caribbean and is said to be in the center of the coral diversity in the Atlantic Ocean (Hughes, 1994). In Jamaica, the effects of overfishing, hurricane damage, bleaching and disease have combined to destroy many reefs, evidenced by reduction in coral cover from 50% on reefs in the late 1970's to less than 5% today (Hughes, 1994; Goreau, 1992). Burgeoning populations, destructive fishing practices, coastal development, unsound agricultural practices, sedimentation from forests clearing, expanding tourism, and increasing pollution (Grimsditch & Salm, 2006) all exacerbate the rapid decline of coral reef systems.

There has been extensive research on coral reefs in Jamaica beginning in the 1950's with Thomas Goreau studying areas on the north and south coasts of Jamaica (Goreau, 1959; Goreau & Wells, 1967; Barnes, 1970; Liddell & Olhorst, 1981; Woodley et al., 1981; Hudson, 1985; Gates, 1990; Goreau, 1992; Aronson & Percht, 1995; Hughes, 1994; LaPointe, 1997; Mendes & Woodley, 2001; Crabbe, Mendes & Warner, 2002). However, the coral reef community of the Foul and Folly Bays, Morant Wetlands, St. Thomas, Jamaica has never been described or quantitatively assessed.

The study site was positioned on the south-eastern coast of Jamaica encompassing two bays (Foul Bay and Folly Bay). They are lined by an extensive mangrove forest which has been designated as a bird reserve since 1984. Beyond the mangrove forest the land use is primarily for sugar cane and a sugar cane factory is associated with the fields. Artisanal fishing is done within the bays and off-shore banks associated with the easternmost end of Jamaica, supports the fishing community (144 registered fishers and 21 registered vessels in 2010) of Rocky Point. Due to the prevailing east to west currents and the lack major developments, the two bays were thought to be pristine with healthy coral reef communities.

Since this coral community has never been studied, this research sought to achieve the objectives of determining the composition and relative abundance of all living and non-living substrate types associated with the reef and to describe the spatial variation of corals and associated benthic organisms across Foul and Folly Bays.

MATERIALS AND METHODS

Coral surveys were conducted between 8:00a.m. and 12:00p.m. Sampling was done on four occasions: December 5, 2007; January 31, 2008; April 11, 2008 and November 21, 2008. Eight stations were chosen using a stratified random process based on areas with live corals across the Morant Wetlands bays (17°52'8.77"N-76°15'2.18"W) using a bathymetry map and reconnaissance surveys (Fig. 1). Stations 1-7 were referred to as the shallow stations (<1-3m) and station 8 the deep station (~12m). A Garmin® GPSMAP® 76CSx was used (accuracy <10m 95% typically) to locate the station previously chosen and accessed by a fishing vessel. Once in the general area of the station, a reef was randomly chosen and 'marked' on the Global Positioning System (GPS) to indicate its exact location.

A camera framer with base dimensions of 0.75m x 0.5m was used to maintain the dimensions of each photo. The camera framer was constructed from 2cm cold water PVC (White & Porter, 1985). A Canon Power Shot G5 Digital camera housed in a waterproof casing was used to capture the contents of the frame. Pictures were taken along the entire length of the reef in the direction parallel to the shoreline. Transects were done in replicate per station.

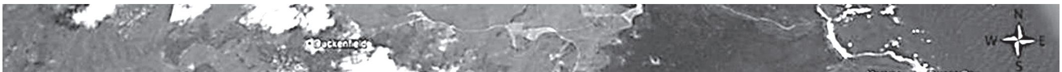

Fig. 1. Sampling areas showing the eight stations numbered from east to west. Plate Inset courtesy of Maptown Ltd.

Coral Point Count with Excel extensions (CPCe) version 3.5 software (Kohler & Gill, 2006) was used to analyze the photographs. Twenty randomly positioned dots were generated on each photograph. The substrate type overlain by each dot was identified using the categories listed in the software. Excel data sheets were produced using CPCe version 3.5 for statistical analysis. Percentage coral cover was assessed.

Cumulative species richness curves were done for each transect at each station to ensure adequate sampling intensity. The percentage cover of all species and substrates associated with the reef were log transformed (Sokal & Rohlf, 1981) and normality confirmed using Shapiro-Wilks W- test. One-way analysis of variance (ANOVA, p= 0.05), tests were done to indicate whether significant spatial variability existed using Statistica V.7. Coral species diversity was calculated using the Shannon-Weaver Index (H´).

RESULTS

The spatially dominant substrates found in the reefal areas of the Morant Wetlands bays (Foul and Folly Bays) were coral, macroalgae, dead coral with algae (DCA), gorgonian, *Porites asteroides, Porites porites, Dictyota* sp.*, Sargassum* sp.*, Turbinaria* sp.*,* and *Halimeda* spp. These were all found to vary significantly (ANOVA, p≤0.01) across stations.

Coral distribution: 17 species of corals were identified including *Millepora complanata* and *Millepora alcicornis, M. complanata* and *M. alcicornis*, though not true corals, were grouped with the true corals as they are important cnidarians on the reef. Corals were identified from all stations except for station five (17°52’27.07”N-76°14’9.78”W). The 17 coral species identified were not equally distributed across all stations as stations 1-7 had means not exceeding seven species while station eight had 16 coral species. The mean coral cover was 5.6% across stations (Fig. 2). The highest mean percentage cover was noted at station eight (17°52’25.43”N-76°16’23.45”W) with 27.03%. Station five had the lowest mean percentage cover (0%) of coral. Stations one to four located within Folly Bay had a coral percentage cover values of <7%. In Foul Bay (stations five to eight) there was a dramatic

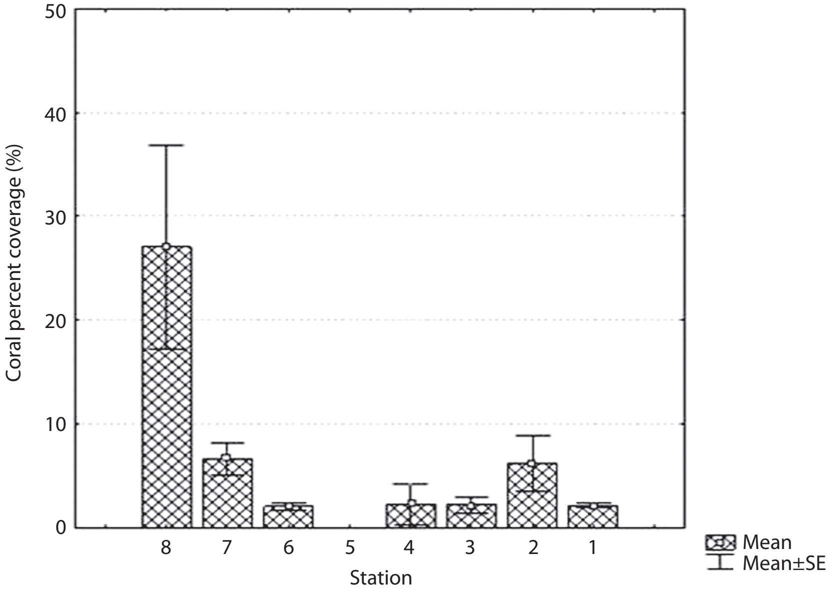

Fig. 2. Mean coral percentage cover across stations. Station 5 is not represented by a bar as it had a percentage cover of zero. Y-axis has been reduced to a maximum of 50%.

increase in coral cover with progression from station five to station eight. The total coral percentage cover was significantly different across stations (ANOVA, p= 0.0342). It should be noted that for good visual effect, graphical presentation of the data has stations numbered in the reverse order (i.e. stations eight à one) which is indicative of the actual position of the stations in the area; station eight being westernmost.

Foul Bay had the higher coverage of *P. asteroides* with station eight having the highest percentage cover. The overall coverage of *P. porites* was very low with the highest mean percentage cover being 3.17% at station two and the lowest at stations five (0%) and six (0%). *A. agaricites* was found only at stations one, three, four, seven and eight. Station eight had the highest mean percentage cover of 23.2%.

Algal cover: Macro-algae was the dominant benthic substrate across all stations and showed significant spatial variation (ANOVA, p= 0.005). The highest mean percentage cover was seen at station six (75.4%) and lowest (8.52%) at station four (Fig. 3). However, in Folly Bay (stations one to four), macroalgae gradually decreased with progression from station one to four. Between the two bays, Foul Bay had the higher percentage cover of macroalgae. There was no gradual decrease in Foul Bay (stations five to eight), as was seen in Folly Bay.

The algal groups examined (*Dictyota* sp., *Sargassum* sp., *Turbinaria* sp. *a*nd *Halimeda* spp.) varied significantly (ANOVA, p≤0.01) across the stations. The more fleshy algae dominated in the shallow areas of Foul and Folly Bays while the calcareous algae (*Halimeda* spp.) tended to be high at station 8. It should be noted that no *Diadema antillarum* were observed along the transects.

Dead coral with algae (DCA): The category DCA was found at all stations with a

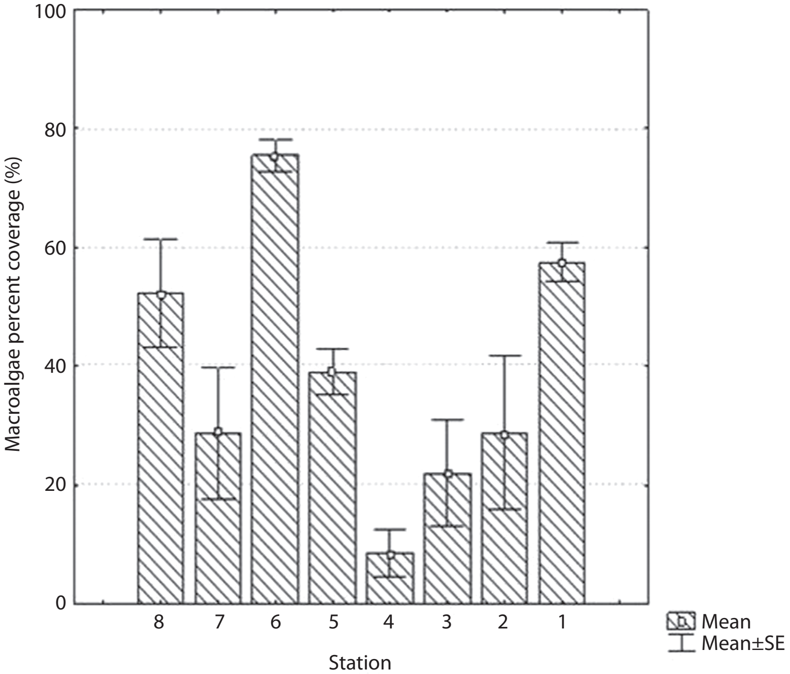

Fig. 3. Mean macroalgae percentage cover across stations. A- Total, -. *Dictyota* sp., B- *Sargassum* sp., C- *Turbinaria* sp., D- *Halimeda* spp.

percent coverage ranging from 15.19-83.86% (Fig. 4). DCA showed a gradual increase in percent coverage in Folly Bay from station one to four. There was no pattern observed for Foul Bay. The highest coverage of DCA was seen at station four (83.86%) and the lowest at station eight (15.19%).DCA was significantly different across stations (ANOVA, $p < 0.001$).

Gorgonians (soft corals): All stations except for stations five and six had gorgonians present. Station two (11.46%) had the highest percentage of gorgonians while stations five and six had the lowest (0%). Folly Bay had a higher percentage of gorgonians than Foul Bay. Gorgonians were significantly different across stations (ANOVA, $p<0.01$).

Diversity: Shannon-Weaver Index (H') diversity across the stations (Fig. 5) ranged from zero at station five (no coral species were found) to 0.34 at station eight. There was no clear trend for stations one to four (Folly Bay). Foul Bay (stations five to eight) however, demonstrated a trend of increasing coral species diversity from station six to eight.

DISCUSSION

Location and extent of the coral reef system: The coral reef system studied across the Morant Wetlands bays was situated at the southeastern tip of Jamaica and as such, the area is exposed to the open waters of the Caribbean Sea. The coral reef area, which runs parallel to the shoreline, spanned approximately 7km that was 80% of the length of the shoreline. Previous representations of the reef in older bathymetric charts show a continuous barrier reef system but this has been severely degraded without the charts being updated. The reasons for the degradation would appear to be a combination of natural and anthropogenic causes.

This study suggests that the reef system was of a patchy barrier reef type with channels along the shallower stations, found mostly in Folly Bay and a section of Foul Bay. The edge of the system has a reef oriented perpendicular to the shoreline (station eight) which is located on the edge of a channel between Foul Bay and Rock Point Bay. This was observed to be a part of a buttress system (I. Wilmot pers. comm.). Buttresses were generally reported to be found only on the north coast of Jamaica (Goreau, 1959), but this area has never received a detailed survey and so the feature may have never been described. Further assessment would be needed in areas outside of the immediate sample location to confirm whether station eight was an anomaly. Surveys of deeper areas south and west of Foul and Folly bays may reveal a similar reef as

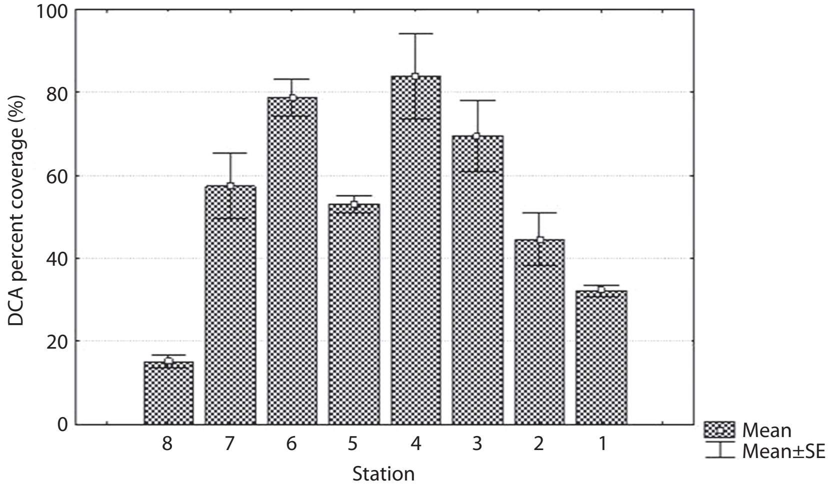

Fig. 4. The mean dead coral and algae (DCA) percentage cover across stations.

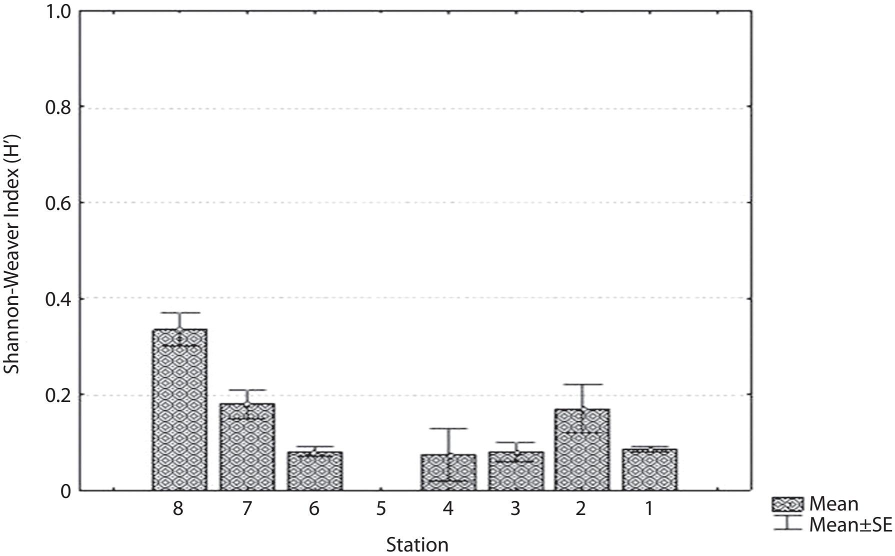

Fig. 5. Shannon-Weaver Index (H') across stations. Station 5 had no corals within sample area.

was observed at station eight. This would be expected as there is a positive correlation of depth and diversity (Bonem & Stanley, 1977; Huston, 1985) in corals.

Composition and relative abundance of coral species: The seventeen hermatypic coral species found in the Morant Wetlands bays included species previously reported from the north coast (Goreau, 1959; Wells & Lang, 1973) as well as the south coast (Goreau, 1959; Mendes, 1992). This represents approximately 1/3 of the species previously reported to be occurring in Jamaica (Goreau & Wells, 1967).

Circulation patterns with very high current speeds (Wilmot, 2010) found within Foul and Folly Bays appear to be unfavorable for coral recruitment (Lugo-Fernandez, 2001; Blanco-Martin, 2006) especially in the shallow algal dominated areas. Station eight situated on the edge of Foul Bay seemed to be most suitable for coral growth as it had the highest diversity and percentage cover of corals. This is further supported by the fact that this station had the highest abundance of massive reef-building corals (Loya, 1976; Goreau, 1959) corals such as *M. annularis, M. cavernosa* and *Diploria strigosa*.

As expected, diversity and coral cover showed a positive correlation with progression from shallow stations to the deeper station eight (Porter, 1974). While the coral cover at station eight was much higher than average, by comparison the average coral cover of the Morant Wetlands was found to be 20% of the average coral cover found at Lime Cay, another south coast area (McNaught, 2007) .

Composition of other living and non-living substrate types: The rock-like pavement which would represent the fore-reef area seen across stations one to seven was thought to have been a part of what was a healthy, continuous barrier reef system as seen in older maps. The presence of this rock-like pavement was one of the reasons for sampling parallel to the shoreline.

The Morant Wetlands, now dominated by algae, seemed to have undergone a coral-algae phase-shift when compared to many reefs across Jamaica and the Caribbean (LaPointe, 1997; Hughes, 1994; Wilkinson, 2008; Bruno, Sweatman, Precht, Selig & Schutte, 2009).

Macroalgae showed a general trend increasing from station one to eight with the more fleshy algae (e.g. *Sargassum, Dictyota* and *Turbinaria*) in the shallow areas (Hudson, 1985) and the calcareous algae *Halimeda* being most abundant at station eight (deep station) was similar to observations by McNaught (2007), working near Lime Cay.

The absence of *Diadema antillarum* and *Echinometra lucunter* would further support the high abundance of algae (Sammarco, 1982). This observation was somewhat similar to Byrd's (2008) study also done within the Morant Wetlands. Although sampling was done only in the day, the strong wave action throughout this area is thought to be unfavorable for *D. antillarum* (Clemente & Hernandez, 2008; Alves, et al., 2001). Sponges had a positive correlation with coral cover; this trend was observed on other reefs such as Curacao, Santa Maria and N.E. Colombia with mean sponge cover below 25% (Aerts, 1998).

This study provides a baseline of the coral community within the Morant wetlands bays. The coral reef studied in the Morant Wetlands should be described as a patchy barrier reef. Seventeen coral species were identified within this area, the mean coral cover was low (5.4%) and macroalgae high (39%). While the coral reef system studied in the Morant Wetlands is situated at the eastern tip of Jamaica, and so is exposed to the pristine waters of the Caribbean Sea. The coral reef is very degraded and is not a continuous barrier reef system as was represented on older bathymetric charts. The degraded state of reefs in the Morant wetlands area is probably attributed to a combination of overfishing, absence of urchins and the resultant algal proliferation, as well as strong waves and currents (Wilmot, 2010) reducing coral recruitment. The anomalous high % coral cover at station eight was attributed to the depth in that area.

ACKNOWLEDGMENTS

This project was funded by The Environmental Foundation of Jamaica. Thanks to the team in Rocky Point, St. Thomas, Judith Mendes, Alison Foster, Nicole Harris, Inilek Wilmot, Marsha Robinson who assisted with sampling and also contributed their expertise and knowledge.

RESUMEN

Las bahías Foul y Folly se encuentran dentro de los Humedales Morant cerca de la punta oriental de la isla de Jamaica. Estos dos bahías nunca han sido investigadas pero se cree que son áreas importantes para la productividad larvaria debido a la extensión de los hábitats bentónicos, ausencia de desarrollos importantes a lo largo de la costa y la ubicación remota de la zona. El estudio tuvo como objetivo proporcionar datos de referencia sobre la distribución espacial y el estado de los corales y del bentos asociado. Investigamos los arrecifes coralinos y áreas asociadas utilizando fototransectos en ocho estaciones analizadas con el programa Coral Point Count. La mayoría de las áreas tuvieron predominio algal, mostrando evidencia del desplazamiento de fase de coral a algas. La cobertura de coral varió significativamente a través de las bahías (ANOVA , p= 0.0342), con un máximo de 27.03% en la estación estación más profunda y una media de 5.6% en todas las demás estaciones combinadas. La media de porcentaje de cobertura de macroalgas fue de 39% y varió significativamente entre las estaciones (α= 0.05, F= 7.472, p= 0.005). La estación mas profunda presentaba el mayor porcentaje de algas calcáreas y coral vivo, mientras que el coral muerto con algas (DCA) fue una variable significativa en todas las demás estaciones (ANOVA , p<0.001). También se evaluaron las gorgonias (ANOVA , p<0.001), esponjas y erizos de mar. No se observó *Diadema antillarum* en todas las estaciones dentro de los transectos. En general, el estado de los arrecifes era pobre, probablemente debido a la pesca excesiva, la ausencia de erizos y la proliferación de algas resultante.

Palabras claves: arrecifes coralinos, variación espacial, Bahía Foul, Bahía Folly, Jamaica.

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Large-scale coral recruitment patterns on Mona Island, Puerto Rico: evidence of a transitional community trajectory after massive coral bleaching and mortality

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Received 01-IX-2013 Corrected 31-IV-2014 Accepted 01-IV-2014

Abstract: Coral reefs have largely declined across the northeastern Caribbean following the 2005 massive bleaching event. Climate change-related sea surface warming and coral disease outbreaks of a white plague-like syndrome and of yellow band disease (YBD) have caused significant coral decline affecting massive reef building species (i.e., *Orbicella annularis* species complex) which show no apparent signs of recovery through larval sexual recruitment. We addressed coral recruit densities across three spur and groove reef locations along the western shelf of remote Mona Island, Puerto Rico: Punta Capitán (PCA), Pasa de Las Carmelitas (PLC), and Las Carmelitas-South (LCS). Data were collected during November 2012 along 93 haphazard transects across three depth zones (<5m, 5-10m, 10-15m). A total of 32 coral species (9 octocorals, 1 hydrocoral, 22 scleractinians) were documented among the recruit community. Communities had low densities and dominance by short-lived brooder species seven years after the 2005 event. Mean coral recruit density ranged from 1.2 to 10.5/m^2 at PCA, 6.3 to 7.2/m^2 at LCS, 4.5 to 9.5/m^2 at PLC. Differences in coral recruit community structure can be attributed to slight variation in percent macroalgal cover and composition as study sites had nearly similar benthic spatial heterogeneity. Dominance by ephemeral coral species was widespread. Recovery of largely declining massive reef-building species such as the *O. annularis* species complex was limited or non-existent. The lack of recovery could be the combined result of several mechanisms involving climate change, YBD disease, macroalgae, fishing, urchins and Mona Island's reefs limited connectivity to other reef systems. There is also for rehabilitation of fish trophic structure, with emphasis in recovering herbivore guilds and depleted populations of *D. antillarum*. Failing to recognize the importance of ecosystem-based management and resilience rehabilitation may deem remote coral reefs recovery unlikely. Rev. Biol. Trop. 62 (Suppl. 3): 49-64. Epub 2014 September 01.

Key words: Climate change, coral decline, coral recruitment, community trajectory, Mona Island, Puerto Rico, transitional state.

Coral larval recruitment is critical for the maintenance of reef biodiversity, ecosystem resilience and benthic community recovery after disturbances across multiple spatial scales (Gittings, Bright, Choi & Barnett, 1988; Sammarco, 1991; Connell, Hughes & Wallace, 1997; Hughes & Tanner, 2000). Coral recruitment refers to the stage when new members of the recently settled juvenile corals become visible to be censused (Harrison & Wallace, 1990). Open reef space is necessary for settling larvae (Hughes & Connell, 1999; Kuffner et al., 2006; Díaz-Pulido et al., 2009), particularly substrates along cryptical microhabitats and areas dominated by crustose coralline algae (CCA), which are recognized by coral larvae (Doropoulos, Ward, Díaz-Pulido, Hoegh-Guldberg & Mumby, 2012). Dynamic processes leading to the creation of free space open for colonization are important for successful recruitment. Nonetheless, Caribbean coral reef ecosystems have shown increasing rates of large-scale disturbance, including hurricanes (Emanuel, 2005; Mann & Emanuel, 2007), massive coral bleaching events (Miller et al., 2006; 2009), widespread disease outbreaks (Cróquer & Weil, 2009; Weil & Cróquer, 2009), and the massive die off of the Long-spine urchin, *Diadema antillarum* (Phillipi 1845) (Lessios, 1988; Gardner et al., 2003), with paramount long-term impacts in adult coral assemblages and in the overall benthic community composition (Hughes, Reed & Boyle, 1987; Hughes, 1994; McClanahan & Muthiga, 1998; Rogers & Miller, 2006; Miller et al., 2009; Edmunds, 2013).

Juvenile coral depth distribution often follows the distribution of adult parental colonies (Bak & Engel, 1979; Harriott, 1985). But Caribbean-wide coral reef decline has been characterized by significant losses in percent live tissue cover of parental colonies followed up by declining trends in coral recruitment (Connell, 1997). There is mounting evidence that recent sea surface warming trends across the Caribbean associated with climate change resulted in significant shifts in coral reef benthic community structure due to the long-term impacts of the 2005 widespread massive coral bleaching that impacted at least 65% of the corals at Mona Island, including 94% of the colonies of the of Star coral *Orbicella (=Montastraea) annularis* species complex (Ellis & Solander, 1786) (García-Sais et al., 2008). This event was followed by the 2005-2006 large-scale coral disease outbreak and mortality (Miller et al., 2009; Edmunds, 2013). Diseases such as yellow band disease (YBD) significantly compromised the reproductive output of *O. faveolata* (Ellis & Solander, 1786) (Weil, Cróquer & Urreiztieta, 2009), and caused a rapid decline within the *O. annularis* species complex in Mona Island (Bruckner & Bruckner, 2006; Bruckner & Hill, 2009). These factors led to massive coral recruitment failure of multiple species, resulting in a major decline in the natural recovery ability of critical reef-building species such as *O. annularis* (Edmunds & Elahi, 2007; Hernández-Pacheco, Hernández-Delgado, & Sabat, 2011). This has further resulted in an irreversible alteration in the trajectory of coral reef benthic community structure across very large spatial scales.

Successful coral recruitment is critical for sustaining slow-growing, low-recruiting massive coral species (Harrison & Wallace, 1990; Szmant, 1991). But several long-term studies have shown very limited sexual recruitment success for the *O. annularis* species complex (Rogers et al., 1984; Edmunds & Elahi, 2007; Irizarry-Soto & Weil, 2009), even at Mona Island (Bruckner & Hill, 2009). Edmunds (2004) also found a positive correlation between juvenile coral density and mean sea surface temperature (SST), with slower growth and higher mortality under high SST, in a pattern leading to changes in relative generic abundance. These findings suggest that even such long-term subtle effects could result in major transitional changes in benthic community composition and trajectory, with far-reaching ecological consequences for the survival and resilience of coral reefs. Further, disturbance history over multiple spatio-temporal scales is also a critical determinant of coral reef community trajectory. Hurricanes, in combination with massive coral bleaching events, have resulted in high mortality of juvenile corals (Harriott, 1985) and declining coral recruitment rates across large spatial scales (Mumby, 1999; Mallela & Crabbe, 2009). This could be the result of indirect impacts on recruitment habitat quality which may alter larval selection. Coral larvae have been shown to be highly selective of habitat conditions for successful recruitment (Baird, Babcock & Mundy, 2003; Kuffner et al., 2006). Elevated SST has been shown to alter microbial biofilm community structure associated to CCA, therefore, altering natural cues for coral larval recruitment (Webster, Soo, Cobb & Negri, 2011). Doropoulos et al. (2012) suggested that ocean acidification (OA) may also reduce coral population recovery by reducing coral larval settlement rates, disrupting larval settlement behavior, and reducing the availability of the most desirable coralline algal species for successful coral recruitment.

Climate change has become one of the most significant and imminent threats to coral reefs at a global scale (Hoegh-Guldberg, 1999; Buddemeier et al., 2008). Recent modeling efforts have suggested that current trends in sea surface warming, increasing atmospheric CO_2 concentration, and OA might have paramount negative consequences on coral reef ecosystems and their services (Buddemeier et al., 2008; 2010), as well as in the overall marine productivity (Hoegh-Guldberg et al., 2007; Veron et al., 2009). According to McWilliams et al. (2005), a rise in regional SST of 0.1˚C resulted in up to 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively. Maximum bleaching extent and intensity are predicted to occur at regional SST anomalies of less than +1˚C (Hoegh-Guldberg, 1999). Coral bleaching is therefore likely to become a chronic source of stress for Caribbean reefs in the near future, with a high potential for coral reef decline, and significantly compromising the natural recovery ability of coralline communities and ecosystem resilience, including remote islands located far from known pollution centers.

Even remote coral reefs have undergone significant recent decline as a result of regional climate change-related impacts (Goreau, Hayes & McClanahan, 2000; McClanahan & Muthiga. 1998; McClanahan, 2000; Walther et al., 2002) and have showed limited recovery ability (Gardner et al., 2005; Sandin et al., 2008; Birkeland et al., 2013). Coral reef recovery on remote habitats depends on the functional redundancy of impacted coral assemblages, on the tissue regeneration ability and regrowth of surviving remnant colonies, and on successful coral recruitment (Golbuu et al., 2007; Díaz-Pulido et al., 2009). Genetic connectivity also plays a critical role in natural coral reef recovery (Zubillaga, Márquez, Cróquer & Bastidas, 2008). But populations for many important coral species, particularly across the Caribbean, show high genetic structuring implying that long-distance larval dispersal is an unusual event (Baums et al., 2005; 2006; Vollmer & Palumbi, 2007; García-Reyes & Schizas, 2010; Mège, Schizas, García-Reyes & Hrbek, 2014), rendering isolated coral reefs to largely rely on remnant colony regrowth, colony fragmentation, and self-recruitment for their natural recovery from disturbance. Nonetheless, there is still scarce information regarding remote coral reef natural recovery rates and the trajectory followed by benthic communities impacted from disturbance. This study was aimed at conducting a large scale survey of coral recruit densities on the western shelf of remote Mona Island, Puerto Rico, to build on earlier reports by Bruckner and Hill (2009), and address the coral community trajectory following the 2005-2006 massive coral bleaching and mass mortality event.

MATERIALS AND METHODS

Study sites: This study was carried out in November 2012 across three spur and groove fringing reef locations along the western shelf of Mona Island, Puerto Rico: Punta Capitán (PCA, 18°06.283’N, 67°56.137’W), Pasa de Las Carmelitas (PLC, 18°06.162’N, 67°56.229’W), and Las Carmelitas-South (LCS, 18°05.995’N, 67°56.290’W). Mona is an oceanic island located 79 km off the western coast of Puerto Rico. Its origin was during the Miocene to Pliocene (10 to 4 Ma) (Rodríguez, 2012) and was suggested by González et al. (1992, 1997) to be the first extensive barrier reef complex reported in the Caribbean.

Coral recruit density: Data was collected along 93 haphazard transects (PCA n=27, PLC n=35, LCS n=31) across three depth zones (<5m, 5-10m, 10-15m). Sampling sites were randomly selected to represent replicate reef habitats along similar depth gradients and similar open substrate space available for recruitment. A maximum of 6-12 transects were analyzed per depth zone at each site. Replicate 10 m-long line transects were haphazardly established along depth contours, often parallel to reef spurs orientation, and separated by at least 10m. Data were collected using high-resolution digital photography along 5 replicate, non-overlapping quadrats per transect (N=465 quadrats) at haphazardly fixed intervals (1, 3, 5, 7, 9m) following a slight modification from the AGGRA method (Lang, 2002), and at a fixed distance from the bottom using a 40 x 27cm ($0.108m^2$) photoquadrat fixed to the camera housing. Any coral colony <5cm was treated as a coral recruit. Coral species with sexually mature small sizes, such as *Siderastrea radians* (Pallas, 1766), were also included in the counts as they were largely abundant across study sites. Efforts were made to avoid sampling areas with high sediment bedload and efforts were made to remove sediments from the bottom when looking from recruits. No special efforts were made to remove algae to test for percent algal cover spatial effects. Percent macroalgal cover was visually estimated from each image following AGGRA methodology (Lang, 2002).

Statistical analyses: A two-way multivariate analysis of similarity (ANOSIM) was used to test the null hypothesis of no significant difference in coral recruit density, biodiversity parameters, including species diversity index (H'n, Shannon & Weaver, 1948), and evenness (J'n, Pielou 1966), and community structure among sites and among depth zones using PRIMER-e v.6.1.14 (Clarke & Warwick, 2001). Principal component ordination (PCO) was used to determine which benthic taxa abundance explained spatial clustering patterns of coral recruit communities (Anderson et al., 2008). PRIMER's RELATE multivariate correlation routine was used to test the relationship between coral recruit abundance and percent macroalgal cover. Proportional data on coral recruit abundance and percent macroalgal cover were √-transformed prior to analysis. All tests were based in 10 000 permutations.

RESULTS

A total of 347 coral recruit colonies of 32 coral species (9 octocorals, 1 hydrocoral, 22 scleractinians) was documented, with 99 colonies at PCA, 113 at LCS, and 135 at PLC (Table 1). This included 17 species at PCA subdivided in 3 species across the shallow reef segment, 11 species across the middle depth segment, and 13 across the deeper segment. There were also 15 species at LCS subdivided in 8 species across shallow, 7 across the middle, and 10 across the deeper segment. A total of 18 species of coral recruits were observed at PLC, with 9 species across the shallow, 8 across the middle, and 16 across the deeper zone. Coral recruit community structure was significantly different among locations (p=0.0260), particularly between PCA and LCS (p=0.0060), but not among depth zones (Table 2). There was a significant site x depth interaction (p=0.0160). Coral recruit assemblages were overall dominated by ephemeral species such as starlet coral *Siderastrea radians* (Pallas 1766) and mustard hill coral *Porites astreoides* (Pallas 1766), representing 33% and 31% of the total coral recruit colony abundance. These were followed by lettuce coral *Agaricia agaricites* (Linnaeus 1767), brain coral *Diploria strigosa* (Dana 1846), and finger coral *Porites porites* (Pallas 1766), for a combined 16% (Fig. 1).

Shallow reef zone abundance of *S. radians* reached 3.7 and 3.4colonies/m^2 at PLC and LCS, respectively. Abundance of *P. astreoides* reached 2.9 and 2.2colonies/m^2 at PLC and LCS, respectively. Middle reef zone abundance of Abundance of *P. astreoides* reached 2.7 and 2.0colonies/m^2 at PCA and PLC, respectively. *S. radians* reached 2.5colonies/m^2 at LCS. *P. astreoides* was dominant at the deeper zones of both, PCA and LCS, with 3.5 colonies/m^2. *Siderastrea radians* was dominant at the deeper zone of LCS with 2.5colonies/m^2. These corals were largely growing on formerly *O. annularis* species complex dominated habitats. Most of the dominant reef-building corals across these habitats died following the 2005 massive coral bleaching event. Nonetheless, recruits members of the *O. annularis* species complex were very rare across the shelf, and were present only in low and sporadic abundance in deeper waters. Only seven juvenile individuals of *O. annularis*

TABLE 1
Mean density (#/m^2) of coral species present across study sites

Species	PCA-I	PCA-II	PCA-III	LCS-I	LCS-II	LCS-III	PLC-I	PLC-II	PLC-III
Gorgonia ventalina	-	-	-	-	-	-	-	-	0.77
Muriceopsis sp.	-	-	-	-	-	-	-	-	0.77
Pseudopterogorgia sp.	-	0.84	-	-	-	-	-	-	-
Plexaura sp.	-	-	-	-	-	-	-	-	-
Plexaurella sp.	-	-	-	-	-	-	0.84	-	-
Eunicea sp.	-	0.84	-	-	-	-	-	-	-
Pseudoplexaura sp.	-	-	-	-	-	0.92	-	-	0.77
Pterogorgia sp.	-	-	-	-	-	-	-	-	-
Briareum asbestinum	-	-	-	-	-	1.85	-	-	-
Acropora palmata	-	-	-	-	-	-	-	-	-
Favia fragum	-	0.84	0.92	-	-	-	-	-	-
Porites astreoides	-	13.43	17.54	10.91	12.93	17.54	14.27	10.00	3.85
Porites porites	-	-	0.92	0.84	0.92	1.85	1.68	2.31	1.54
Porites divaricata	-	-	-	-	0.92	-	-	-	-
Porites furcata	-	-	0.92	-	-	-	-	-	-
Porites branneri	-	-	2.77	-	-	0.92	1.68	0.77	0.77
Siderastrea radians	1.54	7.55	12.00	16.79	11.08	5.54	18.47	5.39	12.31
Agaricia agaricites	-	1.68	7.39	-	-	3.69	5.04	1.54	3.85
Agaricia tenuifolia	-	-	1.85	1.68	-	-	-	-	2.31
Agaricia fragilis	-	-	-	-	-	-	-	-	-
Agaricia humilis	-	0.84	0.92	-	1.85	-	-	-	-
Diploria strigosa	-	1.68	3.69	0.84	1.85	1.85	2.52	0.77	-
Diploria labyrinthiformis	-	-	-	0.84	-	-	-	-	-
Colpophilia natans	-	-	-	0.84	-	-	-	-	-
Meandrina meandrites	-	0.84	-	-	-	-	0.84	-	2.31
Orbicella annularis	-	-	-	-	-	-	-	0.77	1.54
Orbicella faveolata	-	-	0.92	-	-	-	2.52	-	2.31
Orbicella franksi	-	-	-	-	-	-	-	-	0.77
Montastraea cavernosa	3.08	-	-	0.84	-	0.92	-	-	1.54
Dichocoenia stokesii	-	-	-	-	-	-	-	-	0.77
Eusmilia fastigiata	-	1.68	0.92	-	-	-	-	-	-
Millepora alcicornis	1.54	1.68	1.85	-	1.85	0.92	-	0.77	1.54

(2%) and 3 of *O. faveolata* (0.9%) were documented out of the 347 recruit colonies found across the 465 surveyed quadrats, suggesting that natural population recovery seven years following the massive post-bleaching coral mortality in 2005-2006 was still very limited for this critically-important reef-building species complex.

Total coral recruit density was significantly different among sites (*p*=0.0020), but not among depth zones (Fig. 2a). The highest overall densities were documented at the deeper zones of PCA and LCS, with 10.5colonies/m^2 and 7.2colonies/m^2, respectively. The highest density of the middle depth zone was observed at PCA with 6.4colonies/m^2, while the highest density of shallower zones was observed at LCS with 9.6colonies/m^2. Coral species richness was significantly different among sites (*p*=0.0130), particularly between PCA and LCS (*p*=0.0070), and between PCA and PLC (*p*=0.0130) (Fig. 2b). No significant difference among depth zones was observed. The highest species richness was at deeper zones of PCA

TABLE 2
Two-way ANOSIM test of spatial variation in coral recruit community structure and biodiversity patterns

Parameter	Community structure		Species richness		H'n		J'n	
	Global R	*p*	Global R	*p*	Global R	*p*	Global R	*p*
Site	0.034	**0.0260**	0.046	**0.0130**	0.029	**0.0420**	0.010	0.1960
PCA-LCS	0.077	**0.0060**	0.084	**0.0070**	0.046	0.0550	0.013	0.2040
PCA-PLC	0.028	0.1280	0.085	**0.0130**	0.067	**0.0320**	0.038	0.0900
LCS-PLC	0.011	0.2230	-0.021	0.9310	-0.016	0.8320	-0.014	0.7880
Depth (m)	0.008	0.7040	0.005	0.2860	0.014	0.1550	0.023	0.0880
<5 m vs 5-10 m	-0.012	0.6790	-0.020	0.8590	-0.012	0.6150	-0.011	0.5830
<5 m vs 10-15 m	-0.022	0.8850	-0.007	0.2830	0.014	0.1870	0.022	0.1230
5-10 m vs 10-15 m	0.006	0.2970	0.026	0.0880	0.035	0.0620	0.049	**0.0310**
Site x Depth	0.052	**0.0160**	0.032	0.0950	0.023	0.1570	0.019	0.20

(2.9/transect), PLC (2.6/transect), and LCS (2.2/transect). H'n was significantly different among sites (*p*=0.0420), particularly between PCA and PLC (*p*=0.0320) (Fig. 2c). The highest H'n was documented at deeper zones of PCA (0.8912) and PLC (0.7385), followed by the shallow zone of PLC (0.7385). J'n was significantly different between shallow and deep zones (*p*=0.0310) (Fig. 2d). No site-specific effects were observed. The highest J'n was observed at the deeper zones of PLC (0.7281), PCA (0.6830), and LCS (0.6725).

Percent macrocalgal cover showed no significant differences among sites or depth zones. Highest values were documented at the shallow zone of PCA (25.7%), followed by the middle (23.2%) and deeper depth zone (17%) of LCS (Fig. 3). Most macroalgae were Phaeophytes dominated by *Dictyota* spp. and *Lobophora variegata* Lamouroux 1817. There was a highly significant non-linear negative correlation (r^2=0.6864, p<0.0001) between increasing percent macroalgal cover and declining coral recruit density (Fig. 4). PCO analysis showed four general clustering patterns of coral reef bottoms, with one cluster largely dominated by *P. astreoides* recruits, and in a lesser degree by *Montastraea cavernosa* Linnaeus 1767, and *Agaricia tenuifolia* Dana 1846 (Fig. 5). A second cluster was determined by abundant *S. radians* recruits, followed by *A. agaricites* and *D. strigosa*. A third cluster was dominated by

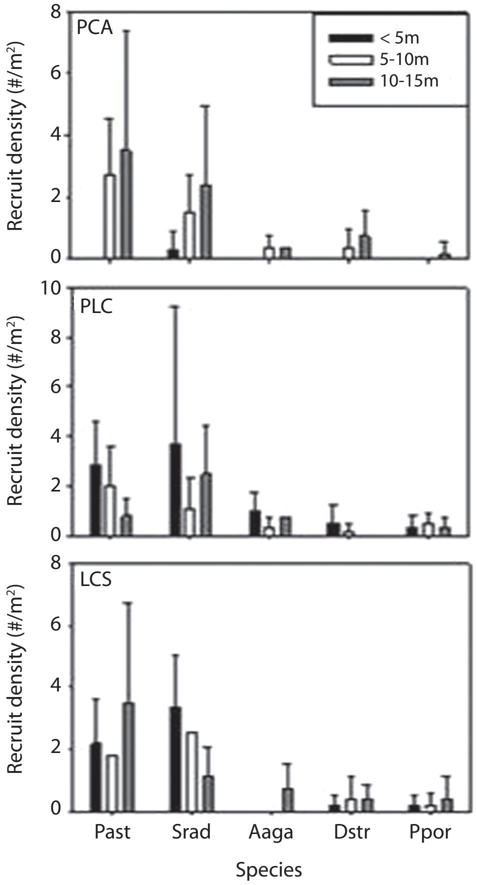

Fig. 1. Coral recruit density (#/m^2) of the overall five more abundant coral species (mean±95% confidence interval). Past= *Porites astreoides*, Srad=*Siderastrea radians*, Aaga= *Agaricia agaricites*, Dstr= *Diploria strigosa*, Ppor= *Porites porites*.

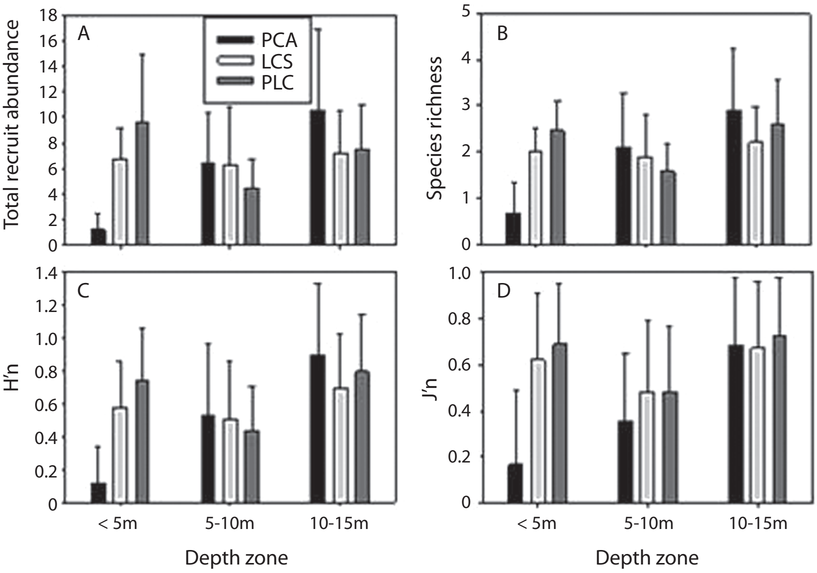

Fig. 2. Coral recruit community metrics (mean±95% confidence intervals): A) Total coral recruit abundance (#/m^2), B) Species richness, C) H'n, D) J'n.

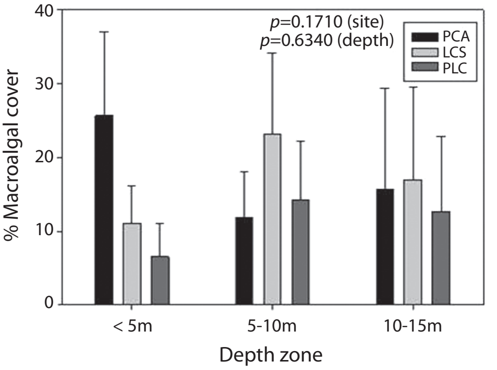

Fig. 3. Percent macroalgal cover (mean±95% confidence interval).

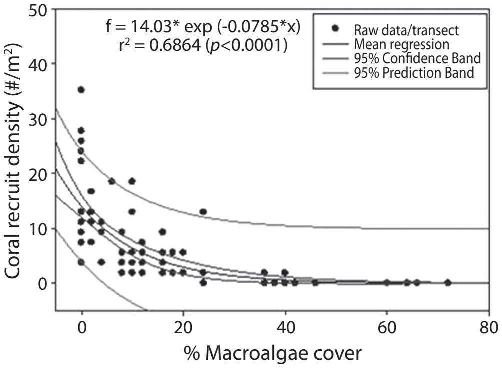

Fig. 4. Non-linear regression of coral recruit density as a function of percent macroalgal cover.

P. astreoides. A final cluster was dominated by open reef bottoms largely devoid of corals, and dominated by brown macroalgal overgrowth.

DISCUSSION

Coral recruit communities at remote Mona Island showed low densities and dominance by short-lived brooder coral species seven years after the 2005-2006 massive bleaching event and the subsequent post-bleaching mass coral mortality. Differences in coral recruit community structure can be attributed to slight variation in percent macroalgal cover as study sites had nearly similar benthic spatial heterogeneity. Nonetheless, trends in dominance by ephemeral coral species were widespread across all study sites. Recovery of largely declining massive reef-building species such as the *O. annularis* species complex was very

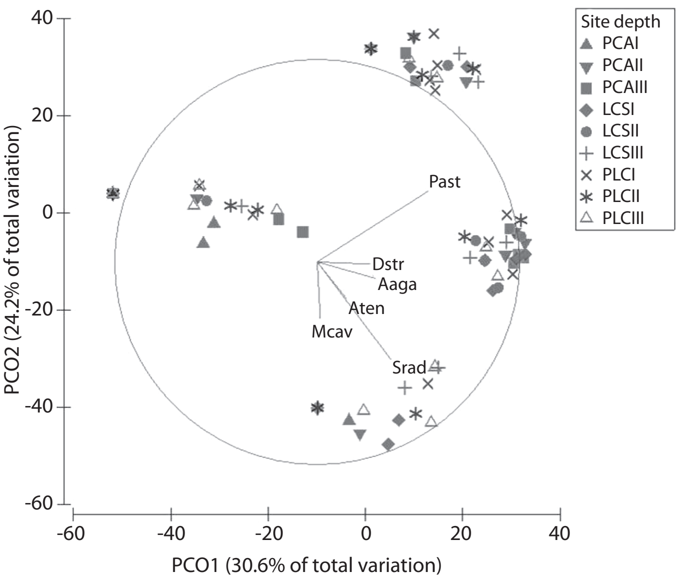

Fig. 5. Principal component ordination (PCO) of coral recruit abundance per site and per depth zone.

limited and even non-existent across extensive reef zones. Instead, dead coral surfaces were largely overgrown by unpalatable brown macroalgae *L. variegata* and *Dictyota* spp. Red encrusting algae *Peysonnellia* spp. were also abundant. Mona's isolated reef systems have followed a transitional trajectory leading to a major phase shift favoring macroalgae and non-reef building, ephemeral coral taxa. Lack of coral reef recovery following major disturbances, including climate change, has been a concerning phenomenon across the Caribbean (McClanahan & Muthiga, 1998; Aronson et al., 2002; Gardner et al., 2003; 2005; Rogers, 2013), and might have significant long-term ecological and socio-economic consequences (Buddemeier et al., 2008; 2010; Paddack et al., 2009; Lane et al., 2013), including regional-scale declines in coral cover and reef complexity (Alvarez-Flip et al., 2011). We suggest that lack of net recovery in remote Mona Island's reefs could be the combined result of several mechanisms involving climate change-related post-bleaching mass coral mortality, chronic YBD disease outbreaks, rapid substrate dominance and out-competition of remnant corals by brown unpalatable macroalgae, declining herbivory due to long-term fishing impacts, lack of *D. antillarum* population recovery, altered microbial communities associated with crustose coralline algae (CCA) that may negatively affect coral larval settlement cues, and Mona Island's reefs limited connectivity to other reef systems which highly limits potential successful larval recruitment from other locations.

The observed trend of low coral recruit densities and dominance by short-lived brooder coral species is very similar to recent observations from other Caribbean reefs where massive reef-building species have largely declined and have shown limited or no net recovery (Rogers & Miller, 2006; Miller et al., 2009; Hernández-Pacheco et al., 2011; Edmunds, 2013), which suggest a long-term coral recruitment decline across the region. Mean coral recruit density ranged from 1.2 to 10.5/m^2 at PCA, 6.3 to 7.2/m^2 at LCS, 4.5 to 9.5/m^2 at PLC in our study. But earlier studies across the wider Caribbean showed higher recruit density values than most recent accounts. Bak and Engel (1979) documented coral recruit densities of 16.8/m^2 across the 3-9m depth zone, and of 12.9/m^2 across the 9-17m depth zone at Curaçao. Rogers et al. (1984) found coral recruit densities ranging from 13 to 42colonies/m^2 at Salt River Canyon, St. Croix, USVI across depth ranges similar to this study. Carpenter and Edmunds (2006) also found coral recruit colony densities of 6.2/m^2 at Belize, 26.7/m^2 at St. Croix, 28.9/m^2 at Barbados, 26.6/m^2 at Port Antonio, 15.6/m^2 at Bonaire, and 33.8/m^2 at Grenada. They also found that highest coral recruit densities correlated with high densities of *D. antillarum* and lower percent algal cover. Tomascik (1991) documented relatively common recruits of *O. annularis*, *Siderastrea siderea* (Ellis & Solander, 1786), and *Diploria* spp. on settlement plates from non-polluted reefs at Barbados. Bak and Meesters (1999) also found relatively common juvenile colonies of *O. annularis* species complex, *S. siderea*, and other massive coral species at Curaçao. There has also been evidence that fishing management can strongly indirectly influence coral recruitment dynamics. Mumby et al. (2007) documented coral recruit densities ranging from 10 to 14/m^2 within a no-take marine protected area (MPA), and from 4.5 to 6/m^2 across non-MPA sites at Exuma Cays, Bahamas. But large massive Caribbean-wide disturbances, such as recurrent massive bleaching events in 1987, 1998, and 2005 (Eakin et al., 2010), recurrent mass coral disease outbreaks (Weil, 2004), and the mass mortality of *D. antillarum* (Lessios, 1988) have resulted in a major transition in the ecological state of coral reefs. A key characteristic of such a change has included rapidly declining coral recruit densities.

Recent studies have documented declining coral recruit densities across the Caribbean. Irizarry-Soto and Weil (2009) found a decline from 4.8 to 2.8 coral recruit colonies/m^2 between 2003 and 2005, and very low recruit abundance of massive reef-building species in La Parguera, Puerto Rico. Coral recruit density within a no-take MPA in Exuma Cays, Bahamas, increased from approximately 3.8/m^2 for *P. astreoides*, 1.4/m^2 for *A. agaricites*, and 2.1/m^2 for *O. annularis* in 2004 to 8.4/m^2, 2.3/m^2, and 3.1/m^2 in 2007 for each species, respectively (Mumby & Harborne, 2010). Coral recruit density outside the MPA shifted from 2.8/m^2 in 2004 to 3.5/m^2 in 2007 for *P. astreoides*. Densities of 0.6/m^2 for *A. agaricites* and 2.2/m^2 for *O. annularis* in 2004 showed no significant change outside the MPA by 2007. Even recent studies from Mona Island have shown a 30-80% loss of *O. annularis* and *O. faveolata* due to YBD outbreaks (Bruckner & Bruckner, 2006), failed recruitment, minimal re-sheeting, and exposed skeletal surfaces largely colonized by macroalgae, bioeroding sponges, and hydrocorals (Bruckner & Hill, 2009). Ongoing studies at Mona Island have preliminarily suggested that a stunning 96% of large-sized colonies of *O. annularis* species complex across the same surveyed sites in this study were either killed or are showing partial mortality due to YBD infections (Hernández-Delgado, unpublished).

Rapidly declining coral recruitment and lack of coralline community recovery across the Caribbean significantly contrasts recovery trends documented in isolated coral reefs off Western Australia where coral cover increased from 9 to 44% within 12 years of the 1998 massive coral bleaching event by a combination of coral tissue regeneration of remnant surviving colonies and coral recruitment (Gilmour et al., 2013). Diaz-Pulido et al. (2009) also documented rapid reef regeneration following the 2006 coral bleaching-related mass mortality across the Great Barrier Reef due to rapid regeneration rates of remnant coral tissue, strong coral out-competition of *L. variegata*, a natural seasonal decline in macroalgal dominance, and an effective MPA system. However, the benefits from MPAs may not be great enough to offset the magnitude of losses from acute thermal stress events (Hughes et al., 2011; Selig, Casey & Bruno, 2012) if such impacts operate in combination with other local human-driven factors, including herbivore overfishing (Mumby & Harborne, 2010).

We argue that shifting benthic community trajectories have largely impacted coral recruitment dynamics. The observed shift in coral recruit biodiversity is a consequence of the massive post-bleaching coral mortality in

2005-2006 and has resulted in a transitional shift in benthic community trajectory under increasing stress associated to climate change favoring non-reef building taxa. Large-scale (temporal, spatial) massive coral bleaching episodes can lead to significant mortality by post-bleaching disease outbreaks (Miller et al., 2006; 2009), which can potentially lead to a dramatic loss of coral reproductive potential (Weil et al., 2009), the onset of Allee effects, and to reproductive failure (Connell, 1997). Coral recruits exhibit an apparent tolerance to massive bleaching (Mumby, 1999), but evidence of long-term survival following such disturbances is still very limited. Weil et al. (2009) observed that YBD had deleterious impacts on sexual reproduction in *O. faveolata*. Significant physiological fragmentation in *O. annularis* and *O. faveolata* colonies from Culebra Island, Puerto Rico, resulted in permanently halting sexual reproduction in fragmented remnants since the 2005 bleaching episode (Hernández-Delgado, unpublished), similarly to declining reproduction in coral physiological fragmentation experiments documented elsewhere (Szmant-Froelich, 1985; Szmant, 1986; 1991; Szmant & Gassman, 1990; Soong 1993). There is also evidence from the eastern Pacific that most of the recruitment following a massive bleaching and mortality event occurs largely due to rapid recruitment of ephemeral, high-recruiting coral taxa which can be different in comparison to the pre-existing coral community (Medina-Rosas, Carriquiry & Cupul-Magaña, 2005). Therefore, a shift in benthic community structure trajectory such as the one documented in Mona Island implies a change from dominance by engineer species to ephemeral, poor reef builders. Under current and forecasted climate change trends (Hoegh-Guldberg, 1999), and under current declining population trends in *O. annularis* (Hernández-Pacheco et al., 2011), the future trajectories of coral reefs may be significantly compromised.

We also argue that shifting herbivory dynamics, in combination with natural eutrophication pulses, may indirectly affect coral recruitment dynamics due to algal out-competition of corals. Severely depleted *D. antillarum* populations, as well as low abundance of large sized fish herbivores (Scaridae), across the Mona Island shelf (Hernández-Delgado unpublished), and grazing preferences of remnant grazer guilds (Szmant, 2002) is probably associated to the significant shift in dominance by *L. variegata* and *Dyctiota* spp., which in turn are significantly affecting coral larval recruitment. Low herbivory of unpalatable brown macroalgal assemblages is a critical factor that may trigger further coral decline due to out-competition of adult corals, and preemptive out-competition of coral spat. Both *L. variegata* and *Dictyota* spp. (Box & Mumby, 2007), and *Ramicrusta* spp. (Eckrich & Engel, 2013) can strongly out-compete juvenile corals due to shading and abrasive effects, or inhibit successful coral larval recruitment. Kuffner et al. (2006) also found experimental evidence that the combined presence of intermingled unpalatable brown macroalgae and cyanobacteria caused either recruitment inhibition, avoidance behavior or larval mortality in multiple coral species. Further, we propose that natural nutrient enrichment pulses can fuel up algal growth. Physical meso-scale oceanographic processes such as internal waves or seiches (Wolanski & Delesalle, 1995; Leichter, Shellenbarger, Genovese & Wing, 1998) and gyre currents (Corredor et al., 2004), in combination with local-scale micro-upwelling associated to strong tidal currents (Shea & Broenkow, 1982), may bring up deep, nutrient-rich waters towards Mona's narrow shelf. Also, groundwater infiltration might contribute natural nutrient pulses further triggering macroalgal (Lapointe, O'Connel & Garrett, 1990) and cyanobacterial blooms (Littler, Litter, Lapointe & Barile, 2006). Mona Island is a carbonate platform with extensive cave systems and groundwater flows documented to occur even at 20-30 m depths (Hernández-Delgado, personal observations). These factors clearly suggest that management of herbivory is critical for the conservation of coral reef resilience and coral recruitment dynamics.

Hughes and Connell (1999) found that coral reef assemblages that are similar in coral community composition, but under different management regimes may show profound differences in recruitment dynamics and species turnover, with major implications for their ecology, evolution and management. Fully functional no-take MPAs and recovering populations of *D. antillarum* and fish herbivore guilds seem to have a significant role in fostering increased coral recruitment rates. According to Mumby et al. (2007), coral recruit density can increase up to 2-fold within no take MPAs as a result of reduced fishing pressure and weak predator–prey interactions that can create trophic cascades that increase the abundance of grazing fishes and reduce the coverage of macroalgae on coral reefs, therefore opening new substrate for coral larvae. Carpenter and Edmunds (2006) found that population recovery of *D. antillarum* is occurring at both local and regional scales, and that urchin grazing is creating conditions favoring coral recruitment. Nonetheless, *D. antillarum* recovery in Puerto Rico has been patchy and spatially limited even three decades after mass mortality (Ruiz-Ramos, Hernández-Delgado et al., 2011). Long-term trends documented in Mona Island and elsewhere around Puerto Rico have also shown that brown macroalgae have become the dominant component of many coral reefs (Hernández-Delgado, 2005; Ballantine et al., 2008; García-Sais et al., 2008). If macroalgae dominate open available substrates, they might permanently inhibit coral recruitment either due to direct out-competition or by overgrowing CCA, and in the long run affect coral reef recovery ability from disturbance (McCook, Jompa & Díaz-Pulido, 2001). CCA are key reef-building primary producers known to induce the metamorphosis and recruitment of many species of coral larvae (Negri, Webster, Hill & Heyward, 2001). Reef biofilms (particularly microorganisms associated with CCA) are also important as settlement cues for multiple marine invertebrates, including corals (Wieczorek & Todd, 1998). CCA is highly vulnerable to macroalgal overgrowth as well as to increasing SST. Webster et al. (2011) provided solid experimental evidence that rapid loss of CCA-covered surfaces and its associated biofilms resulted in a massive failure of coral recruitment due to the permanent effects on CCA's photo-physiology and its inability to produce natural chemical cues for larval recognition. Coral reefs require high levels of grazing intensity to prevent further macroalgal blooms from taking place, and to reopen reef substrate to increasing percent CCA cover to trigger increased coral larval recruitment. Therefore, reversing low herbivory should be a critical component to improve coral recruitment success.

Natural recovery of remote coral reefs may seem increasingly difficult due to regional scale of ecosystem decline across the Caribbean which compromise natural connectivity to other reefs Lack of coral reef recovery also implies declining coral functional redundancy and coral reef ecosystem resilience, which could in turn result in a long-term decline in ecological scales of connectivity. Coral reefs at Mona Island are high-circulation, oligotrophic, oceanic reef systems, located far from known anthropogenic pollution sources, but also far from potential source coral reefs. Therefore, genetic isolation due to the oceanographic barrier associated to strong surface currents across the Mona Channel between La Hispaniola and Puerto Rico play a critical role in maintaining high genetic structuring and rendering isolated coral reefs to largely rely on remnant colony regrowth, colony fragmentation, and self-recruitment for their natural recovery from disturbance. Long-distance coral larval dispersal is an unusual event (Baums et al., 2005; 2006; Vollmer & Palumbi, 2007; García-Reyes & Schizas, 2010; Mège et al., 2014) and suggest the paramount importance of replenishing rapidly declining coral reefs though a combination of novel efforts focused on ecosystem-based approaches (i.e., managing food webs, enhancing herbivory, increasing percent cover CCA, and improving coral reproductive stocks).

Replenishment of depleted coral engineer species will require immediate novel efforts (i.e., low-tech coral farming) to rehabilitate their populations. It will also require large-scale, ecosystem-based management of reef fisheries to foster the rehabilitation of the entire food web, with particular attention of recovering herbivore guilds. Alternatives such as propagating and restocking *D. antillarum* populations should be implemented across shelf-wide scales. These will represent important steps towards fostering improved self-recruitment and buying critical time for rapidly declining coral reefs to rehabilitate ecosystem resilience and cope with increasing climate change impacts. Failing to recognize the importance of recovering herbivory, reducing brown macroalgal cover, increasing crustose coralline algae (to foster increased coral recruitment), and propagating key reef-building coral species may result in losing the last opportunity of saving coral reefs in a transitional state from falling into an alternative, irreversible ecological collapse.

ACKNOWLEDGMENTS

This study was possible thanks to the support provided to E.A. Hernández-Delgado by the National Science Foundation HRD #0734826 through the Center for Applied Tropical Ecology and Conservation of the University of Puerto Rico (UPR). We also acknowledge support provided by UPR Department of Biology and by Capt. Elick Hernández and the M/V Tourmarine crew.

RESUMEN

Patrones a gran escala del reclutamiento de coral en Isla Mona, Puerto Rico: evidencia de una trayectoria transitoria de comunidad después del blanqueamiento y mortalidad coralino masivo. Los arrecifes de coral han disminuido en gran medida en el noreste del Caribe después de los blanqueamientos y muerte masiva de coral en el 2005. El calentamiento superficial del mar relacionado con el cambio climático y brotes de enfermedades en corales como el sindrome de plaga blanca y la enfermedad de banda amarilla (YBD) han causado una disminución significativa de coral de arrecife afectando las especies constructoras de coral (es decir, el complejo de especies *Orbicella annularis*) que no muestran signos evidentes de recuperación a través del reclutamiento larval sexual. Nos centramos en las densidades de coral recluta en tres sitios de coral espuela y surco a lo largo de la plataforma occidental de la remota Isla de Mona, Puerto Rico: Punta Capitán (PCA), Pasa de Las Carmelitas (PLC) y Las Carmelitas-Sur (LCS). Los datos fueron recolectados durante noviembre de 2012 a lo largo de 93 transectos a través de tres zonas de profundidad (<5m, 5-10m, 10-15m). Se documentaron un total de 32 especies de corales (9 octocorales, 1 hidrocoral, 22 scleractinios) entre la comunidad coral recluta. Comunidades de coral recluta mostraron bajas densidades y predominancia por especies criadoras rápidas durante siete años después del evento del 2005. La densidad coral recluta varió entre 1.2 y 10.5/m^2 en el PCA, 6.3 y 7.2/m^2 en LCS, 4.5 a 9.5/m^2 en el PLC. Diferencias en la estructura de la comunidad coral recluta pueden atribuirse a la ligera variación en el porcentaje de cobertura de macroalgas y composición en los sitios de estudio que tenían una heterogeneidad espacial bentónica muy similar. Tendencias en el predominio de las especies de coral efímeras fueron generalizadas. Recuperación de especies de arrecife con alta disminución como la especie *O. annularis* del complejo de especies fue muy limitado e incluso inexistente a través de zonas extensas de arrecife. La falta de recuperación puede ser el resultado combinado de varios mecanismos que implican cambio climático, brotes crónicos de YBD, macroalgas, pesca, erizos y conectividad limitada de los arrecifes de la isla Mona a otros sistemas de arrecife. También hay una necesidad de impulsar la rehabilitación de la estructura trófica de peces, con énfasis en la recuperación de gremios herbívoros y las poblaciones agotadas de *D. antillarum*. Al no reconocer la importancia de la gestión de rehabilitación y capacidad de recuperación basado en los ecosistemas se estima que la recuperación de arrecifes de coral es muy improbable.

Palabras clave: Cambio climático, disminución de coral, reclutamiento, trayectoria de comunidad, isla Mona, Puerto Rico, estado transitorio

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The results of long term coral reef monitoring at three locations in Jamaica: Monkey Island, “Gorgo City” and Southeast Cay

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Received 25-X-2013 Corrected 18-III-2014 Accepted 02-IV-2014

Abstract: The global and regional impacts of climate change are having devastating consequences on the coral reef ecosystems of the Caribbean. Long term monitoring are important tool for assessing reef health. Monitoring was established in 2000 in the Bahamas, Belize and Jamaica. Following the pilot project, the program was institutionalized in Jamaica and monitoring was conducted on eight occasions from 2000 to 2010. Monkey Island and “Gorgo City” near Discovery Bay (both on the north coast) and Southeast Cay at Port Royal on the south coast were selected. Macroalgae dominated the benthic substrate. Monkey Island and “Gorgo City” had the highest coral cover. *Porites astreoides*, *Montastraea* spp., *Porites porities, Siderastrea siderea*, and *Agaricia agaricites* were the most common species. Data from this programme have been used in local and regional coral reef assessment and management initiatives. Rev. Biol. Trop. 62 (Suppl. 3): 65-73. Epub 2014 September 01.

Key words: Discovery Bay, Portland, Port Royal, Jamaica, video monitoring, coral reefs, long term monitoring, climate change.

In 1992 the Intergovernmental Panel on Climate Change (IPCC) highlighted the vulnerability of low-lying island states to the impacts of climate change, particularly as it relates to sea level rise and increased sea surface temperatures (IPCC, 1992). This report pointed out that coastal ecosystems and populated low lying coastal plains would experience the most severe impacts and went on to recommend that the identification and assessment of the potential risks to coastal areas, islands and coastal resources be undertaken. This growing concern about the vulnerability of the small island developing states to the threats of climate change was highlighted in the United Nations Global Conference on Sustainable Development of Small Island Developing States held in Barbados in1994. Climate change, climate variability and sea level rise were identified as issues of grave concern and as such were judged to be priority areas in the Barbados Programme of Action (BPOA), which outlined specific actions to be taken to address these special challenges (UN, 1994). The Caribbean Planning for Adaptation to Climate Change (CPACC) project was subsequently implemented as a regional initiative coming out of the BPOA and was designed to address the issues related to climate change with a view to building capacity to adapt to climate change impacts. CPACC was implemented in the countries of the English speaking Caribbean during the period 1998-2001 with the Organization of America States (OAS) as the executing agency and funding provided by the Global Environmental Facility (GEF) through the World Bank (Deeb, 2002).

Component 5: The Coral Reef Monitoring for Climate Change Impact Programme was one of nine components of the CPACC project established in 1998. A multidisciplinary forum comprising specialists from governments, Non-Governmental Organizations, CARICOM (Caribbean Community Secretariat) institutions and experts from the scientific community formulated this long term coral reef monitoring program for the assessment of reef health and to inform management decisions. Other expected outcomes included obtaining knowledge on the extent and sources of coral reef degradation within the region. The pilot project was implemented at the national level in The Bahamas, Belize and Jamaica, with the objective of having the monitoring programme eventually expanded and to all CARICOM countries (de Berdt Romilly, 2001; Creary, 2006). Recommendations coming out of the evaluation of the pilot project strongly supported the implementation of a regional coral reef monitoring program (Lawrence & Edwards, 2001) however, this did not materialize.

Jamaica is located in the northern Caribbean and is the largest English speaking country in this region. The island has a fringing reef developed on a narrow shelf on the north coast and patchy reef formations developed on a wide shallow shelf on the south coast (Gayle & Woodley, 1998). The Jamaican reefs were thought to be in excellent condition in the 1950's when much of the coral reef research was initiated (Goreau, 1959). Since that time the impacts of hurricanes (Woodley, 1991; Rogers, 1993), coral diseases (Bruckner, Bruckner & Williams, 1997; Knowlton, Lang,, Rooney & Clifford, 1981) and the loss of the herbivorous sea urchins (Hughes, Keller, Jackson and Boyle, 1985), as well as overfishing (Hughes, 1994) and nutrient loading (Lapointe, 1997) have resulted in a decline in the health of these reefs. Superimposed on these anthropogenic factors were the impacts resulting from climate change, particularly elevated sea surface temperatures which have resulted in mass bleaching events (Jones, et al., 2008; Crabbe 2010). These issues have, in large part, led to a change in the general structure of the benthic community, where macroalgae now cover the reefs that were once dominated by corals (Hughes, 1994).

This paper presents the results of the coral reef monitoring programme implemented under the Component 5: Coral Reef Monitoring for Climate Change Impacts of the CPACC project that was carried out at three locations in Jamaica (Monkey Island, "Gorgo City" and Southeast Cay) during the period 2000-2003 and 2007-2010.

MATERIALS AND METHODS

Site selection and description: The protocol for the selection of the Operational Areas was developed by Woodley in 1999 (Creary, 2001; Creary, 2006; Creary, Jones Smith & Green, 2012; Deeb, 2002) for each of the pilot countries (The Bahamas, Belize and Jamaica). Three reef sites were established in Jamaica, according to this protocol, to represent a gradient of anthropogenic impacts. These sites were Monkey Island (also known as Pellew Island) in the Parish of Portland (18º10'56"N, 76º47'5"W), "Gorgo City" near Discovery Bay in the Parish of St Ann (18º28'40N, 77º25'46"W) and Southeast Cay, one of the Port Royal Cays in the Parish of Kingston (17º53'56"N, 76º23'27"W). Monkey Island, which was selected as a minimally impacted site, was located on the northeast coast of the island in an area of limited land-based stressors. There were no built up areas, industrial activity or agriculture production in close proximity to the reef site (NRCA, 1995). The major economic activity was eco-tourism with a few villas located along the coast. The fringing reef was made up of spurs and groves, developed on a narrow submarine shelf with a moderate sloping profile. The Discovery Bay reef site was located centrally along the north coast, just North West of the bay in an area called "Gorgo City" (approximately 1.4km North West of the Dancing Lady site). The main economic activities in and around the Discovery Bay area included artisanal fishing, bauxite loading, tourism and research (Gayle & Woodley, 1998). The reef formation was similar to that of Monkey Island consisting of the gently sloping spur and grove formation developed on a narrow submarine shelf. Southeast Cay, which forms part of the Port Royal Cays, is located on the south coast of the island just offshore of the capital city of Kingston. The Cays are comprised of a series of small coral islets situated on the island shelf which forms a protective barrier for the Palisadoes tombola and the town of Port Royal. The reef formation at Southeast Cay exhibits a gentle to flat profile. Despite being located outside of the eutrophic Kingston Harbour (Morrison & Greenaway, 1989) this area is important for artisanal fishing, recreation, tourism and transshipment activities (Mendes, 1992).

Video monitoring: The location of the transects within the designated Operational Areas were randomly selected following the procedure outlined in the Draft Site Selection Protocol developed by Woodley in 1999 (Creary, 2001; Deeb, 2002). A total of 20 transects, each 20m in length, within the depth range of 7-13m, were established for each reef site. The benthic substrate was monitored using the video monitoring protocol developed for the CPACC project (Miller, 2000; Miller & Rogers, 2002). Coming out of the Technical Review Workshop held at the end of the pilot project in 2001, Woodley recommended the change from random to fixed transects which would eliminate variation and facilitate direct comparison over time (Lawrence & Edwards, 2001). However, because of resource constraints this change in methodology was not implemented until 2007. Monitoring was carried out at Monkey Island, "Gorgo City" and Southeast Cay annually for the period 2000-2003 and 2007-2010 between the months of September to November.

Data processing and analysis: The resultant video tapes were checked for clarity, then numbered, catalogued and the content of each tape logged. Non-overlapping images were captured from the video tapes using a Sony™ Mini DV player connected to a computer loaded with the Pinnacle Studio™ software. During the early stages of the monitoring programme (2000-2003), a specially-developed CPACC software format, involving the use of Adobe Photoshop in combination with Winbatch for Windows, was used to place the10 random dots on the captured images. The benthic component under each dot was identified and entered into a Microsoft Excel spreadsheet designed to tabulate and summarize the data (Miller, 2000; Miller & Rogers, 2002). With the development of the more user friendly Coral Point Count with Excel Extension (CPCe) tool for the determination of coral cover (Kohler & Gill, 2006) the CPACC protocol was modified and the analysis of the captured images for the period 2007-2010 was carried out using this new tool.

RESULTS

Hard coral cover: Coral cover was generally low, falling below 15% at all three monitoring sites (Table 1). Hard coral cover ranged from a low of 6.2% (SE±0.8) in 2002 to a high of 14.6% (SE±2.4) in 2010 at Monkey Island in Portland. Notwithstanding the gap in the monitoring between the years 2004-2006, hard coral cover showed a moderate increase from 12.2% (SE±2.4) in 2007 to 14.6% (SE±1.3) in 2010. For 'Gorgo City" near Discovery Bay hard coral cover ranged from 5.9% (SE±1.2) in 2003 to 11.7% (SE±1.2) in 2010. This site also exhibited a slight increase in coral cover during the second period of the monitoring programme (2007-2010) ranging from 9.4% (SE±0.8) in 2007 to 11.7% (SE±1.2) in 2010. In contrast, the Southeast Cay site at Port Royal exhibited very low levels of hard coral cover throughout the entire monitoring period. Values ranged from 0.9% (SE±0.3) in 2009 to a high of 2.2% (SE±0.4) recorded in 2003. The hard coral cover of 1.3% (SE±0.3) recorded in 2010 points to a gradual decline over the 10-year period (Fig. 1). *Porites astreoides, Montastraea spp, Porites porities, Siderastrea siderea,* and *Agaricia agaricites* were the most commonly occurring coral species at Monkey Island and "Gorgo City" while *P. astreoides*

TABLE 1
Summary of the mean percentage cover for hard coral at Monkey Island, Portland; "Gorgo City" Discovery Bay and Southeast Cay, Port Royal, Jamaica for the periods 2000-2003 and 2007-2010

Year	Monkey Island, Portland		"Gorgo City", Discovery Bay		Southeast Cay, Port Royal	
	Mean	SE	Mean	SE	Mean	SE
2000	7.1	0.9	6.7	0.7	2.1	0.3
2001	11.2	1.1	8.1	0.8	1.2	0.3
2002	6.2	0.8	11.1	1.2	2.1	0.6
2003	11.8	1.8	5.9	1.2	2.2	0.4
2007	12.2	2.4	9.4	0.8	1.3	0.4
2008	10.5	2.1	10.2	1.0	1.5	0.5
2009	14.6	2.4	10.9	0.9	0.9	0.3
2010	14.6	1.3	11.7	1.2	1.3	0.3

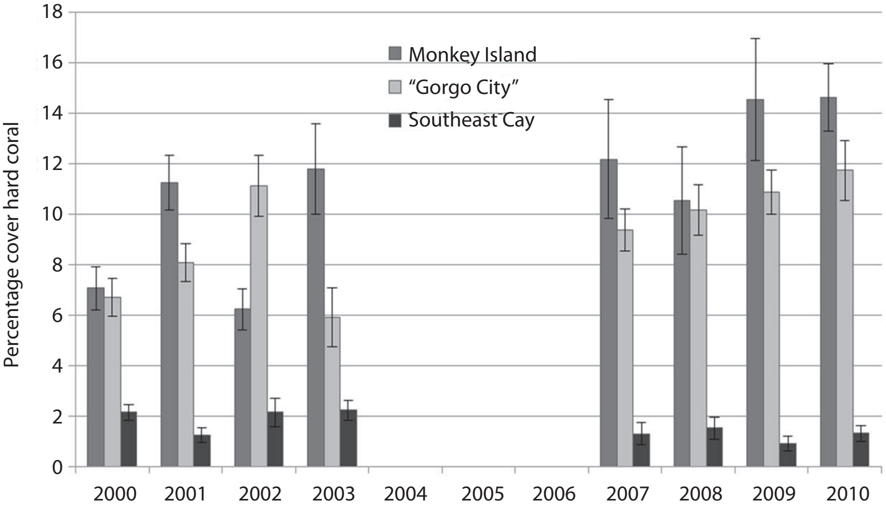

Fig. 1. Mean (with S.E.) percentage cover of hard coral at Monkey Island, Portland, "Gorgo City" Discovery Bay, St Ann and Southeast Cay, Port Royal, Kingston, Jamaica during the period 2000- 2003 and 2007 to 2010.

and *Montastraea spp* were the common species at Southeast Cay.

Macroalgae: The benthic substrate was dominated by macroalgae at all three monitoring sites (Table 2). At Monkey Island the macroalgal cover ranged from a low of 26.9% (SE±4.1) in 2001 to a high of 55.9% (SE±4.0) in 2003. However, macroalgal cover did not exceed 50% during the 2007-2010 period with a value of 40.5% (SE±5.8) recorded in 2010. For "Gorgo City" near Discovery Bay macroalgal cover ranged from 30.4% (SE±1.8) in 2001 to 54.7% (SE±2.9) in 2010. For this site macroalgal cover was showing an increasing trend. The macroalgal cover recorded at Southeast Cay, Port Royal, ranged from a low of 43.0% (SE±1.9) in 2000 to a high of 95.7% (SE±0.4) in 2007. Of note is the dramatic increase in macroalgal cover for the 2007-2010 monitoring period, with values exceeding 90% for all four years (Fig. 2). *Dictyota, Lobophora* and *Sargassum* were the macroalgal species commonly found at all three sites.

TABLE 2
Summary of the mean percentage cover for macroalgae at Monkey Island, Portland; "Gorgo City" Discovery Bay and Southeast Cay, Port Royal, Jamaica for the periods 2000-2003 and 2007-2010

Year	Monkey Island, Portland		"Gorgo City", Discovery Bay		Southeast Cay, Port Royal	
	Mean	SE	Mean	SE	Mean	SE
2000	52.3	2.6	49.5	2.1	43.0	1.9
2001	26.9	4.1	30.4	1.8	55.7	3.8
2002	55.0	2.3	33.6	4.5	58.5	3.1
2003	55.9	4.0	52.1	3.1	53.6	2.3
2007	36.3	5.7	40.1	4.9	95.7	0.4
2008	43.9	6.2	42.5	5.0	94.6	1.0
2009	49.1	6.7	49.0	4.7	94.8	1.1
2010	40.5	5.8	54.7	2.9	94.9	1.0

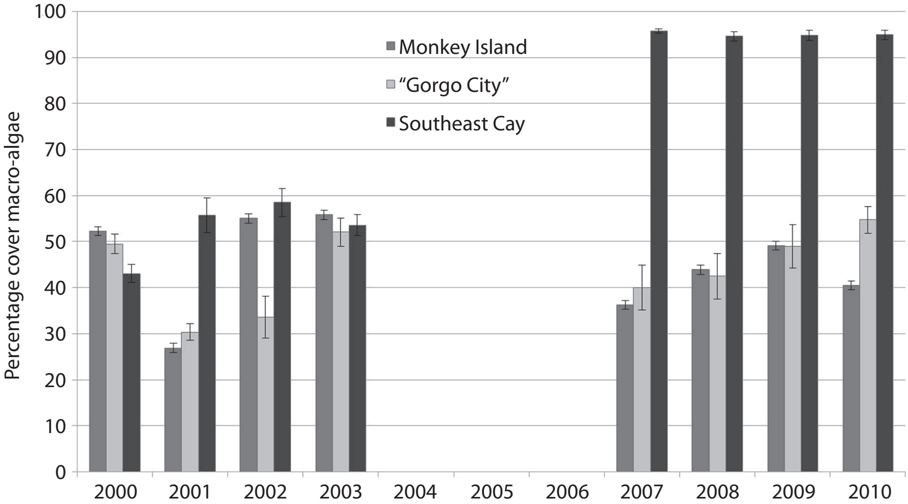

Fig. 2. Mean (with S.E.) percentage cover of macroalgae at Monkey Island, Portland, "Gorgo City" Discovery Bay, St Ann and Southeast Cay, Port Royal, Kingston, Jamaica during the period 2000- 2003 and 2007 to 2010.

DISCUSSION

There is a vast body of literature that has documented the decline of coral cover and the resultant increase in other taxa, particularly macroalgae (Gardner, et al., 2003; Cote, Gill, Gardner & Watkinson, 2005; Mumby et al., 2007; Creary et al., 2008) and in most cases human activity has been implicated (Hughes, Baird, Bellwood, Card & Connolly, 2003). Schutte, Selig and Bruno (2010) in their analysis of 875 sites over a 35 year period showed that region-wide hard coral and macroalgae cover have changed very little since 1980, however, they suggest that there were local spatial-temporal variations in the benthic structure underlying this broad pattern.

The results presented here are of importance because they document the long term dynamics of three Jamaican reef ecosystems. For this monitoring programme coral reef health was assessed by looking at the relationship between hard coral and macroalgae. Coral cover at the two north coast sites (Monkey Island and "Gorgo City") showed a small but gradual increase particularly for the period

2007-2010. In contrast, for the Southeast Cay site on the south coast, coral cover was low and declining. All three sites were dominated by macroalgae; however, the north coast sites maintained cover at around 50% while on the south coast macroalgae cover increased dramatically to over 90% by 2010.

Indications are that for the north coast sites coral cover is making a comeback and that macroalgae cover in remaining relatively stable. Crabbe (2011, 2012) in his studies carried out between 2000 and 2008 concluded that the corals around Discovery Bay exhibited good resilience, particularly with regards to coral recruits. Cho and Woodley (2000) indicated that prior to the start of this study, the reefs at Discovery Bay were recovering and they attributed this to the recruitment and growth of opportunistic coral species such as *P. asteroides, P. porites and A. agaricites,* aided by the increasing abundance of *Diadema antillarum.* These coral species are still an important component of the coral community on the sites monitored during this study. Cho and Woodley's (2000) study also showed that coral cover was variable with a mean of 15.9% at 10m while mean macroalgae was 56.5% at the same depth. Similar results were reported for the CARICOMP (Caribbean Marine Productivity Program) site on the west forereef of Discovery Bay where coral cover remained relatively constant at around 11% during the period 1994 to 2007 (Gayle, Charpentier, Spence & Levre, 2010). A more recent study by NEPA (2011) has also reported that coral cover on a number of sites around the island has stabilized at around 13% over the period 2007 to 2010. This is also in keeping with trends in some other sites throughout the Caribbean where stability as well as gradual recovery on the local scale has been detected (Cote et al., 2005). A review of regional assessment of coral communities by Schutte et al. (2010) suggests that regional coral cover is stable at about 16% with coral cover in the northern Caribbean at about 20%.

In 2005 widespread sea surface temperature anomalies were recorded throughout the Caribbean resulting in extensive coral bleaching (Eakin, 2010). However, reports on the status of the coral reefs in Discovery Bay indicated that bleaching did take place but with little resultant mortality (Jones et al., 2008; Creary et al., 2008), which suggested that the coral reefs in this area were showing some amount of resilience to temperature stress (Crabbe, 2012). So, although no monitoring was carried out during the period 2004-2006 the data collected in 2007 and onwards does not suggest a substantial decline in coral cover prior to this.

When the monitoring programme was established to measure coral reef health it was expected that data obtained in 2000 would represent a baseline against which annual changes would be compared. For the period 2000-2010 monitoring was actually carried out in two four-year blocks (2000-2003 and 2007-2010) with a gap of three years (2004-2006). The sites selected were based on a gradient of anthropogenic impacts. Monkey Island was identified as being minimally impacted, "Gorgo City" moderately impacted and Southeast Cay severely impacted. The results for the period 2000-2010 showed little difference between coral and macroalgae cover for the minimally (Monkey Island) and the moderately ("Gorgo City") impacted sites on the north coast. With regards to the Monkey Island, despite not being located in an area of significant economic activity or coastal development pressure, this site still exhibited relatively low coral cover (i.e. less than 15%). This become more apparent when compared with "Gorgo City" near Discovery Bay where bauxite loading, tourism activities (such as villas and public beaches), artisanal fishing and the presence of a population center was expected to have exerted more anthropogenic pressure on the adjacent reefs. However, studies have shown that the abundance of coral and macroalgae can also vary as a result of other factors such as reef morphology, wave energy and biological factors (Cho & Woodley, 2000).

Although the objective of establishing a long term monitoring programme was to show the effects of global warming factors on coral reefs, this was not entirely achieved due the failure of Component 1of the CPACC project (the establishment of the sea level/ climate monitoring system) which would have provided the climate related data. In addition, with the focus of the programme on coral reef monitoring, this precluded the possibility of collecting additional physical, chemical and meteorological data under Component 5. With the exception of Jamaica, the expectation that CARICOM countries would institutionalize the coral reef monitoring programme after the pilot project was not realized. Wide scale monitoring programmes are expensive and with limited human and financial resources, monitoring institutions can find it difficult to implement and support such programmes over the long term, Financial resources represented the greatest challenge faced in Jamaica and this resulted in data not being collected for the period 2004 to 2006. As with many data collection programmes of this nature (e.g. CARICOMP) their long term success require stronger support if they are to perform at the level that is expected to achieve sustainability. Despite the many challenges, the need for monitoring has been strongly recognized (Rogers & Miller 2006) and the resultant data has provided valuable information to local and regional agencies requiring inputs to their decision making process.

ACKNOWLEDGMENTS

I would like to acknowledge the inputs of the staff from National Environment and Planning Agency (formally the Natural Resources Conservation Authority) for the role they played in data collection, processing and analysis). Staff from various department of the University of the West Indies also played a part in this monitoring programme since 2000; these include the Department of Life Sciences, Port Royal Marine Laboratory, Discovery Bay Marine Laboratory, Caribbean Coastal Data Centre. Inputs were also received from Cave Hill Campus of the UWI, CERMES in Barbados and the Caribbean Community Climate Change Center (CCCCC) in Belize. Direct funding was provided at various times through the Caribbean Planning for Adaptation to Climate Change (CPACC) Project and Mainstreaming Adaptation to Climate Change (MACC) Project.

RESUMEN

Resultados del monitoreo a largo plazo en los arrecifes de coral en tres lugares de Jamaica: **Isla Monkey, "Ciudad Gorgo" y Cayo Sureste.** Los impactos regionales y globales del cambio climático están teniendo consecuencias devastadoras en los ecosistemas de arrecifes de coral en el Caribe. Se establecieron monitoreos en el 2000 en Las Bahamas, Belice y Jamaica. Siguiendo el proyecto piloto, el programa se institucionalizó en Jamaica y el monitoreo se llevó a cabo en ocho ocasiones del 2000 al 2010. Se seleccionaron los sitios: Isla Monkey, "Ciudad Gorgo " cerca de la Bahía Discovery (ambos en la costa norte) y el Cayo Sureste en el Puerto Royal en el sur de la costa. Las macroalgas dominaban el sustrato bentónico. Isla Monkey y "Ciudad Gorgo" tuvieron la mayor cobertura de coral. *Porites astreoides*, *Montastraea spp, Porites porities, Siderastrea siderea*, y *Agaricia agaricites* representan las especies de corales más frecuentes. Los datos de este programa se han utilizado en las iniciativas de evaluación y manejo de arrecifes de coral locales y regionales.

Palabras clave: Bahía Discovery, Portland, Puerto Royal, Jamaica, videovigilancia, arrecifes de coral, monitoreo a largo plazo, cambio climático

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Possible recovery of *Acropora palmata* (Scleractinia:Acroporidae) within the Veracruz Reef System, Gulf of Mexico: a survey of 24 reefs to assess the benthic communities

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Received 03-XI-2013 Corrected 12-III-2014 Accepted 24-III-2014

Abstract: Recent evidence shows that *Acropora palmata* within the Veracruz Reef System, located in the southwestern Gulf of Mexico, may be recovering after the die off from the flooding of the Jamapa River and a dramatic cold water event in the 1970s. Since this decline, few surveys have documented the status of *A. palmata*. The 28 named reefs in the system are divided into 13 northern and 15 southern groups by the River. Between 2007 and 2013, we surveyed 24 reefs to assess the benthic communities. Seven of the 11 reefs surveyed in the northern group and all in the southern group had *A. palmata.* Colonies were typically found on the windward side of the reefs in shallow waters along the reef edges or crest. We also recorded colony diameter and condition along belt transects at two reefs in the north (Anegada de Adentro and Verde) and two in the south (Periferico and Sargazo), between 2011 and 2013. In addition, eight permanent transects were surveyed at Rizo (south). A total of 1 804 colonies were assessed; densities ranged from 0.02 to 0.28 colonies/m² (mean (±SD), colony diameter of 58 ± 73cm, and 89 ± 18% live tissue per colony). Total prevalence of predation by damselfish was 5%, by snails 2%, and <1% by fireworms, disease prevalence was <3%. Size frequency distributions indicated that all of the sites had a moderate to high spawning potential, 15-68% of the colonies at each site were mature, measuring over 1 600cm². The presence of these healthy and potentially reproductive colonies is important for species recovery, particularly because much of the greater Caribbean still shows little to no signs of recovery. Conservation and management efforts of these reefs are vital. Rev. Biol. Trop. 62 (Suppl. 3): 75-84. Epub 2014 September 01.

Key words: *Acropora palmata*, population recovery, Veracruz, Mexico, colony size class frequency.

Acropora palmata and *A. cervicornis* (Lamarck, 1816) historically have been major reef framework builders in the greater Caribbean, Gulf of Mexico and Florida (Adey, 1978; Neigell & Avise, 1983). Their complex three-dimensional structure provides habitat to numerous invertebrate and vertebrate species and coastal protection during storms and hurricanes. Between the 1970's and 1980's populations across the species range were plagued by disease and in some locations researchers documented up to 100% loss by white band disease (Dustan & Halas, 1987; Knowlton, Lang & Keller, 1990; Aronson & Precht, 2001; Bruckner, 2002). There has been very little documentation of species recovery since these declines (Grober-Dunsmore, Bonito & Frazer, 2006; Mayor, Rogers & Hillis-Starr, 2006; Jones et al., 2008) thus, in 2006 they were listed as threatened by the US Endangered Species Act (NOAA, 2006) and critically endangered by the IUCN Red list (Aronson et al., 2008a; 2008b).

Since the listing, many populations have not returned to self-sustainable levels despite increased restoration activities and protection (Knowlton et al., 1990; Aronson & Precht, 2001; Bruckner, 2002; Miller, Bourque &

Bohnsack, 2002; *Acropora* Biological Review Team, 2005); however, there are remnant populations throughout the *Acropora* spp. range. Large *Acropora* spp. populations have been reported in Florida (Vargas-Angel, Thomas & Hoke, 2003; Williams, Miller & Kramer, 2008; Walker, Larson, Moulding & Gilliam, 2012); Punta Rusia, Dominican Republic (Lirman et al., 2010); Roatan, Honduras (Keck, Houston, Purkis & Riegl, 2005); Venezuela (Zubillaga, Márquez, Cráquer & Bastidas, 2008); and St. John, US Virgin Islands (Grober-Dunsmore et al., 2006). Here we add to this list by reporting on the abundant *A. palmata* in Veracruz, Mexico.

The Veracruz Reef System (VRS) is located within the Parque Nacional Sistema Arrecifal Veracruzano (PNSAV) which encompasses 52 000ha of marine ecosystems off the coast of the major port city of Veracruz, Mexico and a small fishing village to the south, Antón Lizardo. The VRS includes 28 shallow-water coral reefs, which are separated into two groups by the Jamapa River outflow. The northern group consists of 13 reefs near the city of Veracruz and the southern group has 15 reefs near Antón Lizardo. Most of the reefs in this system are heavily impacted by urbanization, run-off, sedimentation, close proximity to coastline and fishing activities (Emery, 1963; Horta-Puga, 2007). In 1992, the VRS was declared a natural protected area and was converted into a National Park by the Mexican Government (Diario Oficial, 1992).

Since the late 1800's, *A. palmata* and *A. cervicornis* have dominated the shallow-water coral reefs of the VRS (Heilprin, 1890). However, similar to other Caribbean populations, researchers observed local declines through the 1970's and 1980's. Mortality in this region was attributed to disease and the flooding of the nearby Jamapa and Papaloapan rivers (Rannefeld, 1972; Tunnell, 1988; 1992). In 1971, Rannefeld (1972) documented up to a 100% loss at Enmedio for both species and by 1973, abundance had decreased dramatically on many reef slopes (Tunnell, 1988; 1992). However, Jordan-Dahlgren (1992) documented re-colonization of *A. palmata* to old standing dead colonies in the late 1980's. Another study by Lara, Padilla, García and Espejel (1992) observed *Acropora* spp. at 82% of the reefs surveyed (n=17) and recorded them as dominant (>20% live cover) on the fore reef edge and inner fore reef zones. Despite this, in 2002 population levels of *A. palmata* were reported as low (0–0.3% cover) at six reefs in the VRS (Jones et al., 2008), some of which had previously been documented as having colonies (Lara et al., 1992).

This study was part of a larger, long-term project in which we partnered with PNSAV staff to characterize the benthic communities in the VRS (Rangel Avalos et al., 2007). To date, 24 of the 28 reefs have been visited and it was during these visits that it was noted that a majority of the reefs had the presence of one or both species of *Acropora.* Using the knowledge gained of these populations during the benthic surveys, additional *A. palmata* assessments were completed to document the current status, health and possible recovery of *A. palmata* within the VRS. Population recovery herein is defined by an increase in colony abundance, size and distribution and the potential to sexually reproduce with low prevalence of recent mortality in comparison to previous studies in the VRS.

MATERIALS AND METHODS

Benthic characterization assessment: Reefs within the VRS were visited between 2007 and 2013 as part of a larger benthic characterization project (Rangel Avalos et al., 2007). Fifty-five sites, targeting the windward side and northern and southern ends of the reefs, were surveyed across 24 of the 28 reefs. Of these sites, 28 were in the northern group and 27 were in the southern group. At each site, four or five 30m point intercept transects were completed for benthic characterization. In addition, notes and images were taken of the area surrounding the transects. Special attention was taken to note the presence of *A. palmata.* These data were utilized to document the distribution of *A. palmata* within the VRS and target sites for the *A. palmata* assessment.

***Acropora palmata* assessment:** Five sites where *A. palmata* was found in greatest abundance were used to further investigate the status of *A. palmata* within the VRS. These sites were on two reefs in the northern group (Verde and Anegada de Adentro) and three reefs in the southern group (Rizo, Periférico, and Sargazo). Colony maximum length, height, percent mortality and presence or absence of disease and predation were collected along five or six parallel 10m belt transects at all reefs but Rizo. Divers spread across the reef approximately 10m apart, swimming parallel to each other, collecting data on colonies within 5m to each side of them. A hand-held GPS was used to mark the start and end of each transect to obtain transect length. Belt transects length varied between 15-170m and depended on the population size and time available. At Rizo, eight previously installed permanent transects, 7m x 30m, were utilized for the assessment. For all transects, a colony was only included if it had live tissue and measurements were made of the entire colony skeleton (live tissue + dead skeleton).

A live area index (LAI) was used to compare the amount of live tissue between sites and across years to better understand the population structure within the VRS. LAI indices typically use colony length, width and percent live tissue measurements. However, in order to maximize the number of colonies measured within the limited time available during each sampling, colony width was only measured for a subset of colonies (348) at four of the five sites; width measurements were not collected at Periférico. The mean ratio of length divided by the width of 348 colonies was 0.75, and this value was used as a conversion to estimate width for the LAI. Therefore, for this study LAI = (Length × (0.75) Length × % live tissue)/100, where length was the maximum dimension of the colony and percent live tissue was the percentage of the whole colony covered by live tissue.

The resulting size frequency distribution was used to describe the population structure. Soong and Lang (1992) reported that *A. palmata* was not fertile until colonies were >60cm^2, and as size of the colony increased as did the frequency of fertility, 31% of the colonies between 250 and 1 000cm^2, 43% of the colonies between 1 000 and 4 000cm^2 and 88% of the colonies >4 000cm^2 were fertile. In addition to determining the proportion of fertile colonies within each size class, they concluded that colonies greater than 1 600cm^2 were reproductively mature. Therefore, our chosen size classes, similar to those of Schärer et al. (2008), are as follows: small colonies with no reproductive potential (<60cm^2), medium colonies with low frequency of fertility (60-1 600cm^2) and large mature colonies with moderate to high potential to spawn (>1 600cm^2).

RESULTS

Benthic characterization assessment: Based on the point intercept surveys and site descriptions, *A. palmata* was present at 20 of the 24 reefs surveyed and 34 of the 50 sites. In the northern group, *A. palmata* was present at seven of the 11 reefs and 13 of the 28 sites (Fig. 1). In the southern group, *A. palmata* was present at all reefs (n=13) and 21 of the 27 sites (Fig. 2). Where *A. palmata* was present, colony abundance varied by site ranging from one colony to multiple large overlapping colonies.

Five reefs were of particular interest because *A. palmata* was present in greater abundance. In the northern group, large overlapping *A. palmata* colonies were found at Verde and Anegada de Adentro reefs. Colonies were observed on the reef flat at Anegada de Adentro and on the leeward slope of Verde. Three reefs in the southern group, Rizo, Sargazo and Periférico also had greater abundance. Colonies at Rizo were observed on the reef flat and on the upper fore reef of Sargazo and Periférico.

***Acropora palmata* assessment:** Belt transects targeting *A. palmata* were completed

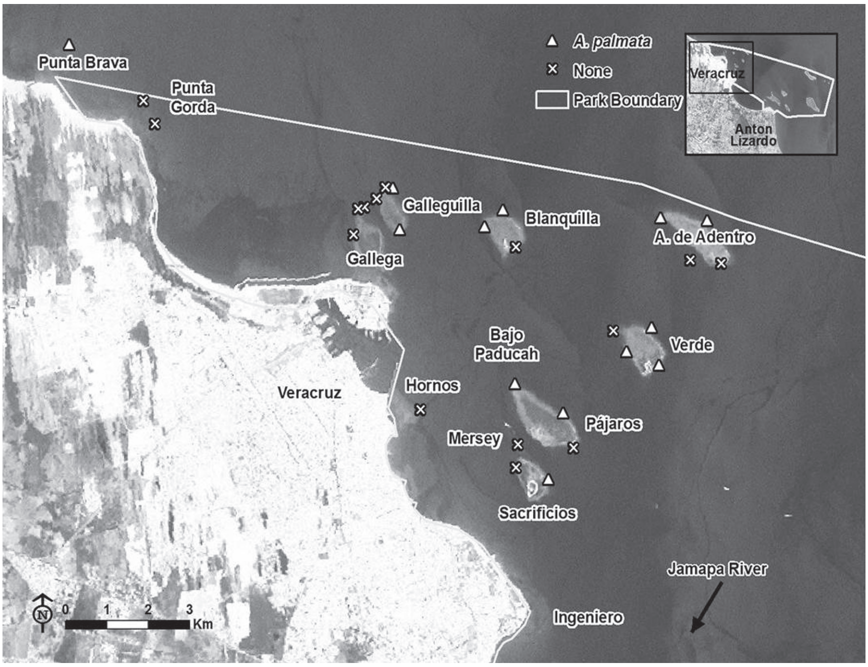

Fig. 1. Presence of *Acropora palmata* in the northern group of the Veracruz Reef System.

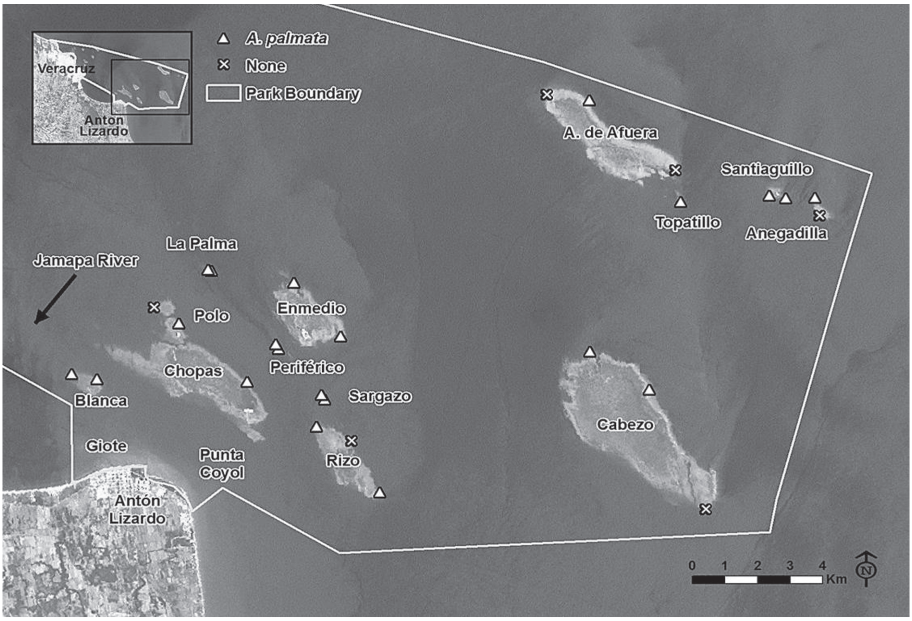

Fig. 2. Presence of *Acropora palmata* in the southern group of the Veracruz Reef System.

between 2011 and 2013 at Verde, Anegada de Adentro, Rizo, Periférico and Sargazo reefs, surveying a total area of 21 420m² (Table 1). A total of 1 804 colonies were measured across all sites and all years. The number of colonies ranged from 40 in 2011 at Rizo to 764 at Verde in 2012 (Table 1).

Colony density (±SD) ranged from 0.02±0.03colonies/m² to 0.28±0.08colonies/m² (Table 1). The greatest abundance of *A. palmata* was found at Anegada de Adentro where the density was significantly greater than that of the other four sites (Kruskal-Wallis, $p<0.05$). When reefs were grouped by location, the northern sites' mean density (0.15±0.12colonies/m²) was significantly greater than the southern (0.06±0.06colonies/m²—Kruskal-Wallis, $p<0.05$). Verde and Rizo were visited during consecutive years and both had an increase in colony density from 2011 to 2012 (Table 1). The increased number of colonies at Rizo was likely due to the VRS being directly impacted by two storms between the 2011 and 2012 surveys. Rizo was surveyed once more in 2013 and density remained similar to that observed in 2012.

Mean colony length (±SD) for all reefs was 58±73cm. Anegada de Adentro had significantly larger colonies than the rest of the reefs (122±163cm —Kruskal-Wallis, $p<0.05$) and the largest colony recorded (length= 1 320cm). At Verde colony length increased from 2011 to 2012. At Rizo colony length decreased from 2011 to 2012, but increased slightly in 2013 (Table 1).

Mean percent live tissue (±SD) per colony for all reefs across all years was 89±18%. Mean percent live tissue per colony varied by reef and was greatest at Rizo in 2011, 96% (Table 1). However, from 2011 to 2013 colonies at Rizo decreased in mean percent live tissue per colony from 96% to 73%. Colonies at Verde also decreased in live tissue from 92% to 87% between the 2011 and 2012 survey.

Predation by the threespot damselfish, Stegastes *planifrons* (Cuvier 1830), snail, *Coralliophilia abbreviata* (Lamarck 1816) and bearded fireworm*, Hermodice carunculata* (Pallas 1766) were present in both groups. Damselfish predation, through the creation of algal gardens was the most common type, observed on 95 colonies. Its impact was difficult to quantify and was only recorded as present or absent on a colony since it was not considered a cause of recent mortality. The most common cause of recent mortality was predation by snails, affecting 35 colonies throughout the three years of data collection. Half of the colonies with snail predation were observed at Sargazo. Fireworm predation was recorded on ten colonies; eight of which were observed at Verde. The mean percent recent mortality of all colonies was 1.1%, and ranged from 3.3% at Sargazo to 0.1% at Rizo.

Disease prevalence was low. Although it was recorded at four of the five reefs, it was

TABLE 1
Quantitative assessment of *Acropora palmata* populations within the Veracruz Reef System (±SD).
Rizo transects utilized permanent belt transects and thus are the same area across years

Group and Reef	Year(s) Surveyed	Survey Area (m^2)	Total Colonies	Site Density (colonies/m^2)	Mean Colony Length (cm)	Mean Colony % Live
Northern Group Verde	2011	2 500	192	0.08 ± 0.04	52 ± 51	92 ± 15
	2012	8 500	764	0.09 ± 0.04	60 ± 55	87±20
A. de Adentro	2013	700	197	0.28 ± 0.08	122 ± 163	90 ± 11
Southern Group Rizo	2011	1 680	40	0.02 ± 0.03	40 ± 22	96 ± 7
	2012	1 680	89	0.05 ± 0.03	33 ± 22	83 ± 19
	2013	1 680	82	0.05 ± 0.03	34 ± 19	73 ± 24
Periférico	2011	1 500	199	0.13 ± 0.10	35 ± 27	95 ± 13
Sargazo	2011	3 180	241	0.08 ± 0.02	41 ± 39	91 ± 17

only observed on 2.7% of the colonies across the entire study. Disease was not observed at Rizo. Rapid tissue loss (RTL) was the most commonly recorded condition (Williams & Miller, 2005), observed affecting 1.4% of the colonies. White band disease (WB) and white pox (WP) were also observed in low levels 0.9% and 0.3% of the colonies respectively. WB was mainly observed at Verde affecting only one other colony at Periférico. RTL was observed at Verde, Anegada de Adentro and Sargazo and WP was only observed at Verde and Sargazo.

Mean LAI ranged from 828cm² to 23 448cm² per reef (Fig. 3). The reefs in the northern group had significantly larger mean LAI's, Anegada de Adentro (23 448cm²) and Verde (3 097cm² in 2011 and 3 580cm² in 2012) than the southern group, where all reefs had a LAI under 2 000cm² (Kruskal-Wallis, p<0.05- Fig. 3).

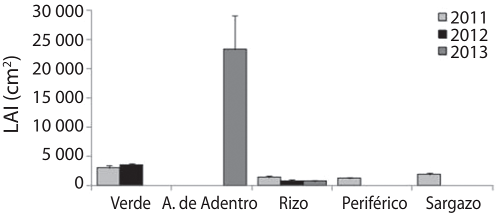

Fig. 3. *Acropora palmata* mean (±SE), live area index (LAI) per colony (cm²) for each reef surveyed.

In 2011, for all reefs combined, 6% of the measured colonies were small (<60cm²), 66% were medium (60-1 600cm²) and 28% were large (>1 600cm²). From 2011 to 2012, there was a small shift from small colonies to medium and large at Verde. At Rizo, there was a decrease in the number of large colonies and an increase in the number of small and medium colonies and by 2013, there was a small increase in medium colonies and decrease in small colonies. Anegada de Adentro was the only site dominated by large colonies with 69% having a mean LAI greater than 1 600cm² (Fig. 3, 4).

DISCUSSION

This study is the most comprehensive study of *A. palmata* within the Veracruz Reef System to date. Its distribution through the VRS indicates that *A. palmata* may be recovering from the 1970's and 1980's die off. *Acropora palmata* was present at a majority of the sites surveyed in both reef groups. For those sites where it was not found it appears that either the habitat was not suitable (too deep) or the sites were within close proximity to shore and/or the major shipping port (northern group). The overall mean density of this study (0.08colonies/ m²) was greater than the previously described for the area (0.03), Puerto Rico (0.03), St. Croix (0.02) and St. John (0.06) and

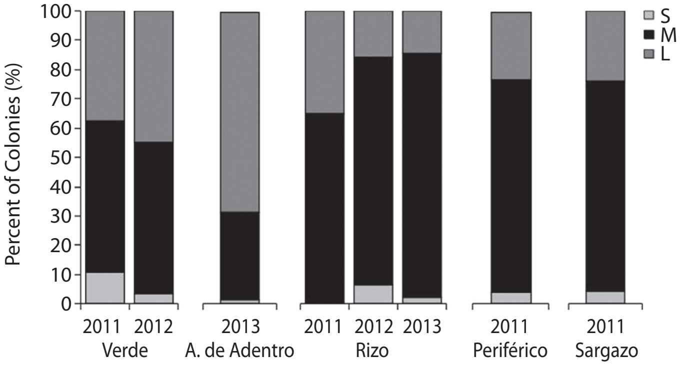

Fig. 4. Size frequency of *Acropora palmata* colonies for each reef surveyed by year (2011-2013). Size classes based on LAI of each colony surveyed, Small <60cm², Medium 60-1 600cm², Large >1 600cm².

similar to Venezuela (0.08) (Jordan-Dahlgren, 1992; Mayor et al., 2006; Schärer et al., 2008; Zubillaga et al., 2008). Colony density and mean colony length were greatest in the northern group (Verde and Anegada de Adentro). This was contrary to what was found by Jordan-Dahlgren (1992), however the three reefs that they surveyed in the southern group were not included in our *A. palmata* assessment.

In order for a population to be recovering it needs to be dominated by 'healthy' colonies, which are characterized by a broad distribution of colony size frequencies (Knowlton, 2001) low prevalence of disease, predation and recent mortality and have reproductive potential (Richmond, 1997; Zubillaga et al., 2008). The mean colony length during this study was 58cm, whereas Jordan-Dahlgren (1992) reported a mean colony size of 22cm. The largest colony measured (1 320cm) was over ten times that of Jordan-Dahlgren (1992). Across the three years of data collection, the mean percent live tissue of all colonies was 89% and mean recent mortality was only 1.1%. Prevalence of disease (2.7%) and predation (2.5%) were observed at very low levels. Other studies have recorded similar or higher levels of disease and predation in other regions (Grober-Dunsmore, et al., 2006; Schärer et al., 2008; Zubillaga et al., 2008; Williams & Miller, 2011).

The *A. palmata* populations in the VRS have a high spawning potential, 38% of the colonies are considered mature (>1 600cm^2), of those colonies 53% were >4 000cm^2. According to Soong and Lang (1992) there is a high potential (88%) that colonies >4 000cm^2 are fertile. All sites were dominated by medium sized colonies; only 4% of the colonies were classified as small across all years. This size frequency distribution indicates that these populations have a high potential for colonies to spawn, whereas two decades prior the majority of the colonies were in the small to medium size classes (Jordan-Dahlgren 1992). Large colonies were found across the VRS, increasing the potential for sexual reproduction, albeit the genetic diversity for this species is currently unknown for this region.

Although the *A. palmata* populations were 'healthy' as defined herein, there was a decrease in the percent live tissue cover (96% to73%) at Rizo from 2011 to 2013. We found no signs of disease and very little recent mortality, however, the VRS was directly hit by two storms between the 2011 and 2012 surveys, Tropical Storm Harvey (August) and Hurricane Nate (September). These storms caused an increase in wave height and flooding of the Jamapa river (Blake, 2011; Kimberlain, 2011). At Rizo in 2011, 40 *A. palmata* colonies were measured within the permanent monitoring transects and in 2012, the count increased to 89. Initially, there were no small colonies within this population, but in 2012, 7% of the colonies were less than 60cm^2. There was also a 20% drop in the number of large colonies, which may indicate that the energy from the storms caused some large colonies to fragment into smaller colonies. Williams (2011) found similar increases in fragmentation, decreases in colony size, and increases in colony tissue mortality following a hurricane. This shift was also apparent in the mean colony length, decreasing from 40cm to 33cm between 2011 and 2012. However, this trend seemed to be reverting in 2013, as we observed a decrease in small colonies and an increase in medium colonies. This could indicate that the small fragments formed in 2012 had survived and grown in the intervening period, showing some resilience, characteristic of a healthy population. We were not able to detect similar patterns at Verde because, unlike Rizo, the transects started in the same location both years, but the 2012 transect continued an additional 1 200m past the end of the 2011 transects, therefore including more colonies in the assessment. In addition, the colonies at Verde may be more protected as they are found on the leeward slope of the reef, whereas colonies at Rizo are more exposed on the windward edge of the reef.

These data suggest that *A. palmata* in the VRS is healthy, abundant, broadly distributed, and has a high spawning potential, whereas most of the Caribbean populations are not. Hence, the next question may be, why has this species been able to proliferate in this area where there are continuous terrestrial and environmental impacts? Especially if it is thought to have endured the same population decrease as the rest of the Greater Caribbean. During a time where this species is under review to be uplisted to Endangered under the US Endangered Species Act, proper management and conservation efforts should be made to protect these recovering populations.

ACKNOWLEDGMENTS

We thank the staff of the Parque Nacional Sistema Arrecifal Veracruzano, M. Rangel Avalos and J. Santander Monsalvo for critical logistical support. Nova Southeastern University Oceanographic Center graduate students, V. Brinkhuis, S. Bush, A. Costaregni, N. D'Antonio, P. Espitia, D. Fahy, A. Halperin, M. Sathe, J. Walczak, and C. Walton, provided essential help with data collection. Partial funding for this research was provided by multiple Nova Southeastern University President Faculty Research and Development Grants, the Guy Harvey Research Institute, and a grant from the National Oceanic and Atmospheric Administration to the National Coral Reef Institute. We thank Margaret Miller and an anonymous reviewer for constructive comments on this work. This is NCRI Contribution 157.

RESUMEN

Posible recuperación de *Acropora palmata* (Scleractinia:Acroporidae) en el sistema arrecifal de Vera Cruz, Golfo de México: evaluación de comunidades bentónicas en 24 arrecifes. Evidencia reciente indica que las poblaciones de *Acropora palmata* del sistema arrecifal de Vera Cruz, ubicado al suroeste del Golfo de México, podría estarse recuperando después de las inundaciones del río Jamapa e intrusiones de agua fría que afectaron la región en los años setenta. Desde la disminución, pocos estudios han documentado el estado *A. Palmata.* Consiste de 28 arrecifes divididos 13 al norte y 15 al sur del río. Entre el 2007 y 2013 se muestrearon 24 arrecifes para caracterizar las comunidades bentónicas. Siete de los 11 arrecifes del norte y en todos los arrecifes del sur tenían *A. palmata*. Las colonias se encontraron por lo general en el barlovento de los corales en agua sómeras a lo largo del borde del arrecife. También registramos los diámetros de las colonias y condición a lo largo de transectos tipo conturón en dos arrecifes al norte (Anegada de Adentro y Verde) y dos en el sur (Periférico y Sargazo), entre el 2011 y 2013. Además, ocho transectos se evaluaron en Rizo (al sur). Evaluamos un total de 1 804 colonias; las densidades variaron entre 0.02 a 0.28 colonias/m^2 (promedio (±DE) del diámetro de colonia 58± 3cm y 89±18% de tejido vivo por colonia). La depredación fue 5% por peces damisela, 2% por caracoles y <1% por gusanos, prevalencia de enfermedades <3%. La distribución de tamaños indicó que las poblaciones tienen un potencial moderado a alto de desove, 15-68 de las colonias eran maduras, y medían más de 1 600cm^2.La presencia de estas colonias saludables y potencialmente reproductivas son importantes para la recuperación de especies, particularmente porque el Caribe muestra muy pocas o ninguna señale de recuperación. Esfuerzos en conservación y manejo en estos arrecifes es vital.

Palabras clave: *Acropora palmata*, recuperación poblacional, Veracruz, Mexico, distribución de frecuencia de tamaño.

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Population assessment of *Acropora palmata* (Scleractinia: Acroporidae): relationship between habitat and reef associated species

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Received 01-IX-2013 Corrected 31-III-2014 Accepted 01-IV-2014

Abstract: Three decades ago, *Acropora palmata* was one of the main reef-building coral species throughout the Caribbean, forming an essential component of the structural complexity of shallow coral reef habitats. These colonies still provide microhabitats for settlement, food and shelter to many vertebrates and invertebrates. The recent decline of *A. palmata* has been followed by a significant loss in spatial heterogeneity and possibly in species diversity. Studies addressing whether dead and living stands of *Acropora* hold different fish and benthic assemblages are scarce. The status of *Acropora* colonies and their associated species were assessed in October 2012, at two reef zones of Cayo Sombrero, Venezuela. Visual censuses of fish abundance and the number of macrofaunal individuals were recorded for both live and dead zones. Living *Acropora* colonies had the lowest abundance (<31%). In both zoned the fish community was dominated by damselfishes (<53%) and wrasses (<36%), the benthic macrofauna by peracarid crustaceans (<40%) and polychaetes (<38%). Fish and benthic communities were not correlated with the condition (live or dead) of the *Acropora* habitats; possibly branching structures provide the necessary shelter and protection no matter if they are dead or alive. More replication is necessary to test this unexpected result. Rev. Biol. Trop. 62 (Suppl. 3): 85-93. Epub 2014 September 01.

Key words: *Acropora palmata*, benthic macrofauna, Caribbean, coral reefs, reef fishes.

Coral reefs are complex systems that typically support high structural complexities with high spatial heterogeneity, representing one of the most diverse ecosystems of the planet (Glynn, 1991). Unfortunately, multiple factors such as overfishing, sedimentation, nutrient enrichment, global warming and diseases (Rogers, 1990; Aronson & Precht, 2001; Cróquer & Bone, 2003; Gómez et al., 2010) have been directly or indirectly linked to the progressive *decline* in coral *communities*, causing important changes on the coral reef structure and *increasing the loss of biodiversity and live coral cover over the last* few *decades* (García, Cróquer & Pauls, 2003).

The branching coral *Acropora palmata* (Lamarck, 1816) has an essential role in coral reefs as it provides the habitat for a myriad of reef-associated species, significant coral cover and adds complex topography to shallow reef environments. Therefore, this species may have an important role in determining the abundance and diversity of many reef fishes and macrofauna populations (Lirman, 1999). The robust and complex morphology of *A. palmata* provides microhabitats for settlement, food and shelter to many invertebrate reef species (Bonin, 2012), which depend on the presence of Acroporid colonies to survive, probably because of the geological, physical and biological support offered by these corals to numerous shallow reef communities (Baums et al., 2002). Unfortunately, *A. palmata* has shown an important decline of live tissue cover (>95%)

throughout the Caribbean after a mass mortality caused by the combination of white band disease and hurricanes in the middle of the 80s (Aronson & Precht, 2001). It is believed that this regional demise has reduced habitat complexity and concomitantly the diversity of the associated fauna. Yet, the scarcity of quantitative studies to test this hypothesis is evident.

In Morrocoy National Park (MNP) live stands of *A. palmata* are rare, despite large patches of dead colonies being common in exposed reefs with strong wave energy. Recently, Martínez and Rodríguez-Quintal (2012) recorded the presence of this branching coral in Cayo Sombrero and they found a predominance of adult and juvenile size colonies with a low impact from partial mortality, bleaching and no signs of diseases. However, factors such as sediment accumulation affected 47.5% of the colonies, followed by algae overgrowth (37.5%), damselfish territories (35%) and anchor damage (22.5%). These findings clearly indicate that this species has managed to survive for decades, despite MNP being subjected to a number of human impacts such as sedimentation, urban development and chronic pollution (Cróquer & Bone, 2003). While different studies have evaluated the structure and distribution of fish communities in MNP (Rodríguez & Villamizar, 2008), no previous comparisons between the organisms associated with live and dead *A. palmata* zones have ever been conducted. This paper addressed a comparison between fish and benthic assemblages associated with dead and living stands of *A. palmata* to test if changes in the abundance and species composition of these assemblages were correlated with the condition (dead or alive) of *A. palmata*.

MATERIALS AND METHODS

Study site: The Morrocoy National Park (MNP) is a coastal marine park located in the west central coast of Venezuela (10º53’04’’N - 68º12’46’’W), in Golfo Triste region between Tucacas and Chichiriviche populations (Rodríguez & Villamizar, 2008). Surveys to assess the condition of *A. palmata* stands and the fish and benthic communities were conducted at Cayo Sombrero, a key located at Morrocoy National Park (MNP). Previous surveys indicate the presence of *A. palmata* to the northwest and the southeast leeward areas of this reef site (Martínez & Rodríguez-Quintal, 2012).

***Acropora palmata*:** We determined the status of *A. palmata* colonies in October 2012, by counting every colony within four 10m long by 1m wide ($10m^2$) belt transects conducted in two different zones at Cayo Sombrero. One of the zones was dominated by live *A. palmata* colonies and the other zone was dominated by dead stands of *A. palmata*. The linear coral cover of all species was recorded at each zone. All *Acropora* colonies were quantified and classified to determine colony size, using digital images that were analyzed with Image Tool v. 3.0, establishing coral area from each colony. Additionally, the fish and benthic macrofauna communities associated to *Acropora* zones were assessed in both sites.

Fish community: The coral reef fishes were surveyed in both live and dead *Acropora* zones using the method of Bortone, Hastings and Oglesby (1986), conducting visual census over *A. palmata* colonies. This visual census technique was based on the best estimation by eye of fish species abundance that were associated with live and standing dead *Acropora* areas.

Benthic community: Six sediment samples were collected around live and dead *Acropora* colonies, using a PVC 7cm diameter cylinder. The samples were preserved in 10% formalin and washed in the lab over a 0.5mm mesh sieve. The material retained on the sieve was fixed with 70% ethanol solution and sorted under a stereo microscope for counting and identification of macrofauna groups associated to *A. palmata* colonies. Additionally, we identified the main polychaete and peracarid families because of the abundance recorded by these two groups inside the benthic communities.

Statistical analyses: The community structure of live and dead *Acropora* zones were evaluated by the relative abundance and mean density of *A. palmata* as well as reef fishes and benthic macrofauna. Changes in the fish and macrofauna assemblages across colony condition were analyzed by Non-Metric Multidimensional scaling (nMDS) calculated from the Bray-Curtis similarity matrix, using square root transformed data. Differences in fish and macrofauna composition between colony conditions were assessed using permutation-based multivariate analysis of variance (PERMANOVA, Anderson, 2001), based on the Bray-Curtis similarity index and using 9 000 randomizations. All these analyses were performed with PRIMER v.6.0 and Statistix v.8.0.

RESULTS

***Acropora palmata*:** The dead *Acropora* zone was dominated by standing dead *A. palmata* colonies (75%), followed by a group of zoanthids (20%) and sand substrate (5%), while the live *Acropora* zone showed that the dominant category was living *A. palmata* (60%), followed once again by zoanthids (30%) and sand substrate (10%). A total of 62 live and dead *A. palmata* colonies were found and assessed within 10m^2 belt transect (Table 1). Mean densities for live and dead colonies were 0.27±0.15 ind/10m^2 (mean±standard deviation) and 0.61±0.52 ind/10m^2, respectively. In addition, size structure was only represented by adult *A. palmata* with sizes varying between 1 900 and 5 500cm^2 for dead colonies and between 1 800 and 3 600cm^2 for live colonies.

TABLE 1
Assessment of live and dead *Acropora palmata* zones in Cayo Sombrero coral reefs, Venezuela

	Acropora palmata zones	
	Live	Dead
Number of Colonies	19	43
Density (ind/10m^2)	0.27 ± 0.15	0.61 ± 0.52
Size (cm^2)	2600 ± 1700	3300 ± 1200

*Live: Zones dominated by living colonies (60%) and Dead: Zones dominated by standing dead colonies (75%). Data is shown as mean ± DE of n= 4 transects of 10 m^2.
* Vivo: zonas dominadas por colonias vivas (60%) y Muerto: zonas dominadas por colonias muertas (75%). Los datos muestran el promedio±E.E. de transectos (n=4) de 10 m^2.

Fish community: A total of 21 species belonging to nine families with similar fish diversity between live and standing dead *A. palmata* colonies were recorded (Table 2). The total fish abundance consisted of 209 individuals in live *A. palmata* zones and 156 individuals in standing dead *A. palmata*. Density in the live zone was 0.10±0.17 ind/m^2 and 0.07±0.12 ind/m^2 for skeletons of *Acropora* colonies. The reef fish families in the dead zone were dominated by Pomacentridae with a relative abundance of 52.56%, followed by Labridae with 26.28%. Some families such as Acanthuridae were mainly present in dead *Acropora* areas. Additionally, the live *Acropora* zone was dominated by Pomacentridae with relative abundance of 47.85%, followed by Labridae with 36.36%,

TABLE 2
Fish community in live and dead *Acropora palmata* zones at Cayo Sombrero coral reefs, Venezuela

	Acropora palmata zones	
	Live	Dead
Number of Fish Species	16	15
Total Fish Abundance (Number of Individuals)	209	156
Fish Density (ind/m^2)	0.10 ± 0.17	0.07 ± 0.12
Relative Abundance of Fish Families (%)		
Blenniidae		1.28
Aulostomidae	0.96	0.64
Chaetodontidae		1.92
Acanthuridae	0.48	10.90
Lutjanidae	2.87	
Scaridae	4.78	5.13
Haemulidae	6.70	1.28
Labridae	36.36	26.28
Pomacentridae	47.85	52.56

* Abundance of Fish Families expressed as %. Live: Zones dominated by living *A. palmata* and Dead: Zones dominated by standing dead *A. palmata*. Density is shown as mean ± DE of n= 4 transects of 10 m^2.

and some families such as Haemulidae and Lutjanidae recorded their highest abundance over these live colonies (Table 2).

Ordination analyses (nMDS) revealed similar fish communities associated with live and dead *A. palmata* colonies (Fig. 1). PERMANOVA results supported the nMDS ordination and showed that fish composition was not significantly different between live and standing dead *Acropora* zones (PERMANOVA, Pseudo-F=0.72, p(PERM)= 0.57). On the other hand, the main fish species observed in live *A. palmata* were *Thalassoma bisfaciatum* (<2 ind/m^2), followed by *Stegastes planifrons* with densities <0.80 ind/m^2 and *S. adustus* with <0.70 ind/m^2 (Fig. 2). Dead *Acropora* zones were dominated by *S. adustus* (<1.50 ind/m^2), *T. bisfaciatum* (<1 ind/m^2) and *Microspathodon chrysurus* (<0.50 ind/m^2).

Fig. 1. Multidimensional Non-Metric Ordination diagram (nMDS) based on Bray-Curtis similarities. Data represented by the abundance of fish families over Live and Dead *Acropora* zones.

Benthic macrofauna: A total of 12 taxonomic groups were identified in the benthic macrofauna inhabiting the reef sediments, recording a similar diversity between live and dead *Acropora* zones (Table 3). The total abundance of the overall macrofauna was higher around dead colonies (88 individuals) compared to living colonies (68 individuals), showing the highest mean density of macrofauna in standing dead *Acropora* zones (160±133 ind/m^2) compare to live *Acropora* (124±126

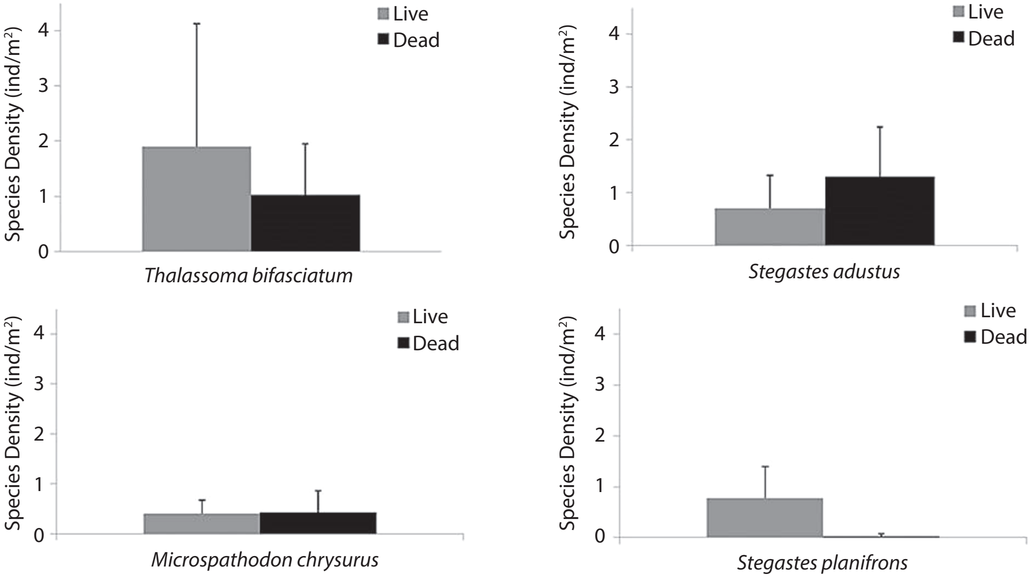

Fig. 2. Density of the main fish species in live and dead *Acropora* zones at Cayo Sombrero coral reefs. Bars represented by the standard error.

TABLE 3
Benthic macrofauna community associated with live and standing dead *Acropora palmata* at Northwest and Southwest Cayo Sombrero, Venezuela

	Acropora palmata zones	
	Live	Dead
Number of Taxonomic Groups	10	9
Total Macrofauna Abundance (Number of Individuals)	68	88
Macrofauna Density (ind/m^2)	124 ± 126	160 ± 133
Abundance of Taxonomic Groups (%)		
Echinoderms		1.14
Gastropods		1.14
Bivalves	4.41	6.82
Sipunculids	4.41	6.82
Cnidarians	1.47	2.27
Copepods	1.47	
Molluscs	1.47	
Ostracods	1.47	
Decapods	5.88	2.27
Nematodes	7.35	10.23
Peracarids	33.82	39.77
Polichaetes	38.24	29.55

* Live: Zones dominated by living colonies and Dead: Zones dominated by standing dead colonies. Density is shown as mean ± DE of n= 6 sediment samples.

ind/m^2). Also, the identified taxonomic groups were mostly represented by peracarid crustaceans, with relative abundance >33%, and polychaetes, with relative abundance >29% for both conditions. On the other hand, the remaining benthic macrofauna were relatively rare, comprising <11% of the total in each of the zones (Table 3).

The peracarids were the most abundant group within the benthic macrofauna and they were only represented by three families, from which Isaeidae family was dominant (>250 ind/m^2) in live and dead *Acropora* zones, followed by Melitidae (>50 ind/m^2) and Sphaeromatidae (>25 ind/m^2) (Fig. 3). Additionally, the "unidentified" group represented those crustaceans that were unable to be classified into families; however, they belonged to the Tanaidacea and Cumacea orders, with densities >25 ind/m^2 for live and dead zones. The nMDS ordination revealed a similar peracarid community associated with live and standing dead *A. palmata* condition (Fig. 4). We found no differences between assemblages present in live and dead *A. palmata* stands (PERMANOVA, Pseudo-F=1.15, p (PERM)= 0.39).

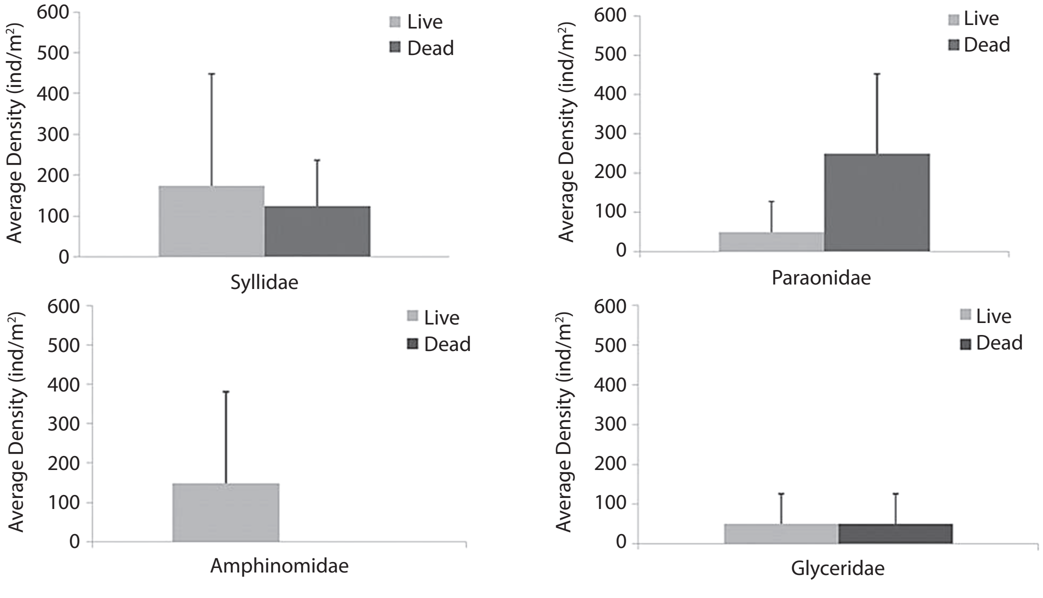

Fig. 3. Average density of the main peracarid families identified around live and dead *Acropora palmata* at Cayo Sombrero. Unidentified: families not recognized. Bars represented by the standard error.

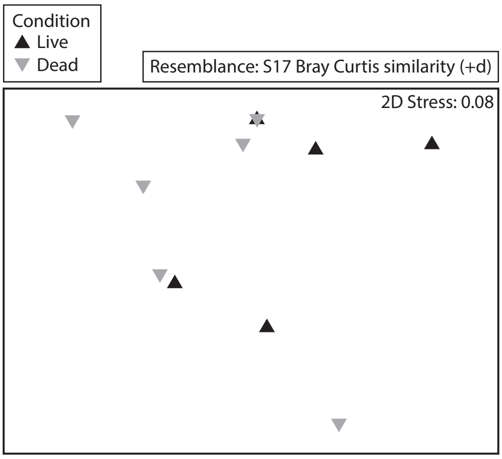

Fig. 4. Multidimensional Non-Metric Ordination diagram (nMDS) based on Bray-Curtis similarities, with data represented by the abundance of peracarid families over Live and Dead *Acropora* zones.

Twelve families of polychaetes were identified in the macrofauna, being dominated by Paraonidae (248±203 ind/m^2) around dead *Acropora* colonies and Syllidae (174±273 ind/m^2) around living colonies (Fig. 5). The Amphinomidae family was only present around living colonies (149±231 ind/m^2), while Glyceridae reveled the same densities for both colony condition (49±77 ind/m^2). As well as peracarids, the nMDS showed a similar polychaete community between live and standing dead *A. palmata* (Fig. 6), forming two main groups that were defined by the abundance of Syllidae and

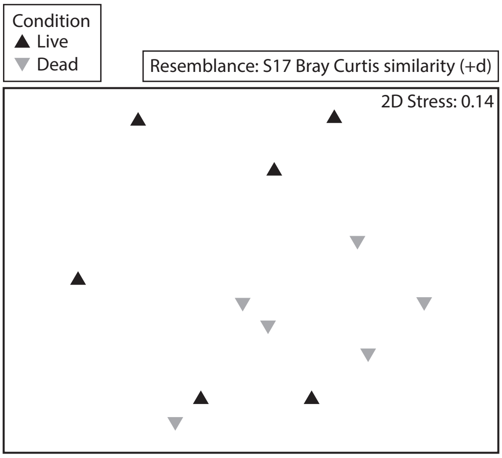

Fig. 6. Multidimensional Non-Metric Ordination diagram (nMDS) for abundance of polychaete families between Live and Dead *Acropora palmata*.

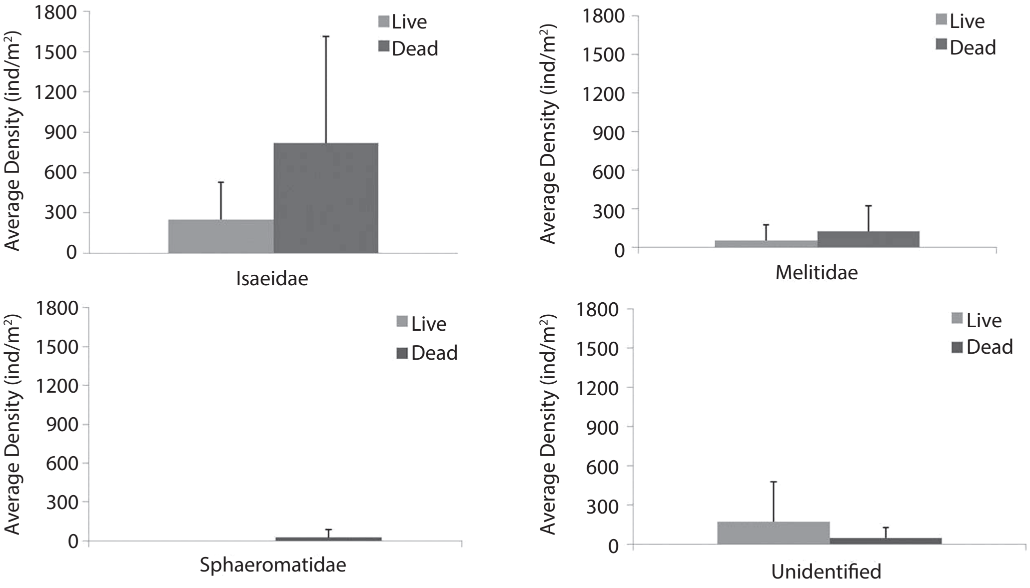

Fig. 5. Average density of the main polychaete families identified around live and dead *Acropora* colonies at Cayo Sombrero. Bars represented by standard error.

Paraonidae families. There was not significant differences between the polychaete assemblages for both conditions (PERMANOVA, Pseudo-F=1.88, p (PERM)=0.08).

DISCUSSION

The complex structure provided by the branching species *A. palmata* has been reported as potential shelter for different reef associated organisms (Lemoine & Valentine, 2012), forming unique habitats with high ecological values at the Caribbean coral reefs. However, over the past few years, many reef areas in Morrocoy have experienced a significant loss of Acroporid corals, leading to the eventual formation of large areas consisting of standing dead *A. palmata*. Thus, live and dead stands of *A. palmata* in Sombrero represent two types of habitats that nearly provide the same structural complexity. Our data showed that the density for live *A. palmata* at Cayo Sombrero was lower than some coral reefs located at Los Roques National Park, such as Cayo Pirata, Crasquí, Carenero, Gran Roque and Cayo de Agua (>0.69 ind/10 m^2) (Zubillaga, Márques, Cróquer & Bastidas, 2008); nevertheless, many other coral reefs such as Boca de Cote, Boca del Medio, Sebastopol and Madrisquí in Los Roques had lower densities (<0.13 indv/10 m^2) than those reported in Cayo Sombrero.

Due to the significant importance of colony condition within a reef environment, we established the hypothesis that those zones dominated by dead *A. palmata* could be mainly composed of herbivorous species, while those zones with live *A. palmata* could be composed of other species such as corallivorous and benthivorous species which feed upon living tissues. Although we set all these predictions based on the colony status, the fish and benthic macrofauna community structure did not show significant differences between live and dead *A. palmata*. Herbivorous fishes were the most abundant condition in both *Acropora* zones, being dominated by the Pomacentridae family which is typically associated with *A. palmata* colonies regardless its status. Species in this family are known to defend their territory which includes a shelter hole, grazing area and nest site, showing at the same time some specificity in their relationship with live and dead colonies (Chasqui-Velasco, Alvarado, Acero & Zapata, 2007).

The dominant species recorded at Cayo Sombrero were *T. bisfasciatum*, *S. adustus*, *M. chrysurus* and *S. planifrons* for both live and dead *A. palmata* zones. These fishes have also been reported by Rodríguez and Villamizar (2008), who found similar results at the same study site, mentioning that the abundance of *T. bisfasciatum* and *S. adustus* could be positively correlated with the substrate type, being mainly associated with dead coral zones covered by algae. Also, these species are very abundant and common in exposed areas with strong wave impact and currents (López-Ordaz & Rodríguez-Quintal, 2010), as was the case in the *Acropora* shallow reefs at Cayo Sombrero.

Additionally, the benthic macrofauna revealed a similar richness and density compared to other coral reefs such as Madrisquí, Sebastopol and Boca del Medio at Los Roques, where it has been reported between nine and 14 macrofauna groups belonging to reefs sediment around *Montastraea faveolata* colonies, with densities >500 ind/m^2 (Bone & López-Ordaz, 2009). Also, the benthic macrofauna did not show significant differences between live and dead *Acropora* zone, however, we observed that live zones harbored a low density of benthic organisms compared to the dead zone. This low density could be the result of benthivorous fishes which dominate live *Acropora* reefs, and have a feeding preference for the macrofauna associated with living coral sediments. On the opposite side, the extensions of standing dead *A. palmata* often harbor herbivorous fishes that only consume the primary producers, leading to the establishment of benthic macrofauna and increasing its abundance around dead colonies.

The most important taxonomic group in terms of abundance was represented by peracarid crustaceans, which are characteristic of the calcareous sediment macrofauna, presenting a spatial distribution that is determinate by several environmental factors such as temperature, chlorophyll concentration and sediment salinity (Escobar-Briones & Jiménez-Guadarrama, 2010). Moreover, the main peracarid families identified around *A. palmata* colonies were Isaeidae and Melitidae, belonging to the amphipod group, which are often related to coral reef sediments and usually record a high abundance and diversity because of the breeding success and gregarious patterns presented by these families (Winfi & Escobar–Briones, 2007). Besides, the live *Acropora* area showed the lowest density of peracarid families, possibly because of the presence of benthivorous fishes that include in their diet a large variety of crustaceans (Randall, 1967).

As well as crustaceans, the polychaete worms were also one of the most abundant groups of macrofauna, which typically present both spatial and temporal variations due to the community natural oscillations that occurs through the life cycles of these benthic species (Bone & López-Ordaz, 2009 unpublished). Some polychaete families such as Amphinomidae were only present around living *A. palmata* colonies, most likely because of the diet preferences. These worms are common in living coral reef zones, being considered as important predators of sessile organisms such as sponges, corals and anemones (Yánez-Rivera, 2009).

A. palmata colonies may function as a physical complex structure, providing shelter and protection for fish and benthic macrofauna communities that are associated with these branching colonies in Cayo Sombrero coral reefs. Although we observed some community variations between live and dead *Acropora* zones, statistically we did not find significance differences between both conditions, thus, the reef associated species are unlikely related to whether or not live tissue is present, but instead the absent or presence of the physical structure of *A. palmata* could be the key factor that enables the establishment of different species associated with reef environments.

ACKNOWLEDGMENTS

We are grateful to the Marine Community Lab of the Universidad Simón Bolívar for giving the necessary equipments and instruments to support this project. We also appreciate the assistant of I. Ortega for the taxonomic knowledge and the field assistant provided by C. Brett and A. Guerra during this research. Thanks to the CEO (Centro de Estudios Oceanográficos) of the Universidad Simón Bolívar for providing lab facilities during the field trips.

RESUMEN

Evaluación poblacional de *Acropora palmata* (Scleractinia: Acroporidae): relación entre el hábitat y especies de arrecife asociados. Hace tres décadas, *Acropora palmata* fue una de las principales especies de coral constructoras de arrecifes a lo largo del Caribe, formando un componente esencial de la complejidad estructural disponible en los hábitats arrecifales someros. Estas colonias todavía proveen microhábitats para el asentamiento, alimentación y refugio de muchas especies de vertebrados e invertebrados. El declive reciente de *A. palmata* ha sido precedido por una pérdida significativa de heterogeneidad espacial y se piensa que ésta reducción ha producido una disminución importante en la diversidad de especies. Los estudios señalan que las colonias muertas o vivas de *Acropora* que sostienen diferentes comunidades de bentos y de peces son escasas. El estado de las colonias de *Acropora* y sus especies asociadas fueron evaluadas en Octubre de 2012, en dos zonas arrecifales diferentes de Cayo Sombrero, Venezuela. Censos visuales de la abundancia de especies de peces y el número de individuos de la macrofauna fueron también registrados para ambas zonas, tanto vivas como muertas. Las colonias vivas presentaron la menor abundancia (<31%). En ambos sitios la comunidad de peces fue dominada por los peces damiselas (<53%) y lábridos (<36%); la macrofauna bentónica por crustáceos peracáridos (<40%) y poliquetos (<38%). Las comunidades de peces y bentos no mostraron correlación con la condición (vivo o muerto) de los hábitats de *Acropora*; posiblemente las estructuras ramificadas proveen el refugio y protección necesario sin importar si están vivos o muertos. Una mayor replicación es necesaria para probar este resultado inesperado.

Palabras claves: *Acropora palmata*, arrecifes coralinos, Caribe, macrofauna bentónica, peces arrecifales.

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Genet and reef position effects in out-planting of nursery-grown *Acropora cervicornis* (Scleractinia:Acroporidae) in Montego Bay, Jamaica

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Received 15-VIII-2013 Corrected 14-III-2014 Accepted 24-III-2014

Abstract: The reef-building coral *Acropora cervicornis* was a dominant ecosystem element on the Caribbean reef until the 1980s, when it declined by some 97% due primarily to anthropogenic ecosystem changes and disease. This branching species expanded its colony footprint and achieved local dominance largely through fragmentation and regrowth, thus is suited to nursery culture towards restoration. In this experiment, fragments of *Acropora cervicornis* of four lineages or *genets* were followed and measured for growth and health over 12 months in 2006 and 2007 on buoyant drop-loop line nurseries at one shallow and one deep fore-reef site in Montego Bay, Jamaica. Sixty-five of these corals were then out-planted to wild reef sites of similar depth and condition to their respective nurseries and monitored photographically for 11 months through 2007 and 2008. A period of rapid death was seen in the out-planted material at both sites over the first four months, followed by a period of relative stability or recuperation. *Hermodice carunculata* predation was the primary problem in the shallow fore-reef, and was combined with a banding syndrome at the deeper site. This syndrome was noted in the samples prior to planting, during a one week storage period on the seafloor. Continued slow decline occurred in the subsequent seven months in the shallow fore-reef site; however, regrowth was noted in the deeper site in the remaining material. Including these losses, final total live coral length was more than fourfold greater than the initial wild harvest: a net increase through multi-stage propagative restoration or coral gardening. Returns were noted particularly in the faster-growing genets of the nursery and larger planted corals tended to retain more material at eleven months, suggesting that propagative restoration programmes invest in stronger genets and larger corals. Adaptive management and maintenance gardening of the planted material and reef would likely have greatly improved outcomes. Rev. Biol. Trop. 62 (Suppl. 3): 95-106. Epub 2014 September 01.

Key words: *Acropora cervicornis*, coral gardening, coral restoration, coral propagation, *Hermodice carunculata.*

The *Acropora* of the tropical western Atlantic are in jeopardy, as are the ecosystems dependent on the intricate branching habitat or defensive reefal accumulations developed by these corals historically (ABRT, 2005). *Acropora cervicornis* was the dominant coral from 5m through 20m depths, an area coined by Goreau (1959) as the *Acropora cervicornis* zone, through most of the Caribbean prior to the early 1980s. Today this species is sparse throughout its range with only a handful of such thicketed habitats remaining and some authors paint a bleak picture for its future. They suggest that a naturally relatively low level of sexual reproduction, a lack of larger spawning animals, the distance between them, chronic stress and the lack of planular settlement habitats has led to an allee effect. Under this effect replacement through sexual reproduction is no longer occurring, yet adult death is continuing in a downward spiral to local extirpation, if not extinction (Stephens & Sutherland, 1999; Knowlton, 2001; Miller & Szmant, 2006).

Several authors have explored the potential for coral gardening to begin to preserve or restore these keystone corals (Bowden-Kerby, 1997; 2001; Rinkevich, 2008). Coral gardening suggests using multi-stage processes akin to silviculture for coral ecosystem restoration, wherein small amounts of coral are harvested from the wild reef and grown in nurseries. After a period of growth these may then be refragmented, propagated for further nursery growth, planted out in reef restoration or used in experimentation, with no further collection from the wild stocks (Bowden-Kerby, 1997; Epstein, Bak & Rinkevich, 2003; Rinkevich, 2006; Shafir & Rinkevich, 2008). As such, an initial harvest may be very small yet provide large amounts of propagated material. Bowden-Kerby (2001) and Ross (2013a) both report more than an order of magnitude increase in useable *A. cervicornis* material within a single year of nursery growth. It is interesting that corals that grow so well in the nursery are still in decline in the wild (Miller, Bourque & Bohnsack, 2002; ABRT, 2005; Alcolano, Caballero & Perera, 2009). This suggests that one may separate the corals from their problems by simply separating them from the substrate: their issues appear to be particularly benthic and not waterborne or intrinsic to the corals themselves. Planting this growth from the nursery to the reef is the next step in elucidating these issues and resurrecting the Caribbean's reefs.

This work is the final in a series of studies in nursery growth of *A. cervicornis* wherein strong differences in growth rate and susceptibility to temperature, fouling and abrasion stresses were noted between genets. In these genets the fastest growers tended to also be the least susceptible to stress (Ross, 2013c), so, here we out-plant propagated corals and follow their progress to see if the differences seen in the nursery hold in the wild. The experimental queries of this work include: i) following the progress of out-planted corals grown in a novel nursery design to assess the efficacy of nursery propagation in ecosystem restoration, ii) following each of the genets to assess whether the relative strength and weakness shown in the nursery carries to the wild reef and its various and different issues.

METHODS

In April 2006, two Buoyant Drop-Loop Line (BDL) nurseries (Ross, 2013a) were set at each of two sites in Montego Bay, Jamaica: a large sand area adjacent to a large reefal stone at 15m depth at the popular dive site Widowmaker's Cave at 18°29'51.59"N, 077°56'5.00"W, and in a sand-channel of the well developed buttress formations of the Airport Reef dive site at 18°29'50.83"N, 077°55'56.24"W. These nurseries were each populated with 5 unbranched 5cm fragments from each of four presumed distinct (Ross, 2013b) coral genets marked with colour-coded wires (N=80). These corals were partially harvested in June 2007 and set to new nurseries, with the remaining nurseries moved intact to concrete block-anchors immediately to one side where they were maintained for a further five months.

Hurricane Dean passed the western tip of Jamaica on August 20, 2007. These maintenance nurseries were sequestered from August 19 for approximately one week by placing them into sediment-free hollows in the reef. Shortly after this storm these corals were planted to adjacent clean reef substrate.

At the deep nursery site the coral nurseries were tucked into a shallow depression immediately adjacent to the nurseries that was clear of sediment; however, there was macroalgae present. Out-planting occurred prior to September 3, 2007 to this same reefal stone at depths of between 14m and 12.5m. No live or dead *A. cervicornis* was present on the reefal stone, though it was present on the continental shelf some 30m away and no active disease was noted in this natural population.

For planting, diseased portions were cut away with clean side-cut pliers 1cm to 2cm ahead of the advancing disease front, as a banding syndrome (likely WBD1) had beset many samples during sequestration. Where the disease front was in the middle of the coral, it was cut into two or more independent fragments, 1cm to 2cm of live-tissue waste was cut away before the advancing disease front in this experiment. In trials at the Doctor's Cave Beach Club and elsewhere in Montego Bay waste of <5mm has proven ample (unpublished), though the author recognizes that every infection or location may be different.

Galvanized masonry nails were immersed in seawater and left outdoors in a mesh bag until they developed a uniform flat grey patina, for approximately two weeks. Fresh galvanized wire or nails will kill the contacting coral tissue; however, aging the galvanizing coating has proven effective in eliminating this contact toxicity in propagated *A. cervicornis* planting trials at the Doctor's Cave Beach Club, Montego Bay, Jamaica (unpublished).

To plant each coral, one pre-aged nail was driven into an exposed, upper portion of reefal stone or dead coral head atop the planting stone and the area around that nail picked clean of macroalgae or any accumulated sediment, though the specific planting locations were chosen to be cleaner points of bare stone. A coral was then cut from the nursery line at random, clipped of any disease and set to the nail with live tissue touching both the nail and substrate to promote attachment. The genet-indicator wire was checked by gently breaking away the thin coral venire at its free end to see its colour. A nylon cable-tie of that same colour was then used to secure the coral to the nail. As necessary, aged galvanized (steel) binding wire was used to make the fragment tight and still. Fragments tended to be horizontal; however, as they were on the upper points of the reef structure they contacted the substrate at a single point. Where a sample was cut into two or more segments to remove disease these were set bundled together, straddling the anchoring nail. Corals were set with a reasonably even distribution around the stone, though somewhat concentrated to the eastern end. The corals were mapped and numbered for repeat monitoring. Twenty-nine corals were planted and followed at this reefal stone.

The nurseries within the buttress system were anchored at 7m depth, thus the nursery corals were growing elevated to between 6.2m and 5.5m from the surface. For Hurricane Dean these shallow nurseries were bundled into a clean, shallow cave at 8m depth within the buttress system. After the storm, these bundles were moved atop a partially urchin-grazed buttress-end at 3m depth at the top, surrounded by caverns on the shoreward sides and a large sand patch on the seaward side all at 9m depth making the planting area something of an island at 18°29’51.49”N, 077°55’57.35”W. This stone held two natural colonies of *A. cervicornis*, both of which were small and stressed, the larger (<0.25m^2) hosting a *Stegastes planifrons* nest. Between 3m and 5m depth and concentrating on the southern face of the planting stone was an area of reasonably urchin- and fish-grazed stone with occasional live coral and macroalgae. Several *Diadema antillarum* urchins were present.

Small limestone projections, knobs and nodules are common on such shallow patch reef-tops, remnants of small massive and branching corals long dead. In coral planting, such knobs were held firmly and shaken to ascertain the knob's strength given boring organisms, primarily *Cliona* sponge colonization: if stone strength was insufficient the piece would break away. For each chosen planting point a coral was cut at random from the nursery bundle and its genet indicator wire exposed. The coral was then fastened against the tested reef nodule with a cable-tie of the genet's indicator colour. The planted corals were then mapped and numbered. Thirty-six corals were planted and followed at this site.

The planted corals of each site were each photographed in turn according to their mapped location and number with a scale bar or measuring tape from the angle judged by the photographer to provide the largest size for each sample. The cable-tie's colour was visible in the photograph. Photo-sessions occurred three times over the first four months (September 3, October 23 and December 22) then again at 11 months (shallow site on July 30 and deep site on August 8). A supplemental set of photographs was taken on September 14 at the deeper site to observe the advancing disease, though this is not discussed in detail here.

The photographs were evaluated using CPCe's Accumulated Lengths function taking both total skeletal and living tissue lengths. Live and dead lengths were taken for each branch and sources of death were assessed, where possible. No consideration was made for error associated with parallax (Ross, 2012a).

Preliminary analysis of CPCe data was carried out using Microsoft Excel software for Macintosh. Statistical tests, including ANOVA, non-parametric correlations and graphing were performed using SPSS18 statistical software. Nonparametric correlations between i) apical polyp count, ii) worm bite count, iii) active disease front count, iv) total live plus dead length, v) dead length and vi) living coral length were assessed using Spearman's rho. Correlations between Log base-10 transformation of the initial live and the final live coral lengths were provided by a Pearson's correlation. General Linear Model (GLM) ANOVA testing used the Natural Log transformed live coral length data with the factors site, visit and genet, hypothesizing:

1. There is no significant difference in living coral length between the deep and shallow sites,
2. There are no significant differences in living coral length between the different visit dates,
3. There are no significant differences in living coral length between the different coral genets,
4. There is no significant interaction between the site, visit and/or genet with regard to living coral length.

RESULTS

The shallow site saw greater survivorship than the deeper site. Sixty-five corals were set in September 2007. Forty-six (70.8%) were still in place and 35 (53.8%) were still alive by the summer of 2008. Of the 36 corals planted at the shallower site, eight were missing and much partial mortality was observed, but all 28 corals present were alive at 11 months (77.8%). At the deeper reefal stone site, of the 29 samples set, 11 were lost (37.9%) and 11 died entirely, leaving only seven surviving (24.1%, Table 1). Damages were observed by the first measurement and continued through the first four months with every coral in this experiment suffering partial mortality.

At both sites partial mortality was substantial, with 47% of tissue lost in the shallow site and 91% in the deep (Table 3). Losses were continuous from planting through the final measure in the deep site even after the initial pulse of predation and disease; however, the shallow site saw a short period of growth prior to its period of decline (Table 3). The deep site saw a rapid decline early, with disease killing corals entirely. However, after an initial pulse, the continued decline was primarily through remaining or continuing disease and sample loss after the December visit. Lost corals may have been attributed to waves in the shallow site, though curious or clumsy spear-fishermen and recreational snorkelers may also have

TABLE 1
Partial and full mortality and losses at 11 months per site and per genet

	Genet	Count	Some Live	All Dead	Missing
Shallow	Orange	9	8	0	1
	White	9	7	0	2
	Blue	10	8	0	2
	Green	8	5	0	3
	Total	36	28	0	8
Deep	Orange	6	3	3	0
	White	7	1	3	3
	Blue	9	3	2	4
	Green	7	0	3	4
	Total	29	7	11	11

TABLE 2
N-values changing through the experimental period with sample loss

Date	Depth	N
1. Sept. 3	Shallow	36
	Deep	29
2. Oct. 23	Shallow	36
	Deep	29
3. Dec. 22	Shallow	35
	Deep	29
4. Jul. 31/Aug. 8	Shallow	26
	Deep	18

TABLE 3
Total live lengths per location

Visit	Shallow (cm)	Shallow (% change)	Deep (cm)	Deep (% change)
1	2 505.7	/	1 684.5	/
2	2 589.2	+3.33	304.0	-81.95
3	1 741.3	-32.75	217.2	-28.55
4	1 338.9	-23.11	149.6	-31.12
Totals	-1 166.8	-46.57	-1 534.9	-91.12

* N-values are in Table 2.

played culprit. At the deeper site an Antillean Z-trap (fish trap) was removed from atop the reefal stone and samples on one occasion, and the location is a popular recreational SCUBA site. Later in the experiment the decomposition of the distal skeleton was rapid, such that dead samples may have simply broken or rotted away.

The September 14 interim observations at the deep site show disease starting either at the benthic contact point, possibly associated with damages incurred during planting, or at the branch tips suggesting vectoring or facilitation by *Hermodice carunculata* (Fire-Worm) with pathogen entry at the bite or lesion. *H. carunculata* attacks were common in this interim visit but were obscured by more general (disease) death by the time of the formal monitoring visit in October. There was no indication that disease started at the points where disease was cut away as an advancing disease front was not necessarily discernable from a *H. carunculata* bite.

The trend over time for mean live coral length is great initial partial mortality, followed by a levelling out in mortality and slight growth at the deep site but a continued slow reduction at the shallow site (Table 4). In the month after planting, the shallow buttress site saw growth, with a per-coral average increase of 3.4%, or 2.4cm per coral. However, in the following period *H. carunculata* worms found these new corals and consumed some 30.8% of the total crop over two months; an average of 22.2cm per coral. This site continued to decline slightly in average live coral length through the remainder of the experimental period through continued *H. carunculata* predation.

The deeper site saw damage almost immediately with disease present in the first photo. Between loss, disease and *H. carunculata* feeding this site’s mean coral length declined by some 82.6% in the first six weeks and a further 28.6% by December. However, from this greatly depressed state it was able to regrow by some 10.7% in the remaining seven months (Table 4) during which it was monitored.

TABLE 4
Gains and losses per location per visit as mean live lengths per coral, excluding lost samples

Visit	Shallow cm	Shallow % change	Deep cm	Deep % change	Deep cm excl. dead	Deep % change, excl. all-dead samples
1	69.6	/	60.2	/	60.2	/
2	72.0	+3.45	10.5	-82.56	-27.6	-54.15
3	49.8	-30.83	7.5	-28.57	-18.1	-34.42
4	47.8	-4.02	8.3	+10.67	+21.4	+18.23
Total	-21.8	-31.32		-86.21	-38.8	-64.45

* Percent change is the length difference between visits as expressed as percent grown or lost. N-values are in Table 2.

New apical polyp formation occurred in the initial period at the shallow site, often associated with healing cut-points or undocumented damage to apical areas from storage. They also formed on the branch trunk as they would in nursery corals and in areas associated with a worm bite or halted disease front. This did not occur immediately afterwards, but after an often-prolonged period of rest or healing, and often only once the dead portions had rotted or broken away. New apical formation was the source of restarted growth between the third and final visit as worm damage left few apical polyps for growth.

Both the shallow and deep sites saw an increase in the average number of apical polyps per coral between the third and final visits as the remaining tissue started to re-grow (Fig. 1). The difference between this and Table 3 at the shallow site was that, as apical polyp and branch formation continued, predation also continued.

A decline was noted generally through the experimental period in each genet. At the shallow site, Orange and Green lost 28% and 41% tissue respectively until day 110 (visit 3). Orange then held at 28% while Green declined by 61% by the final visit. Blue lost 21% of its average length by day 110 and declined a further 25% by the final visit. White also declined by 21% by day 110 but had regained an average of some 3.1cm per coral by the final visit (Table 5).

At the deep site, Orange again remained relatively steady between days 110 and 340, with 77% and 78% loss respectively. White and

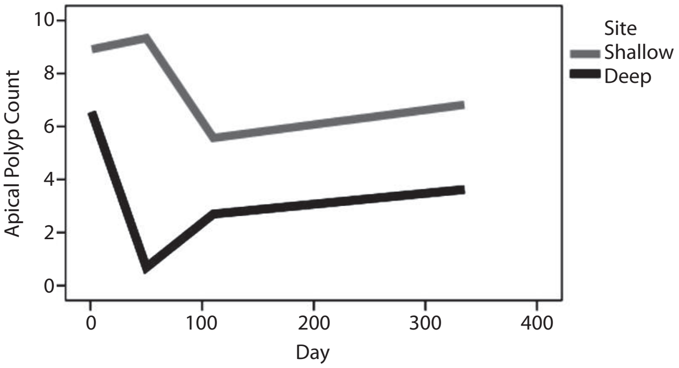

Fig. 1. Apical polyp counts over the 11 months of the experimental period. N= 29 at the deep site, N= 36 at the shallow.

TABLE 5
Advances and declines as mean lengths per genet per visit (V) in cm, excluding lost samples. N-values are in Table 2

	Genet	Living V 1	Living, V 3	% loss	Living, V 4	% loss	Dead, V 3	Dead, V 4
Shallow	1) Orange	91.58	65.05	28	65.56	28	34.61	28.76
	2) White	49.26	38.93	21	42.04	15	19.41	14.54
	3) Blue	60.35	47.86	21	45.53	25	29.38	10.45
	4) Green	79.33	46.69	41	31.18	61	32.45	25.62
	Total	70.13	49.63		46.08		28.96	19.84
Deep	1) Orange	63.07	14.29	77	13.97	78	34.46	18.77
	2) White	52.15	3.16	94	3.35	94	40.49	23.07
	3) Blue	59.94	6.61	89	10.47	83	39.95	24.84
	4) Green	65.92	7.13	89	0	100	42.45	21.83
	Total	60.27	7.80		6.95		39.34	22.13

* N-values are in Table 2.

Blue saw greater losses, losing 94% and 89% respectively at day 110, with White remaining steady through day 340 while Blue improved its average coral size by some 3.8cm per coral. Green expired entirely within the experimental period at this site. A marked decline in dead skeleton length was noted between days 110 and 331/340, by as much as or more than 50% in some cases, due to breakage and erosion.

General Linear Model (GLM) ANOVA testing (Adjusted R Squared 0.235) showed the live length to be significantly different between sites ($p < 0.001$), between different measurement visits ($p < 0.001$) and between genets ($p = 0.008$). Post hoc testing showed that Blue, White and Green genets made up the subset with the least coral length and White, Green and Orange made up the subset with the most coral. As may be seen in Figures 4 and 6, these post hoc differences were largely associated with uneven initial amounts of coral and the particular failure of the Green genet at both sites. A significant interaction between site and day ($p = 0.022$) speaks to rapid disease onset in the early measurements at the deeper site and *H. carunculata* attack in between visits at the shallower site.

The differences between the genets seen in Table 4 are illustrated in Figure 2, whereby a rapid decline in live coral length is seen in the deep site in all genets with a continued fall in the Green genet to zero, but a mild increase in the Blue genet to the final visit. In the shallow site a brief period of growth may be seen in the White and Orange genets and a mild decline in the Green and Blue, followed by a general decline in all genets. After this early decline, the Blue genet saw a further mild decline while the Green genet suffered a much more pronounced decline and the White genet began to regrow. In both cases the Orange genet remained relatively stable after the initial decline, with no particular re-growth or further decline after day 110. Green declined generally throughout and could be described as the weaker performer based on this figure, whereas the Blue and White saw some improvements in mean length and could be described as the stronger performers.

There was no correlation between recent *H. carunculata* attack and length of living tissue occurring through the 11 months (Spearman's rho $r = -.064$, $p = 0.356$). This was in part due to the worm's apparent lack of preference in coral size, but also that once the coral was attacked the amount of living coral for assessment was reduced. Similarly, a strongly negative correlation occurred between *H. carunculata* bites and the apical polyp count (Spearman's rho $r = -0.333$, $p < 0.001$) as the worms actively ate the branch tips.

The worms in this reef patch were large, the largest single bite being 10.6cm long and bite lengths averaging 3.2cm overall. Worm

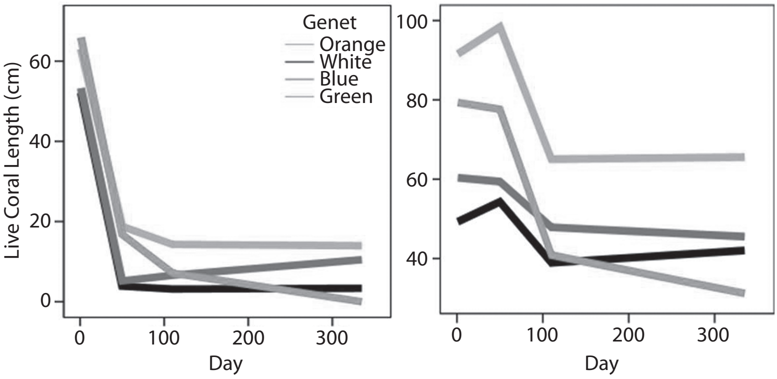

Fig. 2. Mean length of living coral per genet excluding lost samples over the 11 months of the experiment, (A) at the deep and (B) shallow sites. The Y-axis and key apply to both A and B. N= 36 at the deep site, N=29 at the shallow.

bite count was positively correlated with the amount of dead coral (Spearman's rho r= 0.544, p <0.001) but not with the total coral size including live and dead lengths (Spearman's rho r= 0.199, p= 0.086) again suggesting that worm feeding preferences are not associated with the size of the coral. Worm attacks were prevalent in the deep site but were particularly problematic in the shallow buttress site (Fig. 3A) and were the primary factor limiting coral growth at the shallow site.

Disease was negatively correlated to living tissue length (Spearman's rho r= -0.396, p <0.001). This did not mean that disease tended to occur in smaller corals, but rather disease shortened the living portion of the coral for assessment. Similarly, the count of disease fronts was negatively correlated with the number of apical polyps (Spearman's rho r= -0.387, p <0.001) as apical polyps were either killed by the disease or associated with worm attacks. Worm attacks may have played a role in disease distribution, though worm bite count was not significantly correlated with the number of disease fronts in this experiment (Spearman's rho r= -0.025, p= 0.723). Disease front count was positively correlated with the length of dead skeleton (Spearman's rho r=0.520, p <0.001) as the disease was actively killing coral and producing dead skeleton. Disease front count was not correlated with the total amount of coral (Spearman's rho r= 0.051, p= 0.461) suggesting that disease susceptibility was not related to the size of the coral. Banding disease occurred occasionally in the shallow buttress site but was particularly prevalent on the deeper reefal stone where it was the primary killer of tissue and corals (Fig. 3B).

Figure 4A suggests that there is little difference between the genets with respect to worm attack, which may be expected in a coral reliant on rapid growth and overgrowth as its strategy for reef dominance: it would not invest much in chemical defences. Figure 4B suggests a weak trend towards Green being more susceptible to disease than the other genets. This would corroborate its general weakness, though Orange trends towards being the least susceptible to disease.

There was a significant positive correlation between the initial live and the final live coral lengths (Pearson r= 0.387, p= 0.023).

Occasional partial mortality with banding disease was seen where portions of the total

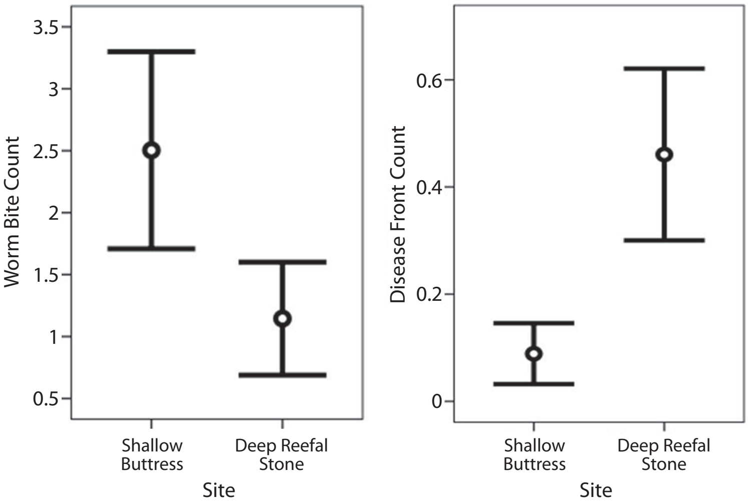

Fig. 3. Mean *Hermodice carunculata* bite count (A) and disease front count (B) per living coral per site pooled through the experimental period, showing the particular prevalence of disease at the deep site and of worm attack in the shallow (±the 95% Confidence Interval). N= 36 at the deep site, N=29 at the shallow.

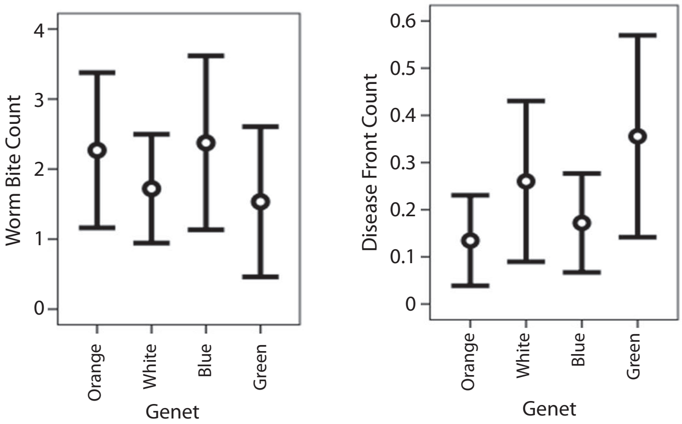

Fig. 4. Mean *Hermodice carunculata* bite count (A) and disease front count (B) per living coral per genet pooled through the experimental period, showing no significant difference between the genets in these factors (±the 95% Confidence Interval). N= 36 at the deep site, N=29 at the shallow.

coral were not killed. These were often sections that were somehow physically separated from the primary coral, e.g. sections broken away by fish-pot or diver damage or broken portions of the drop-loop overgrowth held attached by the underlying nylon line without tissue contact.

Bleaching occurred at the shallow site likely associated with the stress of sequestration, a reduction in depth from the shallow nursery at some 5m and 6m depth to the planting site at 5m to 3m depth and from the seasonal temperatures regardless of relocation activities, though these factors were not assessed in this study. Bleaching did not kill any samples and was only prevalent in the Green genet.

DISCUSSION

Publishing or inclusion of negative outcomes and experimental failures in reporting and published literature is necessary to build a larger picture of the lessons learned by the restoration and manipulation community (Edwards & Gomez, 2007), but also to shed larger light on the factors affecting corals generally including the reasons for presence or absence of a given species in a location. Failure may be as informative as success in restoration, as failure poses its own, arguably more interesting and fundamental questions.

At first glance this study may suggest that propagative coral enhancement of *A. cervicornis* is folly, as the successes of the nursery are not immediately translated into successes on the planted reef. In fact the opposite is true. The amount of coral initially harvested from the wild reef for 65 fragments at five cm each, some 325 linear centimetres, with nursery growth yielded some 4 277.5 centimetres for planting after a preliminary harvest for nursery re-sets and disease pruning. After 11 months, 1 521.15cm remained, giving a net increase of 1196cm or 4.7-fold from the initial wild harvest. Had this been a direct parent-to-planting relocation without an interim nursery phase, the 64.48% decline seen here would amount to some 115cm of total coral length remaining. Considering that this study and others (Knowlton, Lang & Keller, 1990; Bowden-Kerby, 2001) have found greater survivorship in larger disturbed or relocated corals, this final figure would likely have been less.

In this study the corals of the shallow, buttress-end reef grew and attached to the substrate for the first measurements, but by day 100 were heavily set upon by at least one large *Hermodice carunculata* (fire-worm) that consumed much of the branch and apical material, essentially halting growth. After the initial attack period these corals remained at a similar size, with no particular re-growth or further decline noted in the 11 months in mean coral length, though some apical growth and further worm bites were noted. This suggests that a critical mass of coral may be planted on an appropriate area that will maintain a reasonably steady population through predation in the absence of disease, storm or similar catastrophic change.

At the deeper reefal stone site fewer worm attacks were combined with a banding syndrome that was apparently inherent in the sediments, as per Patterson et al. (2002), and possibly exacerbated by macroalgae as this site was largely ungrazed (Nugues et al., 2004) as some corals were showing disease during preplanting storage, before they were planted to the reef. This combination possibly vectored or facilitated by the worms themselves (Sussman, Loya, Fine & Rosenberg, 2003) was able to kill some 91% of the total live coral length by day 340. This illustrates the importance of adaptive management and site choice (Rogers & Montalvo, 2004; Edwards & Gomez, 2007). Had adaptive management been employed, the shallow site would have seen particular investment in worm control, including active hunting and trapping. The deep reefal stone would have been abandoned and the remaining samples either returned to the nursery or moved to another location once disease was seen to be prevalent, likely in limited trials in a cooler season (Patterson et al., 2002; Jones, Bowyer, Hoegh & Blackall, 2004; Bruno et al., 2007). Such adaptive management is also an aspect of coral gardening (Rinkevich, 2005; 2006).

Control of corallivores is a vital aspect of restoration of *Acropora,* and the first, simplest and only viably scalable way to do so is to focus restoration efforts into protected or managed ecosystems with an appropriate compliment of grazers and invertivores. Although it was not assessed here, the shallow site in this study was at a depth that urchin grazing kept the substrate relatively bare of macroalgae and disease was rare relative to the deeper site beyond the habitual urchin-grazing depths. Upright and frondos macroalgae may harbour cryptic corallivores (Bruckner, Bruckner & William, 1997) and develop boundary layers to water flow that collect and harbour sediments (Smith, Smith & Hunter, 2001) including those that may hold disease (Patterson et al., 2002). Thus site choice should look for locations with appropriate grazing and water flow on both macro and micro scales.

Larger corals had significantly more living tissue at the end of the experiment. This suggests that a restoration programme use the largest fragments possible to maximize the amount of material remaining after predation or disease, as well as to maximize productivity through the improved extension rates of larger corals (Ross, 2013d). Although correlations were not found with these assessments, *H. carunculata* only bites as far as it may engulf the branch, thus larger corals should be less susceptible per unit length to this type of attack. Relatedly, once a branch has been bitten it will not be attacked again: the coral's own exposed, dead skeleton protects it from further attack so long at the next worm is not larger. As these worms also only bite down to the first branch fork, a project manager may also maximize branching in the planting stock by targeted damage (Soong & Chen, 2003), nursery site choice (Bottjer, 1980; Ross, 2013b) and even parent coral choice (Bowden-Kerby, 2001; Ross, 2013c) to limit fire-worm feeding efficiency, though it also stands to reason that a coral with more branches for attack would be attacked more often. Had the worms been smaller in this experiment, the corals may have seen more protection due to their relative size, and had the corals been larger or more branched they might have also seen protection from these large worms. Disease or smaller predators, such as snails, may not be so restricted.

The patterns of strong (Blue and White) and weak (Orange and Green) genets seen in the nursery (in Ross, 2013c) were not overtly apparent in these wild out-plants. Predation and disease were the primary issues and apparently not subject to genet influences, as opposed to the bleaching and fouling abrasion seen in the nurseries. The Green genet was the only genet to bleach with the stresses of relocation and summer temperatures, suggesting that the heritable susceptibilities to the nursery stresses persist. The Orange genet did not show particular regrowth, recovery or improvement at either site, remaining at a similar total length from the penultimate to the final measurement, whereas the Green genet continued to decline throughout and eventually disappeared entirely from the deeper site. The White and Blue genets similarly fared poorly early in the experimental period in both locations; however, in the final visit, they showed a modicum of recovery not seen in the weaker genets. Slight regrowth was seen in the shallow site for the White genet and in the deep site for the Blue. Based on these observations, the relative strengths and weaknesses seen in the nursery for improved growth, branching and resistance to bleaching stress continued into the out-planted coral. A trend of increased disease susceptibility in the Green genet also suggests that disease, abrasion and other stresses facilitating disease, will also be more problematic in weaker genets.

ACKNOWLEDGMENTS

This author would like to thank the late Kevin Kohler for adding the “combined lengths” function to CPCe in a single afternoon, the Doctor’s Cave Beach Club for their logistical support and Dale Webber of the Centre for Marine Sciences, UWI Mona, for pointing out that there is valuable data in photographic notes. The author would further like to thank the reviewers of this manuscript for their time and guidance.

RESUMEN

Efectos de la posición en el arrecife y del linaje en el crecimiento de *Acropora cervicornis* (Scleractinia:Acroporidae) en una plantación de vivero en Bahía Montego, Jamaica. La especie constructora de arrecifes de coral *Acropora cervicornis* era un elemento dominante del ecosistema en el arrecife caribeño hasta la década de 1980, cuando disminuyó en un 97% a nivel regional principalmente debido a cambios antropogénicos y por enfermedad. Esta especie de ramificación amplió su huella de colonia para lograr un dominio local a través de la fragmentación y el rebrote, así se adapta al cultivo de vivero para la restauración. En este experimento, fragmentos de *Acropora cervicornis* de cuatro linajes fueron seguidos y medidos para el crecimiento y la salud durante 12 meses en 2006 y 2007 en viveros en línea tipo “buoyant drop-loop“ en un sitio somero y otro profundo en el arrecife frontal de Bahía Montego, Jamaica. Sesenta y cinco de estos corales fueron plantados en sitios de arrecife silvestre con condiciones y profundidad similar a sus respectivos viveros y monitoreados mediante fotográfías por 11 meses durante el 2007 y 2008. Se observó un período de muerte rápida en el material plantado en ambos sitios durante los primeros cuatro meses, seguidos por un período de relativa estabilidad o recuperación. La depredación de *Hermodice carunculata* fue el principal problema en el arrecife frontal poco profundo y se combinó con un síndrome de bandas en el sitio más profundo. Este síndrome se observó en las muestras antes de la siembra, durante un período de almacenamiento de una semana en el suelo marino. A continuación ocurrió un lento descenso en los posteriores siete meses en el sitio de arrecife frontal poco profundo; sin embargo, se observó un rebrote en el sitio más profundo con el material restante. Aún incluyendo estas pérdidas, al final la longitud de coral vivo total fue más de cuatro veces que la inicial: un aumento neto a través de varias etapas de restauración propagativa o de jardinería de coral. Los rechazos fueron observados especialmente en el linaje de crecimiento más rápido del vivero y corales plantados más grandes que tienden a retener más material en once meses, lo que sugiere que los programas de restauración propagativo deben invertir en linajes de coral más fuertes y más grandes. Probablemente se obtengan mayores resultados con un manejo adaptativo y mantenimiento de jardinería del material plantado y de arrecife.

Palabras clave: *Acropora cervicornis*, coral cuerno de ciervo, propagación de cultivo de coral, jardinería de coral, restauración, *Hermodice carunculata*.

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Coral and algal community primary succession on new vertical substrate at Rackham's Cay, Port Royal, Jamaica

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Received 04-X-2013 Corrected 02-I-2014 Accepted 24-III-2014

Abstract: Jamaica's trans-shipment industry is amongst the largest in the Caribbean with 90% of trans-shipment activities occurring in Kingston Harbour. The eastern ship channel is populated with patch and fringing coral reefs. In 2002, approximately 20% of an originally sloping face of Rackham's Cay, on the southern edge of the channel, was cut vertically to 18m and dredged to widen the channel. The successional changes on the newly created vertical limestone wall was assessed between 2009 and 2012 at 5m, 10m and 15m depths using bi-annual photographs of fixed 1 m^2 quadrats. Photographs were analyzed using Coral Point Count. No colonization of either algal or coralline species was observed at 15m. Initially calcareous and fleshy algae dominated at 5m but showed a gradual decrease over time. Calcareous algae dominated at 10m and increaseed gradually over the 4 years. Stony corals at both 5m and 10m had overall low cover and slow colonization; the shallower depth had more coverage (4.1% maximum in 2011). *Siderastrea sidera* -which dominated Rackham's Cay before dredging- was consistently present in low coverage. Colonization by species of *Acropora* and *Scolymia* indicate slower but better succession at 10m. Ten years following dredging activities, colonization and recruitment have been slow but successful at 5m and 10m; species previously described as abundant lead the colonization. We recommend limiting coral relocation activities to depths not exceeding 10m. Rev. Biol. Trop. 62 (Suppl. 3): 107-114. Epub 2014 September 01.

Key words: Rackham's Cay, new vertical substrate, coral colonization, succession.

Jamaica's trans-shipment industry is amongst the largest in the Caribbean with 90% of trans-shipment activities occurring in the Kingston Harbour (latitude 17º58'N and longitude 76º48'W). This has been a lucrative industry for the Jamaican government, with current plans to diversify and expand this sector to keep abreast with a global marketplace and for continued significant contribution to Jamaica's economy. The Port Authority of Jamaica (PAJ), which owns and operates Kingston Container Terminals (KCT), earned JMD$12.57 billion in 2009. The operations at KCT generated JMD$8.50 billion which was 67% of total income for Port Authority. In 2001, the Port Authority of Jamaica commenced infrastructure expansion to increase the capacity at the Kingston Container Terminal (KCT). This infrastructure upgrade was done in an effort to maximize the potential earnings generated by the KCT, which would increase the benefit to Jamaica. The improvement is required to increase access for Post Panamax container vessels to Kingston Harbour and the KCT.

Kingston Harbour's main ship channel which runs on the east side of the Port Royal Cays is approximately 16.5m deep and is populated with the patch and fringing coral reefs known to be found throughout the area. The Port Royal Cays area has seven small cays, including Rackham's Cay which is positioned on the south-west edge of the ship channel. To facilitate the improved access to Kingston Harbour, the PAJ proposed the removal of the northern portion of the coral reef at Rackham's Cay, which was partially obstructing the south-western portion of the ship channel. This 'capital' dredging exercise, carried out in 2002, was also deemed justified based on a record of repeated groundings occurring in the area on e.g. Gun Cay and Beacon Shoal as vessels maneuver during entry to or egress from the Harbour (Gayle, Wilson-Kelly & Green, 2005).

The dredging exercise involved the removal of approximately 20% of Rackham's Cay and deepening of the east channel depth to 18 m at the area of the opening between Rackham and Gun Cays. The result was a vertical wall of new substrate on the east side of Rackham's Cay. As part of the dredging activity, corals were transplanted to help mitigate the loss of coral species, however, the newly created substrate was not subject to any post-dredging transplanting or seeding activities (e.g. Jaap, 2000; Jaap, Hudson, Dodge & Gillian, 2006). The Port Authority of Jamaica was mandated by Jamaica's National Environment and Planning Agency (NEPA) to monitor the transplanted corals for a period of five years however, there was no stipulation for the monitoring of the new vertical substrate to elucidate changes over time on the new substrate.

In 2009 the Centre for Marine Sciences (CMS) of the University of the West Indies (UWI) received a grant from the Environmental Foundation of Jamaica (EFJ) to monitor the newly created vertical substrate at Rackham's Cay for five years. The objective of the study was to investigate the development of pioneer coral and algal communities and follow the initial stages of succession created by the cutting of the hard substrate as an indication of biological recovery.

The aims of this study were therefore:

1. To indicate the establishment of coral and algae species on the new vertical substrate at Rackham's Cay.
2. To assess pioneer coral and algal community development using taxonomic composition and % cover.
3. To identify the water depth for optimal coral recruitment in the area of the ship channel near Rackham's Cay.

MATERIALS AND METHODS

The successional changes on the new vertical substrate (wall) were assessed between 2009 and 2012. Bi-annual photographs of fixed 1 m^2 quadrats at 5m, 10m and 15m depths were taken during the period. A total of three 1 m^2 permanent quadrats were randomly established at each depth along the vertical substrate of the providing a total of nine permanent quadrats. Photographs were taken with the camera positioned 1 m above the substrate and analyzed using Coral Point Count with Excel extensions (CPCe) version 3.5 software (Kohler & Gill, 2006). Genera and species, where possible, were identified from the images of the quadrats with the use of Human & DeLoach (2003) with checks of Coralpedia (http//coralpedia.bio.warwick.ac.uk) as a cross-reference. Tracing each organism identified (using the area measurement feature of CPCe) and calibration of the image, allowed the programme to compute the area occupied by the organism in question as a percentage of the total quadrat area (percentage cover). The percentage cover of major organisms/substrate categories measured over time at each depth was checked for normality and transformed where necessary (Sokal & Rohlf, 1981) before one-way analysis of variance (ANOVA, $p = 0.05$), tests were applied, using Statistica V.7, to indicate whether significant variability existed between depths and years. Diversity was calculated by the CPCe programme using the Shannon-Weaver Index (Kohler and Gill, 2006).

RESULTS

Analysis of the photographs revealed that only quadrats located at 5m and 10m depths had live species present throughout the study period. Examination of quadrats at 15m indicated silt covered carbonate material as no colonization by algae, sponge or coralline species was observed at the 15m depth.

Species identification: Five species of corals were identified throughout the course of this study: *Undaria agaricites, Acropora palmata, Montastrea faveolata, Siderastrea siderea* and *Scolymia cubensis* however they were observed at different depths and established at different times. *U. agaricites* and *M. faveolata* were identified from the pictorial data capture but were not captured in the random data capture based on the CPCe method employed. The algae observed were only identified to genus level. Those identified were *Halimeda* spp. *Caulerpa* spp., *Dictyota* sp., *Sargassum* sp., *Udotea* sp. and an unidentified encrusting algae. *Halimeda* spp. had the greatest percentage cover (13.75 % cover at 5m and 31.1 % 10m depths) and comprised the dominant genera of calcareous algae. The vertical wall of the Rackham Cay was colonized primarily by algae with other taxonomic groups being added over time.

Species and community changes: While the assessment of the photographic records at Rackham's Cay suggested subtle changes in the community over time and depths, diversity was the only parameter that varied significantly over the years (ANOVA, p = 0.037), with only hard corals (ANOVA p = 0.004) and calcareous algae (ANOVA, p = 0.039) varying significantly with depth. This was supported by a notable change in the percentage cover of species which were consistently present over time and a change in the species composition as new species occupied the area over-time.

The algae *Caulerpa* spp., *Halimeda* spp. and *Dictyota* sp. were present at the 5m depth on each sample occasion. However, the abundance as indicated by % cover was variable, increasing from the first sample occasion to a maximum at the second or third sample occasion and declining thereafter (Figure 1). Other common species such as sponge and the coral *Siderastrea siderea* did not demonstrate maximum % cover until the fourth and fifth sample occasion. Species such as *Agaricia agaricites*, *Sargassum* spp., a species of gorgonian and the coral *Acropora palmata* all demonstrated successional changes as they were present on some sample occasions for one, two or three occasions then later would disappear at subsequent sample occasions (Table 1). It was also observed that *A. palmata* replaced the gorgonian species which had earlier replaced *Agaricia agaricities,* suggesting a successional process.

TABLE 1
Percentage cover values for each taxon found at 5m over the sampling period (dates) arranged in reverse sequence of establishment

SPECIES		Jun-09	Nov-09	Jul-10	Nov-11	Dec-12
Acropora palmata	Y2					0.1
Gorgonian	Y1				8.8	
Sargassum sp.	Y2		0.5	0.9	1.2	
Agaricia agaricites	Y2	0.1	0.1	0.1		
Udotea sp.	Y2			0.2		
Encrusting algae	Y2	1.2			0.1	1.7
Halimeda sp.	Y1	7.1	23.1	17.6	7.5	12.9
Caulerpa sp.	Y1	1.3	11.6	1.2	1.1	2.0
Dictyota sp.	Y1	3.9	3.2	13.3	7.7	0.9
Sponge	Y1	4.1	3.6	4.8	4.1	6.9
Siderastrea siderea	Y1	1.3	1.4	3.7	4.1	1.8

* Y1 or Y2 after each taxon name indicates the y-axis scale with which the values for that taxon are associated.

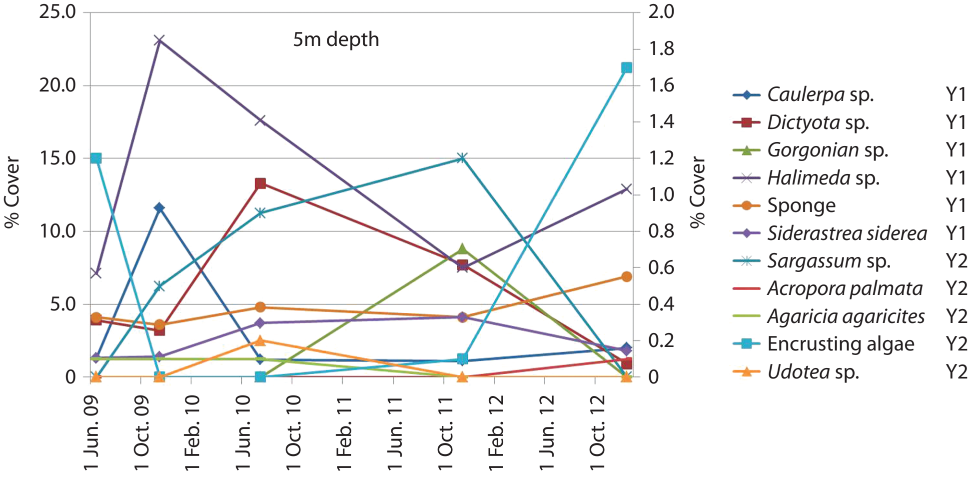

Fig. 1. Percentage cover values for each taxon found at 5m over the sampling period (dates on the x-axis). Y1 or Y2 after each taxon name in the legend indicates the y-axis scale with which the plot for that taxon is associated.

The species pattern was similar at the 10m depth, but with different species being involved in the successional changes. *Caulerpa* spp., *Dictyota* sp., *Halimeda* spp., the sponge and *Siderastrea siderea* were always present with % cover maxima on sampling occasion 4 for *Dictyota* sp. and *Halimeda* spp. and occasion 2 for *S. siderea* and the sponge (Figure 2). In these deeper waters *Udotea* sp. and an encrusting alga, which were present at the start of the sampling programme, disappeared by occasion 3 and 4 respectively and *Scolymia cubensis* and a gorgonian were added to the species composition in the quadrats, providing further successional evidence. These added species remained throughout all other sample occasions and the community at 10m was further enriched with *Agaricia agaricities* being present on the 4th occasion and *A. palmata* on the 5th sampling occasion as species change over time continued (Table 2).

Community change over time, as demonstrated by the significant (ANOVA, p = 0.037) change in diversity, also indicated that

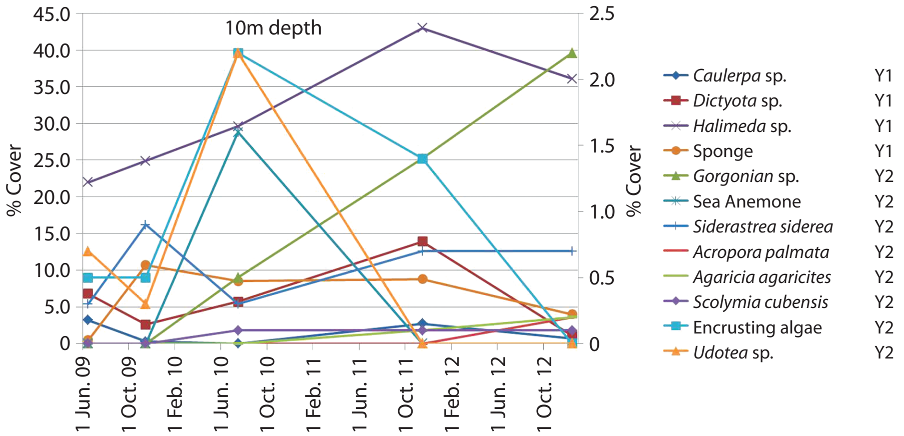

Fig. 2. Percentage cover values for each taxon found at 10m over the sampling period (dates on the x-axis). Y1 or Y2 after each taxon name in the legend indicates the y-axis scale with which the plot for that taxon is associated.

communities at 5m were more diverse that those at 10m for each sampling occasion (Figure 3). Moreover the difference in diversity became larger with the passage of time, with 10m depth samples losing greater diversity than 5m depth samples. While the absolute values are somewhat low (0.63 to 0.81 at 5m and 0.35 to 0.61 at 10m) the pattern of increase then decrease in diversity with the process of succession is clear (Figure 3).

DISCUSSION

The study focused on the medium to long term changes occurring on the newly created bare vertical substrate referred to as the "cut face" of the cay. There are not many examples of colonization of new hard substrate by corals in the Caribbean. Most studies describe primary colonization in relation to artificial substrates (Vermeij, 2006) or newly created

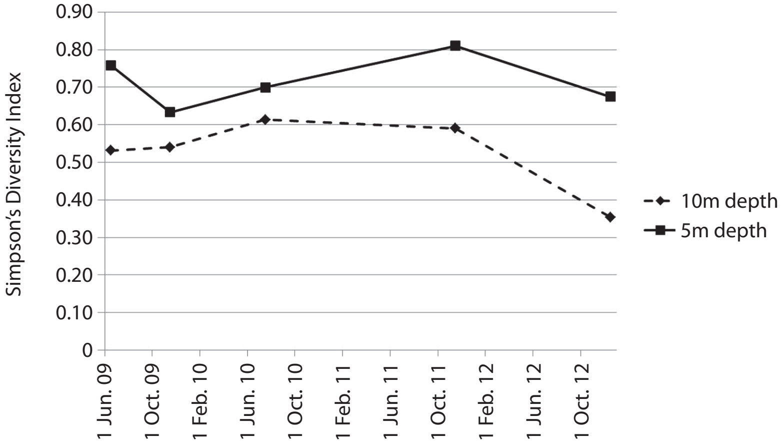

Fig. 3. Simpsons index of diversity for communities at 5m and 10m depths at Rackham's Cay calculated at each of five sample occasions.

TABLE 2

Percentage cover values for each taxon found at 10m over the sampling period (dates) arranged in reverse sequence of establishment. Y1 or Y2 after each taxon name indicates the y-axis scale with which the values for that taxon are associated

SPECIES		Jun-09	Nov-09	Jul-10	Nov-11	Dec-12
Acropora palmata	Y2					0.2
Agaricia agaricites					0.1	0.2
Sea Anemone	Y2			1.6		
Gorgonian	Y2			0.5	1.4	2.2
Scolymia cubensis	Y2			0.1	0.1	0.1
Encrusting algae	Y2	0.5	0.5	2.2	1.4	
Udotea sp.	Y2	0.7	0.3	2.2		
Caulerpa sp.	Y1	3.2	0.3		2.7	0.7
Dictyota sp.	Y1	6.8	2.6	5.7	13.9	1.1
Halimeda sp.	Y1	22.0	24.9	29.6	43.0	36.1
Sponge	Y1	0.5	10.7	8.5	8.8	4.0
Siderastrea siderea	Y2	0.3	0.9	0.3	0.7	0.7

* Y1 or Y2 after each taxon name indicates the y-axis scale with which the values for that taxon are associated.

volcanic rock in areas outside the Caribbean (e.g. Grigg & Maracos, 1974, Tomascik, Van Woesik & Mah, 1996) and so this study presents a unique opportunity, albeit in the Port Royal Cays area where percentage cover of corals (Mendes, 1992) and community diversity (McNaught, 2007) has been reported to be low. Percentage cover of coral at Rachkam's cay "cut face" was one fifth the average from a coral reef at Dairy Bull near Discovery Bay sampled in the same years, which had 15 % cover (NEPA, 2012). However, algal cover which was nine times higher than coral cover was also lower that island averages of 35.5% (NEPA, 2012).

With the absence of a pre-dredging survey, it is impossible to determine the exact nature of the benthic community at the specific depths assessed in this investigation. However, studies in the general area of the Port Royal cays gave insight to the dominant members of the community (Mendes, 1992; Miller, 1996). Throughout this study, the dominance of calcareous and fleshy algae was as reported previously (McNaught, 2007; NEPA, 2012), with the concomitant overall low cover and slow colonization of hard corals and shallower depth having greater coral coverage. Previous reports also indicated that S*iderastrea siderea* dominated Rackham Cay before dredging (Mendes, 1992; McNaught, 2007; Center for Marine Sciences, 2005) and therefore would be expected to colonize fastest and be the dominant coral species. Current data supports this suggestion, with S*iderastrea siderea* being present in all quadrats and on all sample occasions but with very low percentage cover. With no colonization observed at 15m it is clear that the threshold for recovery in the area of Rackham's Cay is between 10 and 15m. This threshold requires further investigation to identify the causative factors.

The primary community succession (Walker & Delmoral, 2003), on the vertical wall at Rackham's Cay, was evident at both the 5 and 10m depths and mirrored the classical description of disappearance of initial species having modified the substrate, to be replaced by more competitively advanced species and a shift to seral communities (Houston & Smith, 1987). In the early stages of this succession, widely accepted pioneer algal genera (*Halimeda*, *Dictyota* and *Caulerpa*) as well as the coral S*iderastrea siderea* dominated with sponges, while the later introduction of gorgonians and the once Jamaican dominant coral *Acropora palmata,* suggest the seral stage has begun. The community in deeper waters (10m) demonstrated additional successional rigour with the coral *Scolymia cubensis*, a seral deep water species occupying consistently after the third sample occasion and the pioneer algae *Udotea* sp. disappearing at the same time. Furthermore, where the species replacement trend was not observed the more widely observed successional trend of change in abundance of common species over time was also observed at both depths. Although only sampled over a period of four years, the successional trends at Rackham's were clear.

The difference in communities at 5m and 10m was supported by the results of the diversity index, where diversity at 5m was consistently higher than that at 10m with the difference increasing with continued succession. Communities in deeper waters are expected to be less diverse resulting from the reduction in light, temperature and nutrient levels, especially adjacent to a major land based source of stress. As succession proceeds, species diversity increases initially due the colonization by new species. However, as competition increases and environmental conditions begin to stabilize, diversity will decrease as the original pioneer species are displaced (Huston, 1994).

The success of coral reef communities in close proximity to the Kingston Harbour is documented as being low (Mendes, 1992; Miller 1996). Even without the additional human disturbance of vertical cutting of the reef structure, these areas have low coral cover and high fleshy algae density due to the environmental conditions of an estuarine impacted coral reef. Rackham's Cay is only 1.2km from the entrance to the eutrophic Kingston Harbour and receives high sediment load, industrial chemicals, fresh water and sewage at least occasionally (Miller, 1996). The Kingston Harbour's environmental conditions and the documented ships propeller wash (Gayle et al., 2005) stunted the areas average coral cover (6-10%) recovery and normal succession that would be expected in 4-6 years (Ohba et al., 2006).

The poor colonization, of coral reefs on Rackham's Cay new vertical substrate may be an indicator that more careful planning and mitigation should be a part of future projects of this nature. The area would be more likely to show coral colonization if parent material was installed there following the completion of dredging. This is particularly true for species such as *Acropora palmata* which reproduces significantly better asexually (from fragmentation) and shows lower colonization from spawning activities. This would also move the succession process much further ahead by enriching the community with this seral species.

A number of recommendations can be derived from the current study. Without pre-dredging base line data, while the dramatic cut face produces opportunities for the study of primary succession, the expectations for recovery will be unknown as existed in this current study. Coral recovery rates are highly variable and difficult to explain when the benchmark to original community structure is unknown. With the knowledge that a dramatic cut face was to be undertaken a coral nursery using fragments from the impacted area should have been created. This would have facilitated accelerated succession by the re-introduction of coral from a created nursery or neighbouring coral community. The time and effort applied to the current study would have yielded more compelling results if a standard monitoring programme was implemented and this should proceed longer than 5 years as currently stipulated by the National Environment and Planning Agency (NEPA).

ACKNOWLEDGMENTS

We would like to thank the Environmental Foundation of Jamaica for providing the grant funding to conduct a four year study on the Port Royal Cays and specifically the Rackham's Cay newly created vertical substrate "cut face". The staff of the Department of Life Sciences, Centre for Marine Sciences and Port Royal Marine Laboratory also played vital roles in facilitating the various aspects of this research.

RESUMEN

Sucesión primaria de una comunidad de coral y algas en el nuevo sustrato vertical en el Cayo de Rackham, Puerto Royal, Jamaica. La industria de transbordo en Jamaica es de las mas grandes en el Caribe con el 90% de las actividades de tránsito que ocurren en el puerto de Kingston. El canal oriental de la bahía está poblado de un fragmento y franja de arrecife de coral. En el 2002, aproximadamente el 20% de una cara del Cayo Rackham fue cortado verticalmente a 18m y dragado para facilitar la ampliación del canal. Los cambios sucesionales en la pared de piedra caliza vertical se evaluó entre el 2009 y 2012 en 5m, 10m y 15m de profundidad usando fotografías bianuales en cuadrantes de 1m^2. Las fotografías fueron analizadas usando "Conteo de Puntos de Coral". A 15m de profundidad, no se observó ninguna colonización de especies coralinas o algas. Las algas calcáreas y carnosas dominaron inicialmente los 5m de profundidad y mostraron una disminución gradual en el tiempo. Algas calcáreas dominaron los 10m de profundidad y también mostraban un incremento gradual en los 4 años. Corales pétreos en 5m y 10m de profundidad mostraron un % de cobertura bajo y lenta colonización, con la menor profundidad y teniendo la mayor cobertura coralina (4.1% máximo en 2011). *Sidera Siderastrea* que dominaba Cayo Rackham antes del dragado fue la especie coral constantemente presente aunque en bajo % de cobertura. La colonización por especies de los géneros *Acropora* y *Scolymia* son indicación de sucesión más lenta pero mejor a 10m de profundidad. Los diez años siguientes después de las dragas, la colonización de coral y reclutamiento ha sido lento pero exitoso en 5m y 10m de profundidad con especies previamente descritas como siendo abundantes en la zona. Recomendamos limitar las actividades de reubicación de coral a profundidades no superiores a 10m.

Palabras clave: Cayo Rackham, nuevo sustrato vertical, colonización, coral, sucesión.

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Estructura de las comunidades de corales y octocorales de Isla de Aves, Venezuela, Caribe Nororiental

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Recibido 24-IX-2013 Corregido 08-IV-2014 Aceptado 10-IV-2014

Abstract: Structure of the coral and octocoral communities of Isla de Aves, Venezuela, Northeast Caribbean. The Isla de Aves Wildlife Refuge is the northernmost portion of the Venezuelan territory generating 135 000km^2 of Exclusive Economic Zone. Studies on coral communities are scarce and old (1970s), due to its location 650km northeast of La Guaira Port and because it has military facilities. To upgrade baseline information we estimated size structure, percent live cover, species composition and abundance of corals and octocorals. We evaluated 16 sites around the island using the AGRRA Protocol (band-transects 10 m^2) between 1.5 and 21m depth (n=67 transects), and visual surveys conducted in other five sites. We recorded 2 327 colonies belonging to four hydroid species and 36 species of stony corals in 11 families. The values for diversity, dominance and evenness of the coral community ranged between 0.78 and 2.12 (SW), 0.15 and 0.61 and 0.57 y 0.92 respectively. Most coral species had relative abundance values under 3%, except *Porites astreoides* (25.57%), *Pseudodiploria strigosa* (18.22%) and *Siderastrea siderea* (14.44%). They were represented mostly by smaller colonies, between 3 and 30cm in maximum diameter and between 0 and 5cm high. A total of 13 octocoral species belonging to three families were identified. *Pseudopterogorgia americana* was the most abundant species. The mean percent of live coral (including hydrocorals) was 22.30% (SE=1.73) (15.45% for dead coral, SE=3.28). Dead coral had the highest percentage of dissimilarity between sites (9.21%) (ANOSIM) and 16.57% contribution (SIMPER analysis). Octocoral live cover ranged from 0 to 21.35% with a mean of 6.38% (SE=0.99). Research on benthic communities of Isla de Aves should continue, especially in the deeper areas, to assess ecological conditions. Rev. Biol. Trop. 62 (Suppl. 3): 115-136. Epub 2014 September 01.

Key words: corals, octocorals, abundance, diversity, Isla de Aves, Venezuela.

El estudio de comunidades coralinas en Venezuela se ha desarrollado especialmente en localidades como el Parque Nacional Archipiélago de Los Roques (Hung, 1985; Weil, 1985; Villamizar, Posada & Gómez, 2003; García, Cróquer & Pauls, 2003; Cróquer, Weil & Zubillaga, 2005; Villamizar et al., 2008; Bastidas et al., 2012) ; el Parque Nacional Morrocoy (Villamizar, 2000; Bone et al., 2001; Cróquer & Bone 2003; Bastidas, Cróquer & Bone, 2006; Cróquer et al., 2010) y otras localidades del país (Olivares, 1971; Urich, 1977; Pauls, 1982; Ramírez- Villaroel, 2001; Sant, Prieto & Méndez, 2002; Weil, 2003; Del Mónaco et al., 2010). En contraste, las comunidades coralinas del Refugio de Fauna Silvestre Isla de Aves (RFSIA), han sido escasamente estudiadas, principalmente debido a la dificultad de acceso a la isla, ya que se encuentra a 650km al noreste de la costa central de Venezuela. Esta Isla de apenas 3.72ha es el único afloramiento de la extensa cordillera submarina conocida como Prominencia de Aves y representa la porción más septentrional del territorio venezolano, generando 135 000km^2 de Zona Económica Exclusiva. Su ubicación constituye un punto estratégico para Venezuela dentro de la geopolítica del Caribe en la elaboración de acuerdos de delimitación de áreas marinas y submarinas con los estados insulares vecinos (Arteaga, 2002) y se encuentra bajo custodia militar.

En lo que respecta a su importancia biológica - ecológica, Isla de Aves constituye el principal sitio de anidación de la tortuga verde (*Chelonia mydas*) en Venezuela y el segundo en el Caribe, luego de tortuguero en Costa Rica (Guada & Solé, 2000) .Es además el área de reproducción de diversas especies de aves marinas y de descanso de numerosas aves migratorias (Phelps, 1945; Gremone & Gómez, 1983). La importancia del Refugio de Fauna Silvestre Isla de Aves, tanto desde el punto de vista geopolítico como biológico y ecológico, motivó la realización del presente estudio, ya que el conocimiento de la diversidad de organismos marinos presentes en los fondos aledaños a Isla de Aves, fortalece la soberanía de nuestro país sobre este pequeño territorio (Arteaga, 2002). Este trabajo es el inicio de la caracterización de las comunidades bentónicas alrededor de la Isla. Únicamente Almeida and Goddard (1974) hicieron un estudio en la isla hasta los 10 m de profundidad, reportando 8 especies de corales e hidrocorales y 3 especies de octocorales, y Brownell y Guzmán (1974) realizaron algunas descripciones sobre los ambientes marinos en los alrededores de la Isla, enfocándose principalmente en la ictiofauna. Esta investigación tiene como objetivo actualizar y obtener una línea base cuantitativa sobre la distribución y estructura de las comunidades de corales y octocorales alrededor de la Isla.

MATERIALES Y MÉTODOS

Zona de estudio: El Refugio de Fauna Silvestre Isla de Aves (15°40’23.7” N; 63°36’ 59.9” O) se encuentra a 650Km al noreste del Puerto de La Guaira, y 510Km al Norte de la Isla de Margarita, a 200Km al Oeste de Dominica y Guadalupe y a 350Km al Sureste de Puerto Rico (Fig. 1). Esta Isla tiene un área

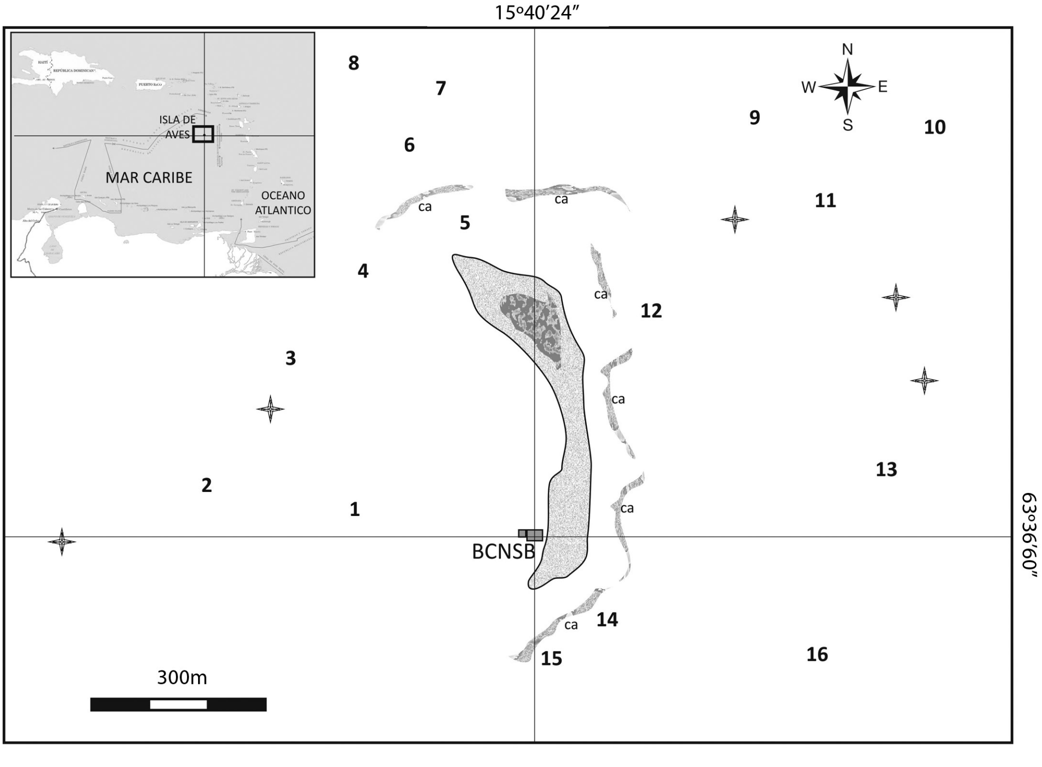

Fig. 1. El Refugio de Fauna Silvestre Isla de Aves.

de 3.72ha, con una altura que oscila entre 0 y 3m sobre el nivel del mar y constituye el único afloramiento de la Prominencia de Aves, extensa cordillera submarina de unos 500km de longitud que está conformada por un antiguo arco de islas volcánicas. Presenta una topografía plana con una superficie ligeramente ondulada por el arrastre de arena y el viento, siendo estrecha en el centro y abultada en sus extremos en dos prominencias principales que constituyen las partes más elevadas del relieve. La longitud aproximada de la isla es de 580m y su ancho 130m en su parte más ancha y 30m en la más angosta (Arteaga, 2002). Se encuentra frecuentemente expuesta a fuertes vientos (Alisios ENE) tormentas y huracanes (Pérez Nieto, 1990), por lo que está sometida a procesos de erosión que generan cambios en su forma y dimensiones según la época del año. Particularmente en la costa central y occidental donde se presenta el seccionamiento de la isla en su parte media, durante el paso de fuertes huracanes (Pérez Nieto, 1990).Se han establecido 4 unidades litológicas a lo largo de la isla: (1) calcarenitas conformadas por fragmentos de corales, algas y gasterópodos cementados de calcita (extremos norte y sur-oeste de la isla); (2) caliza de mástil en la parte norte de la isla y en menor proporción al sur la cual es de origen coralino compuesta por caracoles, esponjas calcáreas, moluscos, arenas calcáreas y fosfáticas cementadas; (3) rocas de playa que conforman la plataforma de material clástico consolidado que rodea la isla y sobre las cuales se acumulan arenas y (4) arena de playa blanca calcárea y de granulometría media (Pantin, 1972). La única vegetación terrestre presente en el área de estudio está representada por verdolaga (*Sesuvium portulacastrum* y *Portulaca olearacea*), ambas son hierbas rastreras o levemente erguidas que cubren en forma de manto áreas de las zonas más elevadas donde desempeñan la importante función de fijar las arenas en el sector norte de la isla (Gremone & Gómez, 1983). Al suroeste del Refugio se encuentra la Base Científico Naval Simón Bolívar, donde reside el Personal de la Armada Bolivariana de Venezuela, únicos residentes de la isla.

Se empleó el Protocolo AGGRA, utilizando bandas-transectas de 10m^2 paralelas a la costa, en las cuales se estimó la cobertura lineal (justo debajo de la cinta) y se registraron todos los corales y octocorales presentes, con el fin de determinar la composición de especies y sus respectivas abundancias. Además se estimaron las tallas tanto de corales como octocorales (diámetro máx. y altura). La cobertura lineal estimada estuvo representada por las siguientes categorías: (1) coral vivo, (2) coral muerto, (3) coral muerto con algas, (4) octocoral vivo, (5) octocoral muerto, (6) algas, (7) roca, (8) arena, (9) algas con escombros, (10) arena con escombros y (11) escombros . La categoría "coral muerto" se define como: colonias coralinas sin vida, con pocos filamentos algales dispersos a lo largo de su superficie, que al ser interceptadas por la cinta métrica, deja ver claramente la estructura esqueletal. Por otro lado, la categoría "coral muerto con algas" representa la superficie de una colonia coralina desprovista de tejido coralino y con presencia con presencia evidente (densa) de una o mas especies de algas cespitosas o macroalgas. La categoría "roca" se refiere a aquella superficie constituida por roca de playa. Según Dalongeville y Sanlaville (1984) este sustrato se define geológicamente como un depósito sedimentario con capas inclinadas hacia el mar, formado en la zona intermareal, y cuyo endurecimiento se debe a la formación de un cemento carbonático (aragonita o calcita magnesiana). Y la categoría *"algas"* se refiere a todo sustrato que presenta una cobertura notable de algas, no dejando ver la naturaleza del fondo.Las evaluaciones se realizaron en 16 sitios alrededor de la Isla (Fig. 1; Cuadro 1) distribuidos en 4 sectores: Sotavento, Barlovento, Norte y Sur, entre 1.5 y 21m de profundidad (n= 67 transectas). De forma complementaria se realizaron censos visuales en otros 5 sitios alrededor de la isla, con el fin de obtener el listado de especies lo más completo posible. Este estudio comprende los muestreos realizados en las Campañas de Investigación Científica organizadas anualmente (desde el 2009 al 2012) por la Dirección de Hidrografía y Navegación (DHN), durante los meses de julio y agosto.

CUADRO 1
Sitios de muestreo en el Refugio de Fauna Isla de Aves, Venezuela

TABLE 1
Survey Sites at Isla de Aves Wildlife Refuge, Venezuela

Sitio	Ubicación	Prof. (m)	Exposión al oleaje	Intensidad de corrientes	Tipo de fondo	Características Generales	N° transectas
1	Sotavento - Suroeste	6.6	0	2	Homogéneo	Fondo plano con roca de playa intercalado con áreas arenosas- . Predominancia de corales del género Pseudodiploria y el octocoral *Pseudopterogorgia americana.*	2
2	Sotavento - Suroeste	9	0	2	Heterogéneo	Fondo plano con roca de playa intercalado con áreas arenosas- Ligera pendiente que alcanza los 15 m de profundidad aprox.	4
3	Sotavento - Oeste	10	0	2	Homogéneo	Fondo plano con roca de playa intercalado con áreas arenosas, corales y esponjas en parches	6
4	Sotavento - Noroeste	9	1	2	Homogéneo	Pequeños parches rocosos colonizados por corales, esponjas y octocorales. Presencia de *Acropora palmata*.	4
5	Norte	1.5	4	3	Homogéneo	Laguna con predominancia del alga calcárea Lithothamium y corales del género Porites: *P.astreoides* y *P.porites.*Hacia el área más externa de la laguna se encuentran colonias muertas del género Montastraea de grandes dimensiones ,colonizadas principalmente por especies del género Agaricia y Porites.Presencia de *Acropora palmata.*	6
6	Norte	8-10	0	3	Homogéneo	Fondo plano arenoso con colonias de corales, octocorales y esponjas distribuidas en parches	6
7	Norte	11	0	2/3	Homogéneo	Fondo con pendiente leve (<10°) en dirección mar afuera. Presenta canales de arena y zonas con gran abundancia de macroalgas (único sitio con esta característica).	6
8	Noroeste	14-15	0	2	Heterogéneo	Unico sitio con estructura física de carbonato de calcio (arrecife consolidado) y con una pendiente que alcanza los 26 m de prof. donde se encuentra el quiebre hacia el talúd vertical que llega hasta los 70 m y luego desciende abruptamente hasta > de 100 m. Esta zona profunda forma parte de un halo de arena que rodea a la Isla.	5
9	Barlovento- Noreste	15	0	3	Heterogéneo	Fondo de roca plano cubierto por corales aislados. Esponjas y gran abundancia de octocorales.	2

CUADRO 1 (Continuación) / TABLE 1 (Continued)

Sitio	Ubicación	Prof. (m)	Exposición al oleaje	Intensidad de corrientes	Tipo de fondo	Características Generales	N° transectas
10	Barlovento-Noreste	21	0	4	Heterogéneo	Fondo plano arenoso con colonias de corales, octocorales y esponjas distribuidas en parches	2
11	Barlovento-Noreste	17-18	0	3	Heterogéneo	Fondo plano arenoso con colonias de corales, octocorales y esponjas distribuidas en parches	3
12	Barlovento-Noreste	5	4	3	Homogéneo	Predominancia del hidrocoral *Millepora squarrosa* y roca de playa en algunas zonas	6
13	Barlovento-Sureste	16	0	3	Heterogéneo	Fondo plano arenoso con colonias de corales, octocorales y esponjas distribuidas en parches	2
14	Sur	8	3	2	Homogéneo	Fondo plano con roca de playa intercalado con áreas arenosas. Presencia de *Acropora palmata.*	6
15	Sur	9	1	3	Homogéneo	Grandes rocas de playa (algunas entre 1 y 2 m de altura aprox). Presencia de *Acropora palmata*	6
16	Barlovento-Sureste	12-14	0	2/3	Heterogéneo	Fondo espacioso con colonias de octocorales, esponjas y corales aislados.Presencia de sustratos coralinos antiguos recubiertos por esponjas.	1

Nota: 6 transectas/estación. La diferencia en el esfuerzo de muestreo de algunas localidades obedece a razones logísticas .Categorías Oleaje y Corrientes: 0= sin impacto; 1= leve; 2= moderado; 3= Alto.
Note: 6 transects/site. Differences in sampling effort in some of the sites are due to logistical reasons. Waves and currents categories: 0= nonimpact; 1= slight; 2= moderate 3= high.

Las especies de corales y octocorales fueron identificadas *in situ* y cuando se dificultó su identificación se tomaron pequeños fragmentos de los mismos para su identificación en el laboratorio. Para la clasificación de los corales se siguió principalmente la nomenclatura de Wells (1973), Humann y DeLoach (2002), Cairns y Kitahara (2012), e incorporó la reubicación de algunas especies de la familia Agaricidae según Stemman (1991) en el género *Undaria* y el estudio de Budd, Fukami, Smith y Knowlton (2012) para la reubicación de varias especies. Asimismo se consideró la lista de especies de Cairns, Hoeksema y Van Der Land (1999) sobre corales extintos y corales sobrevivientes, como otro medio de corroborar la validez de los corales pétreos reportados en este estudio. En el caso de los octocorales se empleó la clave de Bayer (1961) y la información de Bayer, Grasshoff & Verseveldt, 1983 y Janes y Wah (2005).

Análisis de datos: Se hicieron dos Análisis de Ordenamiento MDS (Índice Bray-Curtis) con el fin de explorar posibles agrupamientos entre sitios de muestreo, un MDS de acuerdo a su similaridad en la abundancia y composición de las diferentes especies coralinas y otro según la cobertura lineal de las distintas categorías bentónicas. Con el propósito de comparar la abundancia y composición de especies, así como la cobertura lineal entre sitios, se utilizó el Análisis de Similaridades (ANOSIM) y el análisis de Porcentaje de Similaridades (SIMPER); este último con el fin de cuantificar la contribución de las categorías bentónicas y de la abundancia de las distintas especies en las diferencias observadas. En ambos análisis se usó el índice de Bray – Curtis. Por otro lado, se determinaron los índices de diversidad de Shannon-Wiener (H’), dominancia de Simpson (D) y equitatividad de Pielou (J) tanto de la comunidad de corales como de octocorales. Todos los análisis se realizaron con el Programa estadístico PAST.

RESULTADOS

Abundancia, composición de especies y diversidad: Se registraron un total de 2 327 colonias de corales e hidrocorales vivas pertenecientes a 365 especies de corales pétreos, en 11 familias y 4 especies de hidrozoos (Cuadro 2). Considerando la suma de colonias coralinas para el total de sitios evaluados, se estimó que la mayor parte de las especies de coral presentaron valores de abundancia relativa menores al 3% (Fig. 2), a excepción de *Porites astreoides* (25.57%), *Pseudodiploria strigosa* (18.22%) y *Siderastrea siderea* (14.44%). Dos especies del género *Millepora* le siguieron en abundancia: *Millepora squarrosa* (10.31 %) y *M. alcicornis* (4.30 %). Tanto *P. astreoides* como *S. siderea* estuvieron presentes en todos los sitios de muestreo (Cuadro 3) y *P.strigosa* en 15 de los 16 sitios. De hecho se hallaron diferencias estadísticamente significativas en composición y abundancia de las especies entre sitios (ANOSIM: R global=0.657 $p<0.001$) siendo *P.astreoides* la especie de mayor porcentaje de disimilaridad (6.884%) contribuyendo con 11.45% a las diferencias entre los sitios (Análisis SIMPER). La única otra especie que estuvo presente en todos los sitios de muestreo fue el hidrocoral *M. alcicornis*. Entre las especies del género *Orbicella*, *O.faveolata* se encontró en 10 sitios y *O. annularis* únicamente en tres. *M. cavernosa* presentó una mayor abundancia (3.91%) y se encontró en 14 de los 16 sitios de muestreo. Entre los otros géneros registrados, es importante destacar la presencia del género *Acropora*, representado únicamente por la especie *Acropora palmata,* y sólo en 4 sitios de muestreo.

El número de especies de corales escleractinidos registrados en las transectas osciló

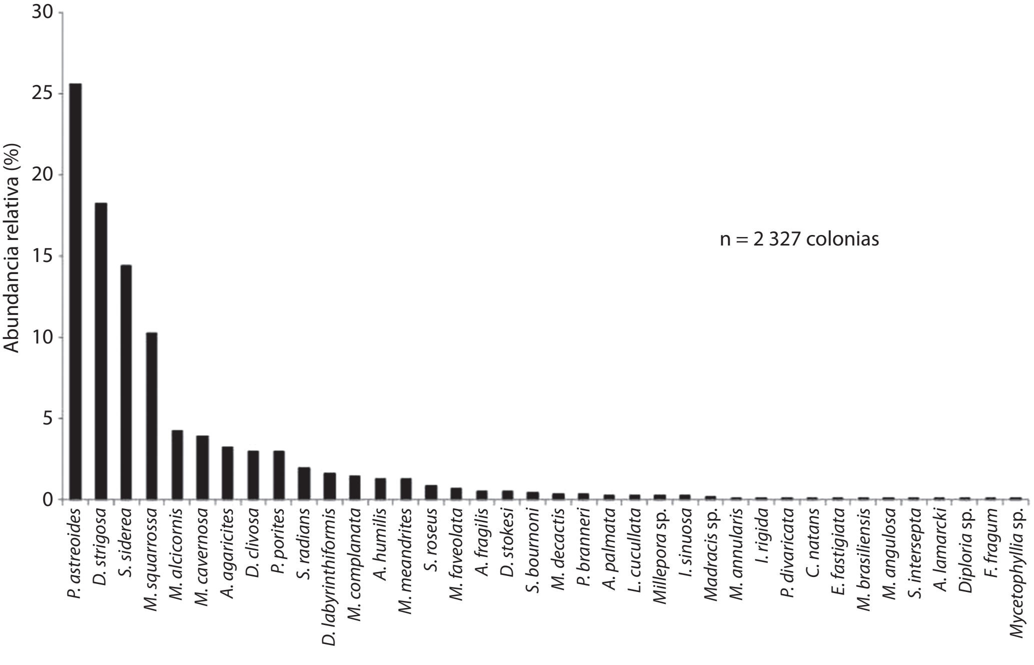

Fig. 2. Abundancia relativa de corales pétreos e hidrocorales en el Refugio de Fauna Silvestre Isla de Aves, Venezuela. Se incluyen 16 estaciones de muestreo; n = 67 transectas

Fig. 2. Relative abundance of corals and hydrocorals in the Isla de Aves Wildlife Refuge, Venezuela. Includes 16 sampling station, n = 67 transects.

CUADRO 2
Lista taxonómica de corales pétreos e hidrocorales del Refugio de Fauna Silvestre Isla de Aves, Venezuela

TABLE 2
Taxonomic list of hard corals and hidrocorals from Isla de Aves Wildlife Refuge, Venezuela

ORDEN	SUBORDEN	FAMILIA	ESPECIE
	ASTROCOENIIDA	Acroporidae	*Acropora palmata* (Lamarck,1816)
SCLERACTINIA	FUNGIIDAE	Agariciidae	*Agaricia fragilis* Dana, 1846
			Agaricia lamarcki M. Edwards & Haime, 1851
			Leptoseris cucullata (Ellis & Solander, 1786)
			Leptoseris sp. Milne Edwards & Haime, 1849
		Merulinidae	*Orbicella annularis* (Ellis & Solander)
			Orbicella faveolata (Ellis & Solander, 1786)
		Montastraeidae	*Montastraea cavernosa* (Linnaeus, 1767)
		Undaria	*Undaria agaricites* Stemman,1991
			Undaria humilis Stemman,1991
		Poritidae	*Porites astreoides* Lamarck, 1816
			Porites porites (Pallas, 1766)
			Porites divaricata Le Sueur, 1821
			Porites branneri Rathbun, 1888
		Siderastreidae	*Siderastrea radians* (Pallas, 1766)
			Siderastrea siderea (Ellis & Solander, 1786)
	FAVIINA	Mussidae	*Pseudodiploria clivosa* (Ellis & Solander, 1786)
			Pseudodiploria strigosa (Dana, 1846)
			Diploria labyrinthiformis (Linnaeus, 1758)
			Colpophyllia natans (Houttuyn, 1772)
			Favia fragum (Esper, 1795)
			Manicina areolata (Linnaeus, 1758)
			Solenastrea bournoni M. Edwards & Haime, 1850
			Mussa angulosa (Pallas, 1766)
			Isophyllia sinuosa (Ellis & Solander, 1786)
			Isophyllastrea rigida (Dana, 1846)
			Mycetophyllia aliciae Wells, 1973
		Meandrinidae	*Meandrina meandrites* (Linnaeus, 1758)
			Meandrina danae Milne-Edwards and Haime, 1848
			Dichocoenia stokesi M. Edwards & Haime, 1848
			Eusmilia fastigiata (Pallas, 1766)
			Dendrogyra cilindrus Ehrenberg, 1834
		Pocilloporidae	*Madracis decactis* (Lyman, 1859)
			Madracis auretenra Locke, Weil & Coates, 2007
		Astrocoeniidae	*Stephanocoenia intersepta* (Lamarck, 1816)
		Rhizangiidae	*Astrangia* sp. Milne-Edwards & Haime, 1848
ANTHOATHECATA	CAPITATA	Milleporidae	*Millepora squarrosa* Lamarck, 1816
			Millepora alcicornis Linnaeus, I758
			Millepora complanata Lamarck, 1816
			Stylaster roseus (Pallas, 1766

CUADRO 3

Especies de corales pétreos e hidrocorales e índices de dominancia,
diversidad y equitatividad por sitio de muestreo en el Refugio de Fauna Silvestre Isla de Aves, Venezuela

TABLE 3

Hard corals and hidrocorals species and diversity, dominance and evenness index
per sampling site at the Isla de Aves Wildlife Refuge, Venezuela

ESPECIE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A. palmata				x								x		x	x	
U. agaricites				x	xx		x	x		x	x	x		xx	x	
U. humilis	x		x	x		xx						xx		x	x	
A. fragilis					xx	x									x	
A. lamarcki								x								
Agaricia sp.			x					x		x	x	xx		x	xx	
P. clivosa	x		x	xx	x	xxx		x				x		xxx	xx	x
P. strigosa	xxx	xxx	xxx	xxx		xxx	xxx	xx	xx	x	x	x	xxx	xxx	xxx	xx
D. labyrinthiformis		xx	xx	xx			xx	x			x		x		x	x
Pseudodiploria sp.																x
D. stokesi		x				x	x	x				x	x			
C. natans			x					x								
F. fragum							x									
E. fastigiata										x	x					
L. cucullata										xx					x	
M. alcicornis	x	x	x	xx	x	xx	xx	xx	x	xx	xx	xx	x	x	x	x
M. complanata		x	xx		xx	x						xx		x		
M. squarrosa												xxx		x		
Millepora sp.												x		xx		
M. cavernosa	x	x	x	x		x	xx	xxx	x	xx	x	xxx	xx	x		x
O. annularis							x	x	x							
O. faveolata			x	x	x		x	x	x	x	x		x	x		
M. meandrites	x	x					x	xx		x	x		x			
M. danae								x			x					
M. decactis		x	x				x	x		x						
Madracis sp.														x	x	
M. aliciae								x								
M. angulosa			x						x							
I. sinuosa	x			x			x			x					x	
I. rigida															x	
P. astreoides	xx	xxx	xxx	xxx	xxx	xxx	x	x	xx	xx	xxx	xx	xxx	xxx	xxx	x
P. porites	x		x		xxx	x		x	x			xx	x	x		x
P. branneri								x				x		x	x	
P. divaricata																x
S. radians	x		x		x	xxx	x					x		xxx	x	
S. siderea	xx	xxx	xxx	x	x	xx	xxx	xxx	xx	xxx	xxx	x	xxx	xxx	xxx	xxx
S. intersepta														x	x	
S. bournoni		x					x	x								x
S. roseus			x	x		x		x		x	xx	x			x	
N° de especies	11	11	17	13	10	13	16	22	9	14	13	18	10	19	19	11
N° de colonias	61	87	238	93	321	152	143	98	48	85	79	334	99	219	222	48
N° de transectas	2	4	6	4	6	6	6	5	2	2	3	6	2	6	6	1
Dominance_D	0.26	0.22	0.25	0.30	0.61*	0.22	0.29	0.15*	0.19	0.15*	0.19	0.49	0.26	0.25	0.26	0.24
Shannon_H	1.61	1.70	1.60	1.53	0.78*	1.70	1.51	2.12*	1.79	2.11	1.88	1.15	1.55	1.66	1.69	1.75
Evenness_e^H/S	0.79	0.85	0.79	0.79	0.57	0.88	0.81	0.88	0.92	0.88	0.86	0.57	0.84	0.83	0.76	0.82

Se incluyen solo especies observadas en transectas. x=rara (1 a 5 colonias); xx= común (6 a 15 colonias), xxx = abundante (>15 colonias). It includes only the species observed in transects. x = rare (1 to 5 colonies); xx= common (6 to 15 colonies), xxx = abundant (>15 colonies).

entre 9 y 22 (Cuadro 3), siendo los sitios 8 y 10, de 14.5 y 21 m de profundidad y situados al noroeste y noreste respectivamente, los de mayor diversidad (H'= 2.12 y H'= 2.11) y el sitio 5, (laguna situada al norte de la isla) el de menor diversidad (H'= 0.78). Por su parte, los valores de equitatividad fueron menores en los sitios 5 y 12 (J = 0.57 para los dos sitios) ambos puntos ubicados en el sector norte de la isla, con profundidades comprendidas entre 1.5 y 5 m. El sitio 9, situado a 15 m de profundidad hacia Barlovento de la isla, presentó los mayores valores de equitatividad (J=0.92). En lo que respecta a la dominancia, esta fluctuó entre 0.15 y 0.61, siendo el sitio 5 el de mayor dominancia y los sitios 8 y 10 los de menor dominancia (Cuadro 3).

En el caso de los octocorales (Cuadro 4), se identificaron un total de 13 especies pertenecientes a 3 familias, siendo *Pseudopterogorgia americana* la especie dominante. De un total de 460 colonias, *P.americana* presentó un 74.78% de abundancia relativa y se observó en la mayor parte de las sitios de muestreo (Cuadro 5), a diferencia de especies de otros géneros que se observaron solo en 3 sitios (ej: *Eunicea* sp.; *E. caribaeorum*). En lo que respecta a los índices de diversidad, dominancia y equitatividad para este grupo (Cuadro 5), la alta abundancia y amplia distribución de *P.americana* a lo largo de los sitios de muestreo, dio como resultado bajos índices de diversidad y altos valores de dominancia.

Cobertura

Se observaron 15 categorías bentónicas, de las cuales se muestran las once más representativas en el Cuadro 6. En este caso se reportan 15 sitios de muestreo, dado que no se pudo estimar la cobertura en el sitio n° 16. La cobertura promedio de *coral vivo* varió entre 8.33% (SE= 2.71) en el sitio 4 (situado hacia sotavento de la isla, a 9m de profundidad) y 50.50% (SE=9.50) en el sitio 10 de 21 m de profundidad, ubicado en el sector noreste hacia Barlovento, con un promedio para todo el muestreo de 22.30% (SE=1.73). Mediante el Análisis de Similitud (ANOSIM; R global=0.624 p = 0.001) se determinó que la categoría *coral muerto* aportó el mayor porcentaje de disimilaridad entre sitios (9.21%); con un porcentaje de contribución de 16.57% (Análisis SIMPER). Esta categoría bentónica presentó un promedio de 15.45% (SE=3.28) y solo cuatro de las quince sitios presentaron coberturas de coral muerto

CUADRO 4
Lista taxonómica de octocorales del Refugio de Fauna Silvestre Isla de Aves, Venezuela

TABLE 4
Taxonomic list of octocorals from Isla de Aves Wildlife Refuge, Venezuela

ORDEN	SUBORDEN	FAMILIA	ESPECIE
ALCYONACEA	SCLERAXONIA	Anthotelidae	*Erythropodium caribaeorum* (Duchassaing & Michelotti, 1860)
		Gorgonidae	*Pseudopterogorgia americana* (Gmelin, 1791)
			Pseudoterogorgia bipinnata (Verrill, 1864)
			Pseudoterogorgia sp. Kükenthal, 1919
			Pterogorgia sp. Ehrenberg, 1834
			Gorgonia ventalina (Linnaeus,1758)
	HOLAXONIA	Plexauridae	*Plexaura flexuosa* Lamouroux, 1821
			Plexaurella sp. Valenciennes, 1855
			Pleudoplexaura sp. Wright & Studer, 1889
			Eunicea sp.1 Lamouroux, 1816
			Eunicea sp.2 Lamouroux, 1816
			Eunicea sp.3 Lamouroux, 1816
			Muricea sp.1 Lamouroux, 1821

CUADRO 5
Especies de octocorales e índices de dominancia,diversidad y equitatividad por sitio de muestreo en el Refugio de Fauna Silvestre Isla de Aves, Venezuela

TABLE 5
Octocoral species and diversity, dominance and evenness index per sampling site at the Isla de Aves Wildlife Refuge, Venezuela

ESPECIE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
E. caribaeorum			x											xx	x	
P. americana	xx	xxx	xxx	xxx		xxx	xxx	xxx	x	xxx	xxx		xxx	xx	xxx	xx
P. bipinnata		x				x	x	x		xx	xx		x	xx		
Pseudopterogorgia sp.		x					x	x						x		x
Pterogorgia sp.										xx	x		xx			x
G. ventalina										x	x		x			
Eunicea sp.						x				x	x					
N° de especies	1	3	2	1	0	2	3	3	1	5	5	0	4	4	2	3
N° de colonias	7	30	36	53	0	24	38	31	3	55	70	0	45	29	28	11
N° de transectas	2	4	6	4	6	6	6	5	2	2	3	6	2	6	6	1
Dominancia_D	1	0.73	0.90	1	-	0.81	0.86	0.70	1	0.39	0.56	-	0.68	0.86	0.88	0.61
Shannon_H	0	0.45	0.14	0	-	0.29	0.23	0.47	0	1.15	0.79	-	0.55	0.23	0.17	0.58
Equitatividad_J	0	0.49	0.20	0	-	0.41	0.25	0.68	0	0.78	0.62	-	0.50	0.26	0.19	0.84

Se incluyen solo especies observadas en transectas. x = rara (1 a 5 colonias); xx= común (6 a 15 colonias); xxx = abundante (>15 colonias).
Include only the species observed in transects. x = rare (1 to 5 colonies); xx= common (6 to 15 colonies), xxx = abundant (>15 colonies).

superiores al 30%, siendo 59.75% (SE=11.79) el valor máximo (sitio n° 3, ubicado hacia sotavento de la isla, a 10 de profundidad). La categoría *Roca*, que representa el sustrato conformado por roca de playa, se registró en cinco sitios. El porcentaje de cobertura para esta categoría fue incluso superior a la de coral muerto en los sitios 1 y 5 (el primero ubicado a 6.6 metros de profundidad hacia sotavento y el segundo representado por la laguna del sector norte), lo que no es de extrañar, dado el basamento de roca que tiene la isla. Por otro lado la categoría *coral muerto con algas* a pesar de presentar una baja cobertura promedio, 5.06 % (SE=1.50), se registró en varias de los sitios que poseen una baja cobertura de coral muerto.

En lo que respecta a los octocorales, se pueden destacar los sitios 4 y 8 como los de mayor cobertura lineal, con 21.35% (SE=3.65) y 19.64%(SE=3.63) respectivamente, siendo 6.38% (SE=0.99) el valor promedio para todos los sitios. Ambos puntos de muestreo donde se registraron los mayores porcentajes de cobertura lineal (4 y 8) presentan una intensidad de corrientes moderada y se encuentran ubicados al noroeste de la isla, el primero a 9 de metros de profundidad y el segundo entre 14 y 15 metros. En dos de los sitios de muestreo (5 y 12) ambos ubicados al norte y caracterizados por fuertes corrientes y oleaje, no se registró cobertura lineal para estos organismos La cobertura promedio de octocoral muerto fue baja: 0.09% (SE=0.09), ya que esta categoría se registró únicamente en dos de los quince sitios. Entre el resto de las categorías bentónicas se pueden destacar las algas, con una cobertura lineal promedio de 11.60 % (SE=1.80) siendo el sitio 7, situado al norte franco de la isla, a 11 metros de profundidad, el de mayor cobertura (31.13%; SE= 4.45).

Estructura de tallas: Dada la importancia de los corales *P. astreoides*, *P. strigosa* y *S. siderea* y del octocoral *P. americana*, en

CUADRO 6

Porcentaje promedio (error estándar) de cobertura de coral vivo (incluyendo hidrocorales) y otras categorías bentónicas para 15 sitios de muestreo en el Refugio de Fauna Isla de Aves, Venezuela

TABLE 6

Average percentage (standar error) of live coral coverage and others benthic categories for 15 sampling sites of the Isla de Aves Wildlife Refuge, Venezuela

Sitio	Coral vivo	Coral muerto	Coral muerto con algas	Octocoral vivo	Octocoral muerto	Algas	Roca	Arena	Algas-escombros	Arena-escombros	Escombros	N° transectas
1	12.10 (4.10)	13.35 (10.35)	-	2.05 (1.95)	-	-	45.10 (38.90)	26.65(26.65)	-	-	-	2
2	21.53 (2.73)	0.68 (0.68)	11.83 (6.44)	10.33 (2.90)	-	6.63 (5.26)	-	3.40 (2.77)	3.63 (2.94)	-	-	4
3	12.90 (3.49)	59.75 (11.79)	-	2.10 (1.00)	-	-	15.32 (9.91)	4.22 (2.74)	-	2.73 (2.46)	1.08 (0.69)	6
4	8.33 (2.71)	43.45 (4.45)	-	21.35 (3.65)	1.43 (1.43)	0.63 (0.63)	-	17.28 (6.77)	-	0.13 (0.13)	1.40 (1.40)	4
5	28.97 (4.86)	5.52 (3.18)	-	-	-	-	55.40 (5.40)	10.02 (5.58)	-	-	-	6
6	10.97 (4.36)	38.10 (12.69)	-	0.53 (0.36)	-	28.31 (9.64)	-	13.04 (4.69)	-	4.73 (4.18)	1.00 (0.82)	6
7	27.00 (4.04)	-	-	8.20 (2.10)	-	31.13 (4.45)	-	6.83 (3.39)	7.93 (4.19)	0.78 (0.61)	0.33 (0.33)	6
8	21.24 (3.06)	1.20 (1.20)	10.16 (3.36)	19.64 (3.63)	-	3.32 (0.60)	-	3.14 (1.28)	7.06 (2.21)	0.52 (0.52)	-	5
9	15.44 (5.44)	54.69 (3.69)	-	2.75 (2.25)	-	-	5.50 (5.50)	16.94 (2.06)	-	-	-	2
10	50.50 (9.50)	-	-	11.50 (5.50)	-	15.25 (1.75)	-	3.25 (1.25)	6.75 (1.25)	0.25 (0.25)	-	2
11	16.80 (1.31)	-	15.17 (6.50)	17.57(0.70)	-	14.63 (3.28)	-	4.17(2.20)	4.93 (1.04)	0.83 (0.83)	-	3
12	42.33 (6.64)	-	-	-	-	29.33 (4.09)	-	0.50 (0.34)	7.42 (3.52)	0.67 (0.67)	2.25 (2.25)	6
13	20.10 (2.60)	26.20 (11.80)	-	11.85 (3.85)	-	5.25 (5.25)	-	24.75 (6.75)	-	3.70 (3.70)	-	2
14	19.17 (5.80)	5.53 (3.56)	29.38 (10.66)	3.43 (1.53)	0.10 (0.10)	1.82 (1.44)	-	8.44 (4.51)	14.35(8.1)	5.88 (3.00)	2.98 (2.73)	6
15	26.78 (5.55)	-	-	0.92 (0.45)	-	13.96 (2.42)	7.28 (5.28)	2.32 (0.98)	11.78(7.0)	-	-	6
X	22.30 (1.73)	15.29 (3.03)	5.06 (1.50)	6.38 (0.99)	0.09 (0.09)	11.60 (1.80)	8.63 (2.50)	7.85 (1.34)	4.95 (1.18)	1.53 (0.54)	0.77 (0.34)	

términos de su abundancia y amplia distribución a lo largo de los sitios de muestreo, a continuación se presentan las estructuras de tallas únicamente para estas especies.

En términos generales, la mayor parte de las colonias de las tres especies de corales se ubicaron en las primeras categorías de tallas, es decir las más pequeñas, tanto en su diámetro máximo como altura (Fig. 3 A y B). En el caso de *P.astreoides*, el 53.48% de las colonias eran pequeñas (3 a10 cm de diámetro máximo; Fig. 3A) y bajas (72.83% entre 0 - 5cm de altura; Fig. 3B). En ambos casos (diámetro y altura) se registró una disminución en la proporción de colonias de *P.astreoides* hacia las tallas más grandes. En lo que respecta a *P.strigosa,* el 74.62 % de las 327 colonias midieron entre 3 y 30 cm de diámetro máximo, ubicándose en las tres primeras categorías de tallas (Fig. 3A), mientras que la altura del 43.73 % de las colonias no superó los 5cm (Fig. 3B). Finalmente en el caso de *S.siderea*, la mayor parte de las

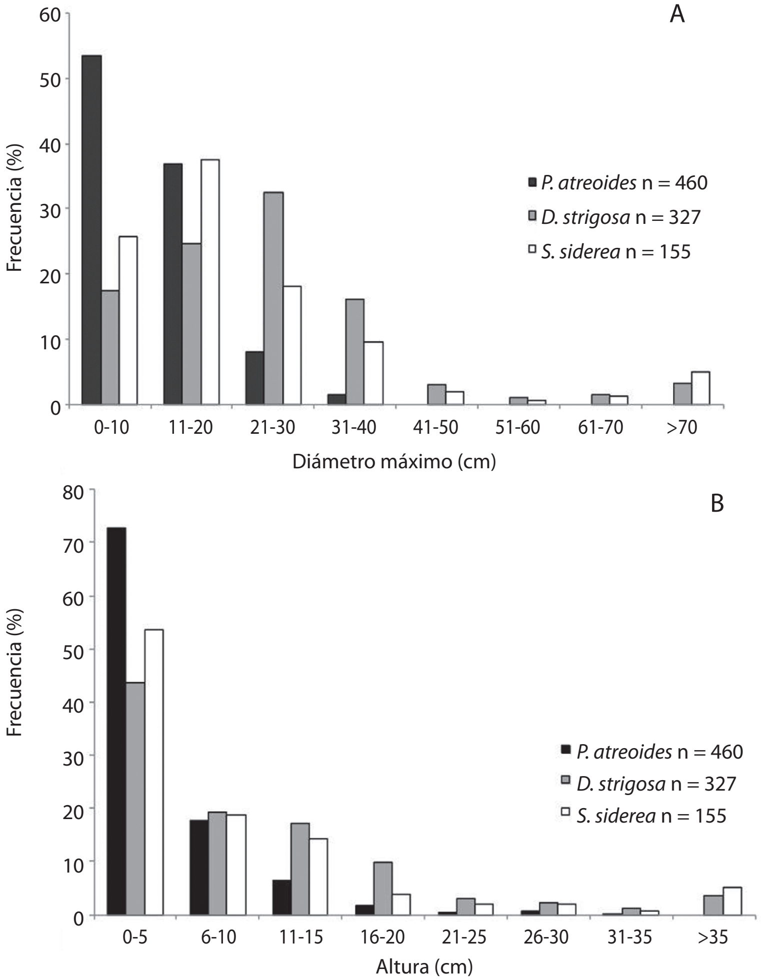

Fig. 3. Histograma de frecuencia de tallas: diámetro máximo (A) y altura (B) de las tres especies de corales pétreos de mayor abundancia en el Refugio de Fauna Silvestre Isla de Aves. Para cada especie se incluye una muestra representativa de colonias sin distinción de sitio. Diámetro mínimo incluido = 3 cm; altura mínima incluida= 0 cm (colonias incrustantes).
Fig. 3. Size frequency histogram: maximum diameter (A) and height (B) of the three hard coral species most abundant in the Isla de Aves Wildlife Refuge. For each species includes a representative sample of colonies regardless of site. Minimum diameter included= 3 cm, minimum height included = 0 cm (encrusting colonies).

colonias (55.48%) presentaron entre 11 y 30 cm de diámetro máximo (Fig. 3A), situándose especialmente entre los 21 y 30cm. La altura de las colonias de esta especie (Fig. 3B) al igual que las de *P.strigosa* en su mayoría no superó los 5cm (53.55%).

Una aproximación más detallada de las dimensiones de las colonias para estas especies en algunas de las localidades de muestreo, se puede observar en el Cuadro 7. Las altas desviaciones estándar que se presentan en la mayor parte de los casos, reflejan la variabilidad en

CUADRO 7

Diámetro y altura promedio (cm) de *Porites astreoides*, *Diploria strigosa* y *Siderastrea siderea* en algunos sitios de muestreo en el Refugio de Fauna Silvestre Isla de Aves, Venezuela

TABLE 7

Average diameter and height (cm) of *Porites astreoides*, *Diploria strigosa* y *Siderastrea siderea* in some survey sites of the Isla de Aves Wildlife Refuge, Venezuela

Especie	Sitio	Diámetro máx. (cm)	Altura (cm)	N° de colonias
Porites astreoides	1	9.55 ± 5.22	6.36 ± 2.34	11
	2	8.08 ± 3.51	4.78 ± 3.95	24
	3	10.19 ± 4.75	6.04 ± 3.03	54
	4	14.56 ± 6.66	9.82 ± 5.76	16
	5	15.66 ± 8.00	7.73 ± 6.03	248
	6	9.20 ± 4.99	4.9 ± 4.00	20
	9	10.50 ± 3.69	5 ± 0.0	10
	11	12.67 ± 4.42	4.67 ± 4.69	18
	13	10.25 ± 5.95	4.9 ± 1.68	20
	14	11.56 ± 7.74	3.92 ± 5.64	39
Pseudodiploria strigosa	1	28.75 ± 17.52	14.38 ± 12.01	24
	2	22.86 ± 16.72	9.07 ± 9.88	15
	3	22.90 ± 9.12	9.28 ± 6.54	68
	4	40.36 ± 31.44	18.57 ± 20.31	28
	6	34.67 ± 19.64	14.67 ± 13.71	45
	7	24.78 ± 15.45	10.66 ± 10.47	45
	8	21.67 ± 23.29	13.78 ± 16.93	9
	9	17.86 ± 7.56	6.43 ± 3.78	7
	13	20.77 ± 7.60	5.7 ± 2.77	13
	14	24.33 ± 10.73	9.67 ± 9.35	67
	16	34.16 ± 7.36	9.17 ± 7.36	6
Siderastrea siderea	1	26.82 ± 24.42	11.82 ± 15.85	11
	2	14.5 ± 7.96	3.86 ± 4.33	14
	3	23.20 ± 13.92	8.78 ± 7.77	50
	6	54.62 ± 51.94	23.85 ± 21.23	13
	7	20.83 ± 13.58	9.37 ± 11.46	41
	8	28.89 ± 27.78	10.58 ± 15.50	19
	9	19.62 ± 11.98	9.23 ± 4.49	13
	11	34.62 ± 25.94	18.45 ± 17.78	13
	13	25.71 ± 30.55	10.24 ± 13.92	31
	14	20.50 ± 8.13	11.7 ± 5.37	30
	16	16.76 ± 7.28	3.41 ± 4.58	17

Nota: el n° de colonias mostrado por sitio representa una muestra del total registrado.
Note: the number of colonies shown by site represents a sample of the total registered.

las tallas de las colonias en un mismo sitio de muestreo, sin embargo se puede señalar que, en el caso de *P.astreoides*, las colonias de mayores dimensiones están en el sitio 5, el cual representa la laguna situada al norte de la isla, tanto en relación al diámetro máximo (15.66±8.00 cm) como la altura (7.73±6.03cm). Las colonias de *P.strigosa* presentaron sus mayores dimensiones promedio en los sitios 4 y 6, el primero ubicado al Noroeste, hacia sotavento de la isla, a 9 m de profundidad caracterizado por corrientes de intensidad moderada y el segundo situado al norte franco, entre 8 y 10 metros de profundidad, con alta intensidad de corrientes. En lo que respecta a *S.siderea*, se repite el sitio 6 como el de colonias con las mayores dimensiones.

Por otro lado, en lo que respecta al octocoral *P. americana* (Fig. 4 A y B), el diámetro máximo del 73% de las colonias se ubicó en las primeras tres categorías de tallas (Fig. 4A), que abarcan de 5 a 30cm, mientras que la altura de las colonias presentó una distribución más uniforme a lo largo de las diferentes categorías de tallas (Fig. 4B) sin predominancia de alguna en particular.

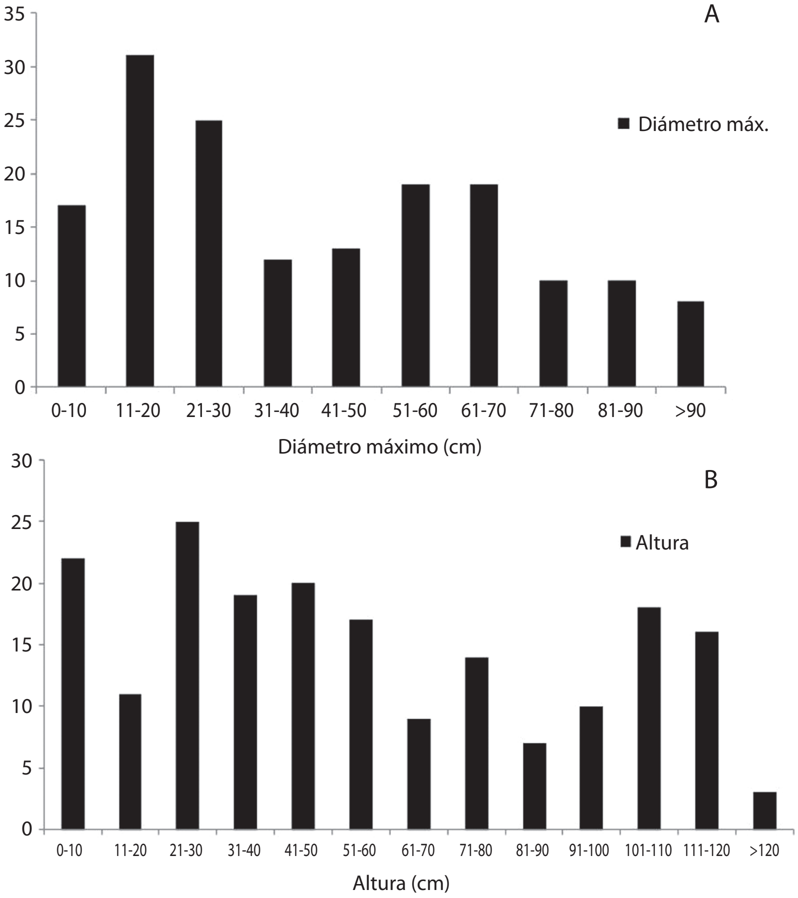

Fig. 4. Distribución de tallas (diámetro máximo y altura) del octocoral *Pseudopterogorgia americana* en el Refugio de Fauna Silvestre Isla de Aves

Fig. 4. Size frequency histogram (maximum diameter and height) of the octocoral *Pseudopterogorgia americana* in the Isla de Aves Wildlife Refuge.

DISCUSION

Las comunidades marinas bentónicas del Refugio de Fauna Silvestre Isla de Aves, están formadas principalmente por 36 especies de corales pétreos y cuatro especies de hidrocorales. Esta riqueza es menor que la reportada para otras islas del territorio venezolano. Así, en el Parque Nacional Archipiélago de Los Roques, se han reportado 57 especies por Hung (1985); 69 (61 hermatípicos con zooxantelas y 8 ecomorfos) por Weil (2003) y 55 (Villamizar et al. en prep.). Asimismo para un arrecife de la Orchila, Urich (1977) reporta 62 especies (54 hermatípicos) y en La Blanquilla Weil (2003) encontró 47 especies (43 con zooxantelas). En otras áreas del país por el contrario, la riqueza de especies de corales es menor que la de Isla de Aves. Del Mónaco et al. (2010) registraron 23 especies en la isla de La Tortuga; Buccimazza (1984) encontró 25 para la Isla de Coche; Weil (no publicado) registró 31 especies (26 hermatípicos) en las islas de Coche y Cubagua al sur de Margarita y Boadas (2011) reportó un total de 12 especies para la isla de Los Frailes, cerca de la isla de Margarita. En relación a las Islas cercanas a la costa continental del país, en el zona occidental, en las Islas Ratón, El Rey, Isla Larga, Alcatraz y Santo Domingo, se han registrado 19 especies de corales pétreos (Rodríguez et al. 2011), Bahía de Adícora, con 13 especies (Eizaga, 2013) y en el Parque Nacional Morrocoy, 45 especies (Pauls 1995) y posteriormente, 26 especies (Villamizar 2000). En el oriente del país, del Parque Nacional Mochima se conocen 37 especies (Olivares 1971, Pauls 1982); en dos localidades del Golfo de Cariaco Sant *et al*. (2002) encontraron 33 especies de corales pétreos y en las Bahías de Santa Fe, Bahía de Mochima y Manzanillo, hallaron 22 especies.

Tomando como referencia el número de especies de corales (principalmente con zooxantelas y en menor extensión sin zooxantelas) en otras localidades del Caribe como Panamá (62), Costa Rica (47), República Dominicana (56), Martinica (53) y Cuba, Jamaica y Puerto Rico con 72 especies, (Miloslavich et al. 2010, Weil, 2003, 2006; Ballantine et al., 2008; Vandel, Pichon & Joannot, 2012), podría decirse que Isla de Aves presenta un bajo número de especies coralinas. Sin embargo, la riqueza estimada se aproxima a reportes de localidades más cercanas a la Isla hacia el este, como Guadalupe con 42 especies y Dominica con 36 y supera al número de especies reportado para otras islas como Saint Martin con 30 especies (Steiner, 2003, Vandel et al. 2012). En el caso de los octocorales, el número de especies registrado (13) se puede considerar muy bajo en relación a otros sitios como Cuba (81); Panamá (61), Antillas Holandesas (48), Republica Dominicana (44) Jamaica (43); Costa Rica y Puerto Rico (26 sp.) (Miloslavich & Klein, 2005; Weil, 2006; Etnoyer, Wirshing & Sánchez, 2010).

En lo que respecta a las diferencias de las comunidades de corales entre las estaciones de muestreo, los dos sitios que presentaron la mayor diversidad (sitios 8 y 10) se caracterizaron por ser zonas relativamente profundas. La estación 10, ubicada hacia Barlovento de la Isla, área caracterizada por fuertes corrientes, fue el sitio de muestreo de mayor profundidad entre todos los evaluados (21 m) y la estación 8 situada entre 14 y 15 m de profundidad, se diferenció del resto de las estaciones de muestreo por presentar un arrecife desarrollado, es decir con una estructura heterogénea de carbonato de calcio, dando lugar a un mayor número de hábitats (mayor heterogeneidad espacial) y en consecuencia a una mayor riqueza de especies. En términos generales las zonas profundas presentaron una mayor diversidad de corales que las zonas someras, a pesar de que el esfuerzo de muestreo en estos sitios (n° de transectas) fue menor debido a razones logísticas.

Con relación a la equitatividad, destacan los menores valores estimados en las estaciones 5 y 12. Esto se debe a la dominancia de *P.astreoides* en el primer sitio y del hidrocoral *M. squarrosa* en el segundo, por lo cual los índices de diversidad de estas estaciones fueron los más bajos. Estos dos sitios fueron los más “diferentes” del resto, el primero por ser una laguna de poca profundidad, expuesta a constante oleaje, y el segundo, también una zona somera (5 m.), situado al noreste, se caracterizó por la presencia de grandes "bloques" de *M. squarrosa* y de roca de playa en algunas áreas. Cuando el oleaje y las corrientes son muy intensas pueden afectar el establecimiento y desarrollo de los octocorales (Kinzie, 1973; Guzmán & Cortés, 1985) por lo cual la ausencia del octocoral dominante *Pseudopterogorgia americana* para estos dos únicos sitios, pudiera estar relacionada con estas variables físicas. Es posible que haya ocurrido la remoción de colonias de este octocoral por el paso de huracanes o ciclones en la zona, una posible evidencia de esto fue el encuentro anual (entre el 2009 y 2012) de numerosas bases y esqueletos de octocorales en la costa, sin embargo la ausencia de registros cuantitativos previos limitan las conclusiones que se puedan realizar al respecto.

En las comunidades coralinas de Isla de Aves las especies de corales pétreos más abundantes son *P. astreoides*, *P.strigosa* y *S.siderea*. Estas especies son abundantes en diversas localidades del Caribe (Guzmán & Guevara, 2001; Bastida-Zavala, et al., 2000; Valdivia & De la Guardia, 2004; Caballero, Rosales & Alcalá, 2005; Weil, 2003; 2006; Lirman & Fong, 2007; García-Sais et al., 2009; Domínguez et al., 2010) y se caracterizan por presentar una alta resistencia a diferentes factores de perturbación, entre los que se pueden mencionar la sedimentación, dada a la capacidad que tienen de eliminar partículas de sedimento acumuladas en la superficie de sus colonias (Rogers, 1983; Sullivan, Chiappone & Lott, 1994). *S. siderea*, presenta gran tolerancia a cambios de temperatura (Kemp et al., 2011) y alta plasticidad fenotípica, manifestada en cambios de morfología esqueletal de acuerdo al ambiente donde se encuentre (Foster 1979). *P.astreoides*, la especie de mayor abundancia relativa en el presente trabajo, se caracteriza por presentar altas tasas de fecundación y corta longevidad (Bak & Engel, 1979; Chornesky & Peters, 1987). Esta especie en particular se ha señalado como una de las más abundantes actualmente en arrecifes someros del Caribe, dado el incremento significativo de su abundancia en los últimos 30 años (Green, Edmunds, & Carpenter, 2008) producto de la combinación de altas tasas de reclutamiento y tolerancia a condiciones adversas como el incremento de la temperatura, ya que poseen zooxantelas de clados resistentes a fenómenos de blanqueamiento (LaJeunesse, 2002; Lirman & Miller, 2003; Green, et al., 2008). Las pequeñas dimensiones registradas en la mayor parte de las colonias de *P.astreoides* de la presente investigación, sugieren tasas de reclutamiento elevadas para esta especie en el área de estudio (Bak & Meesters, 1999). Igualmente *P. strigosa* y *S.siderea* presentan estructuras de tallas donde predominan las colonias de tamaños reducidos, que posiblemente corresponden a colonias jóvenes. Incluso es importante acotar aunque no se presentan resultados al respecto, la observación *in situ* de numerosos reclutas de las tres especies durante los muestreos.

La mayor abundancia de especies como *S.siderea*, *P.strigosa* y *P.astreoides* reportada en diversos arrecifes de la región del Caribe, se encuentra relacionada con el deterioro progresivo que han sufrido las principales especies de corales constructores de arrecifes, lo que ha generado cambios en la composición de especies de los mismos (Green et al., 2008). En el caso de Isla de Aves, no se conocen reportes previos que puedan tomarse como referencia sobre posibles cambios en la composición de las especies dominantes, sin embargo, la presencia de grandes colonias muertas de especies como *Orbicella faveolata* en varias zonas en los alrededores del Refugio, especialmente en áreas profundas, así como de esqueletos de *A. palmata* y el hallazgo de restos coralinos de *Acropora cervicornis* en la costa, sugieren una historia similar a la de la mayor parte de los arrecifes del Caribe, donde epidemias de enfermedades (ej: Banda blanca en Género *Acropora* ; Gladfelter 1982, Aronson & Precht, 2001) y el cambio climático global desencadenante de fenómenos de blanqueamiento, en conjunción con la mortandad del erizo *Diadema antillarum* (Lessios, 1988; Carpenter, 1990) entre otros factores, .han generado un deterioro progresivo de estas comunidades (Szmant & Gassman, 1990; Bak & Luckhurst, 1980; Bythell, Gladfelter & Bythell, 1993; Bruckner & Bruckner, 2003; Steiner & Kerr, 2008). Es importante mencionar que aunque en muy baja proporción, se han observado en los corales algunas enfermedades en la localidad de estudio (banda negra, banda amarilla, lunares oscuros, al igual que palidez y blanqueamiento. Es posible que este resultado esté relacionado con la época del año en la cual se realizaron las expediciones al area de esudio (julio y agosto), ya que es durante los meses de septiembre y octubre cuando comienzan a evidenciarse los efectos del estrés fisiológico en las colonias, debido al incremento y mantenimiento de altas temperaturas en la columna de agua (por mas de 12 semanas), así como las subsecuentes afectaciones por enfermedades. Con relación a las poblaciones de *D.antillarum*, se observaron muchos individuos adultos de la especie entre escombros coralinos y rocas de playa en los fondos someros, sin embargo, no se dispone de información alguna sobre sus densidades.

Entre los parámetros indicadores de la salud de un arrecife se encuentra el porcentaje de cobertura viva que presente (Jackson, 2013). La cobertura promedio de coral vivo estimada para Isla de Aves (22.30%) se puede considerar dentro de la amplitud de valores que se ha reportado actualmente para el Caribe , los cuales han descendido notablemente en las últimas décadas dado el deterioro que han sufrido los arrecifes (Jackson, 2013). En la zona geográfica donde se encuentra Isla de Aves, uno de los factores que pudiera tener gran impacto en la cobertura de coral vivo son los huracanes y tormentas, ya que en esta área son muy frecuentes estos fenómenos climatológicos (Arteaga, 2002). Aunque no se tienen datos específicos sobre la localidad de estudio, se pueden mencionar casos ocurridos en islas relativamente cercanas a Isla de Aves, como Martinica donde la cobertura promedio de coral vivo pasó de de 37.3%. a 23.2 %, luego del Huracan Dean en el año 2007 (Rousseau, Galzin & Maréchal, 2010) Asimismo, en Dominica, la cobertura, pasó de 17% (Steiner, 2003) a menos de 5% (Arnold et al., 2010) luego de un huracán y Anguilla donde la cobertura descendió de 14% en 1990 a 4% en 2009 (Wynne, 2013). En otra isla cercana, Guadalupe, Bouchon et al. (2008) reportaron la destrucción de corales, esponjas y octocorales hasta los 25m de profundidad por olas de 13m de altitud generadas por los huracanes Luis, Marylin y Lennin, en la década de los 90. Considerando la información recabada por Olivares & Piñero (2010) en un recuento histórico sobre ciclones tropicales ocurridos en el Océano Atlántico entre 1871 y 2008, se puede tener una idea del impacto que estos fenómenos han generado en la zona a lo largo del tiempo. En dicho compilado se reportan 113 ciclones cercanos a la Isla, 67 de estos huracanes, 36 tormentas tropicales y 10 no clasificados por no presentar datos. Los meses de agosto y septiembre representaron las épocas con mayor porcentaje de ocurrencia de ciclones, afectando principalmente los sectores Sur y Norte de la Isla.

Una característica particularmente importante de Isla de Aves es el bajo impacto antropógenico que tiene, comparado con otras islas del Caribe. En esta isla no hay presión de pesca ni de turismo y el desarrollo de actividades humanas es muy bajo, ya que la población residente en la isla es mínima (15 personas aprox.). La única actividad que se pudiera considerar de impacto es el vertimento de los desechos orgánicos al mar sin planta de tratamiento, situación sobre la que se tomarán medidas próximamente y por otro, lado las grandes cantidades de guano de las aves residentes en la Isla, probablemente tengan un efecto sobre las aguas circundantes en el sector occidental, que debe ser evaluado. Es muy distinta la situación en varias de las Islas cercanas como Guadalupe, Martinica, Antigua y Bermuda, las cuales tienen un gran desarrollo turístico y costero (Smith, Rogers & Bouchon, 1997). Incluso en Martinica se reportó una invasión de *Sargassum* probablemente por eutrofización producto de descargas humanas en la década de los años 90, que afectó también a Guadalupe (Bouchon, Bouchon, Louis, 1992).

Aún se deben seguir las investigaciones sobre las comunidades bentónicas de Isla de Aves, especialmente en las zonas más profundas y se deben hacer evaluaciones en diferentes épocas del año, esto último permitiría evaluar los efectos que puedan generar los cambios en variables ambientales como la temperatura, o la presión atmosférica (relacionada con la frecuencia e intensidad de tormentas y huracanes) en las comunidades de corales y octocorales de la Isla, así como de otras comunidades de invertebrados presentes, factores que posiblemente son los responsables de gran parte del deterioro o perdida coralina en estos fondos. Los resultados de este tipo de estudios en Isla de Aves, no sólo son de gran valor para Venezuela, por las razones anteriormente citadas en este trabajo, sino para las islas cercanas ubicadas al este y al norte de Isla de Aves (sujetos a condiciones ambientales similares), ya que sus arrecifes y comunidades coralinas podrían ser consideradas como “pristinas” con relación al impacto directo de actividades humanas derivadas del uso de la tierra, modificación de las costas, tratamiento de las aguas, turismo desmesurado, pesquerías, u otro tipo de actividad antropogénica contaminante, representando un “blanco”, de gran interés comparativo.

AGRADECIMIENTOS

Este trabajo forma parte del Subproyecto “Caracterización biótica y condición de salud de las comunidades coralinas y arrecifes de Isla de Aves” Coordinado por E.Villamizar, (IZET, UCV). Se encuentra enmarcado dentro del MacroProyecto Institucional del Instituto de Zoología y Ecología Tropical de la UCV, que lleva por título “Evaluación Integral de las Condiciones bióticas y abióticas de Isla de aves: estudio de línea base”. Los autores agradecen al personal de la Base Científico Naval Simón Bolívar por toda la colaboración prestada durante la ejecución de las Campañas Científicas, a la Dirección de Hidrografía y Navegación (DHN) por el apoyo logístico y a la Universidad Central de Venezuela por colaborar parcialmente con los viáticos y al Fondo Nacional de Ciencia y Tecnología (FONACIT) por la subvención otorgada para participar en la 36^{ava} edición de los Laboratorios Marinos del Caribe. Agradecemos igualmente a Freddy Bustillos por la elaboración del mapa y a los evaluadores del presente manuscrito, cuyo análisis crítico permitió enriquecerlo.

RESUMEN

El Refugio de Fauna Silvestre Isla de Aves (RFSIA) representa la porción más septentrional del territorio Venezolano, generando 135 000km^2 de Zona Económica Exclusiva. Los estudios sobre sus comunidades coralinas son escasos y en su mayoría datan de la década de los setenta, por su ubicación a 650km al nor-este del Puerto de la Guaira y por su condición de zona militar. Para actualizar y obtener una línea base cuantitativa sobre la estructura de las comunidades coralinas de la isla, se estimó la cobertura lineal, estructura de tallas, composición y abundancia de corales y octocorales. Evaluamos 16 sitios alrededor de la isla empleando el Protocolo AGGRA (banda-transectas de 10m^2) entre 1.5 y 21m de profundidad (n= 67 transectas) y se realizaron censos visuales en 5 sitios más. Observamos un total de 2 327 colonias pertenecientes a cuatro especies de hidrozoos y 36 especies de corales pétreos pertenecientes a 11 familias. Los valores de diversidad, dominancia y equitatividad de la comunidad de corales oscilaron entre 0.78 y 2.12 (S-W); 0.15 y 0.61 y 0.57 y 0.92 respectivamente. La mayor parte de los corales presentaron valores de abundancia relativa menores al 3%, a excepción de *Porites astreoides* (25.57%), *Pseudodiploria strigosa* (18.22%) y *Siderastrea siderea* (14.44%). La estructura de tallas de estas especies estuvo representada en su mayoría por las categorías de tallas más pequeñas, entre los 3 y 30cm de diámetro máximo y entre 0 y 5cm de altura. Se identificaron un total de 13 especies de octocorales pertenecientes a 3 familias, siendo *Pseudopterogorgia americana* la especie dominante en abundancia. La cobertura promedio de coral vivo (incluyendo hidrocorales) fue de 22.30% (SE=1.73) (coral muerto 15.45%,SE=3.28). El coral muerto es la que presentó el mayor porcentaje de disimilaridad entre sitios (9.21%) (ANOSIM); con un porcentaje de contribución de 16.57% (Análisis SIMPER). La cobertura viva lineal de octocorales varió entre 0 y 21.35% (SE=3.65) con un promedio de 6.38% (SE=0.99). Las investigaciones sobre las comunidades bentónicas de Isla de Aves deben continuar, especialmente en las zonas más profundas, para evaluar las ocndiciones ecológicas.

Palabras claves: corales, octocorales, abundancia, diversidad, Isla de Aves, Venezuela.

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Evidence of initial coral community recovery at Discovery Bay on Jamaica's North Coast

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Received 01-VIII-2013 Corrected 04-II-2014 Accepted 24-III-2014

Abstract: Current challenges to coral reef sustainability include overfishing, destructive fishing practices, bleaching, acidification, sea-level rise, starfish, algae, agricultural run-off, coastal and resort development, pollution, diseases, invasive species and hurricanes. We used SCUBA belt transects to record coral cover and digital image analysis in the Dairy Bull Reef off the north coast of Jamaica and found that it is a positive example of how reefs can recover after major environmental disturbance. Live coral cover increased from 13±5% in 2006 to 31±7% in 2008, while live *Acropora cervicornis* increased from 2±2% in 2006 to 22±7% in 2008. Coral cover levels were maintained until 2012. Rev. Biol. Trop. 62 (Suppl. 3): 137-140. Epub 2014 September 01.

Key words: hurricanes, bleaching, MPAs, climate change, global warming, Belize, Jamaica.

Current challenges to coral-reef sustainability, include overfishing, destructive fishing practices, coral bleaching, ocean acidification, sea-level rise, algal blooms, agricultural run-off, coastal and resort development, marine pollution, increasing coral diseases, invasive species, hurricane/cyclone damage, and, in Indo-Pacific regions, crown-of-thorns starfish outbreaks. The fringing reefs around Discovery Bay in Jamaica have seen a number of climate-related challenges in recent years, notably several hurricanes as well as a mass bleaching event in the Caribbean in 2005 (Jones et al., 2008). Diary Bull reef has for several years been the fringing reef with the most coral cover, with a benthic community similar to that of the 1970s (Huston, 1985), and it was the subject of the study which suggested a rapid phase-shift reversal (Idjadi et al., 2006). After the 2005 bleaching event there was a major loss of live coral cover, particularly of *A. cervicornis* (Quinn & Kojis, 2008). Here, we investigate coral cover at Dairy Bull reef over a ten year period, from 2002-2012.

MATERIALS AND METHODS

Jamaican sites and sampling: Four randomly located transects, which were not continuous, each 15m long and separated by at least 5m, were laid at between 5-8.5m depth at Dairy Bull reef (18°28.083'N; 77°23.302'W) near Discovery Bay, Jamaica. GPS coordinates were determined using a hand-held GPS receiver (Garmin Ltd.). The belt transect method using SCUBA was used to record coral cover (English, Wilkinson & Baker, 1997) after photography and then by digital image analysis using UTHSCSA (University of Texas Health Science Center, San Antonio, Texas) Image Tool image analysis software. Corals 2 m either side of the transect lines were photographed for archive information. Percentage cover was determined for total live coral, and the dominant species *Acropora cervicornis*, *Porites astreoides*, and *Acropora palmate* as well as for *Diploria strigosa, Sidastrea siderea* and *Acropora palmata*.

This work was conducted at Discovery Bay during March 26-April 19 in 2002, March 18-April 10 in 2003, July 23-August 21 in 2004, July 18-August 13 in 2005, April 11-18 in 2006, December 30 in 2006-January 6 in 2007, and July 30-August 16 in 2008, July 27-August 8 in 2009, April 14-16 in 2010 and July 30-August 2 in 2012. Surveys were made at the same locations at the same sites each year. One or two-factor ANOVA was used to compare coral data among sites; ± error values represent standard errors of the data.

RESULTS

Dairy Bull reef: Figure 1 shows mean percentage cover +1 S.E. of total live coral, and dominant species *Acropora cervicornis*, *Porites astreoides*, and *Acropora palmata* at Dairy Bull reef from 2002 to 2012. Table 1 shows mean percentage cover +1 S.E. for *Acropora cervicornis*, *Porites astreoides*, *Diploria strigosa, Sidastrea siderea and Acropora palmata*.

The major Caribbean-wide bleaching event was in 2005 (Eakin et al., 2010). Live coral cover increased from 13±5% in 2006 to 31±7% in 2008, while live *Acropora cervicornis* increased from 2±2% in 2006 to 22±7% in 2008. Coral cover levels were maintained until 2012. Statistical analysis of the recovery showed that only *Sidastrea siderea* and *Diploria strigosa* had coral cover in 2012 that was statistically significantly similar to coral cover in 2002 and 2005 before bleaching.

DISCUSSION

Diary Bull reef has for several years been the fringing reef around Discovery Bay, Jamaica, with high rugosity, the most coral cover,

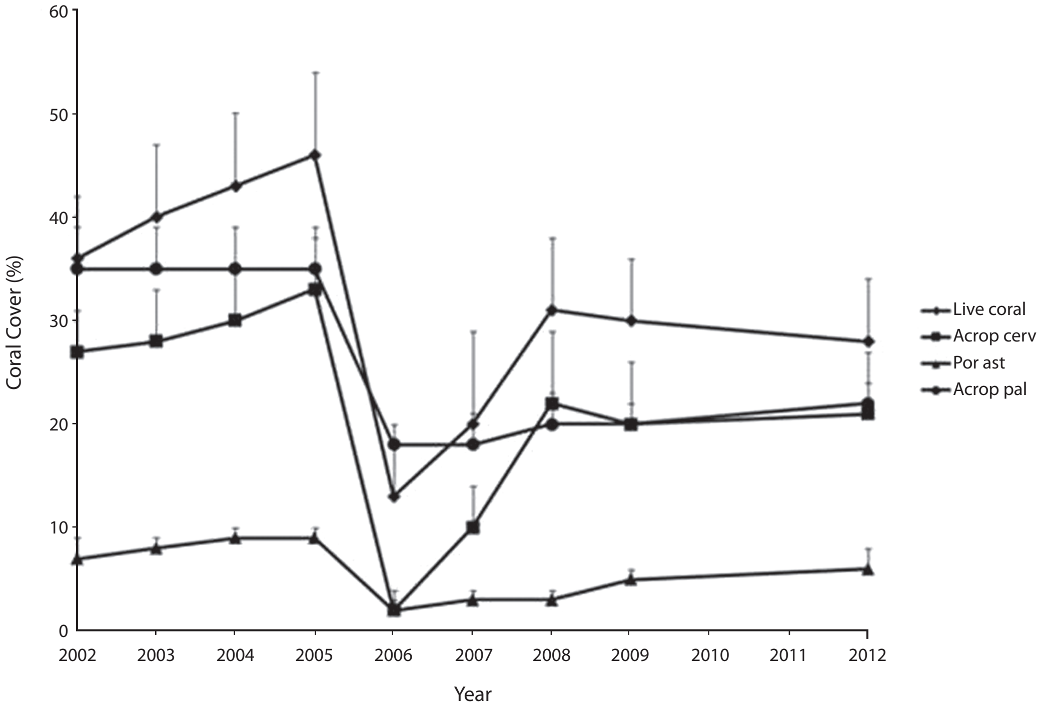

Fig 1. Coral cover at the Dairy Bull reef site from 2002-2012, for: live coral (♦); *Acropora cervicornis* (■, Acrop cerv); *Porites astreoides* (▲, Por ast); *Acropora palmata* (●, Acrop pal). Values are shown + 1 S.E.

TABLE 1
Mean percentage coral cover of live coral, *Acropora cervicornis*, *Porites astreoides*, *Diploria strigosa, Sidastrea siderea and Acropora palmata* species along transects at Dairy Bull, from 2002-2005 (pre-bleaching), 2006-2009, and 2012

Year	Live coral	*A. cervicornis*	*S. siderea*	*D. strigosa*	*P. astreoides*	*A. palmata*
2002	36±6	27±4	6±2	2±0.3	7±2	35±4
2003	40±8	28±5	7±2	2±0.3	8±1	35±4
2004	43±9	30±5	7±2	3±0.3	9±1	35±4
2005	46±8	33±5	6±2	2±0.3	9±1	35±4
2006	13±5	2±2	2±1	0±0	2±1	18±2
2007	20±9	10±4	3±1	1±0.2	3±1	18±3
2008	31±7	22±7	4±1	1±0.3	3±1	20±3
2009	30±6	20±6	5±1	2±0.3	5±1	20±2
2012	28±6	21±6	5±2	2±0.3	6±2	22±2

* Values are ± standard errors.

with a benthic community similar to that of the 1970s (Huston, 1985), and it was the subject of the study which suggested a rapid phase-shift reversal (Idjadi et al., 2006). Cover of live corals for 2005 and 2006 determined here are similar to figures reported by Quinn and Kojis (2008). It is encouraging that coral cover and the rapidly growing *A. cervicornis* colonies have returned to the reef at levels approaching pre-bleaching values. This site shows relatively high rugosity (Crabbe, 2010) and the influence of *M. annularis* colonies on the reef, acting as structural refugia (Idjadi et al., 2006) and maintenance of biological legacies and reasonably fast growth (Diaz-Pulido et al., 2010) may have facilitated this recovery. Coral resilience has also been noted on the reefs of Bonaire (Bruckner, 2012). Interestingly, we found a variety of clades of zooxanthellae, including clade C, in corals at Dairy Bull reef (Crabbe & Carlin, 2007), and that may also be a factor in their recovery (Stat, Loh, Hoegh-Guldberg & Carter, 2008).

It may be that under conditions of low coral cover, low reef rugosity and low biodiversity, a major disturbance such as the 2005 bleaching event crosses a ‘threshold’ which then induces a cascade to induce the crossing of other thresholds, leading to a stable but less desirable alternative state (Kinzig & Pacala, 2001). An example where this has happened may be the reefs of Tobago (Mallela & Crabbe, 2009). On the reefs of North Jamaica, there is a variable response and resilience, strongest in the case of Dairy Bull reef, which exhibits relatively high rugosity, coral cover and biodiversity with no significant macrogal cover (Crabbe, 2009). What our work suggests is that marine park managers may need to assist coral recruitment and settlement in years where there are severe acute disturbances, including hurricanes and bleaching events, by setting up coral nurseries and/or natural or artificial high rugosity substrate on the reef. In addition, where the insults to coral reef are of a long term human-induced chronic nature, such as overfishing and land development (Mumby, Hasting & Edwards, 2007), engagement with fisherfolk and land developers is vital to minimise the human-induced threats which are so damaging to coral reefs. Unfortunately, previously successful efforts to engage the local fisherman in controlling catches around Discovery Bay (Sary et al., 1997) have not been maintained, and it may be that the development of a sustainable Discovery Bay Marine Protected Area is the only solution.

ACKNOWLEDGMENTS

I thank the Earthwatch Institute for funding in Jamaica, Mr. Peter Gayle, Mr. Anthony

Downes, and the staff of the Discovery Bay Marine Laboratory for their invaluable help and assistance, and volunteers for their help underwater during this project.

RESUMEN

Evidencia de la recuperación inicial de la comunidad coral en Bahía Discovery, Costa norte de Jamaica. Los retos actuales para la sostenibilidad del arrecife de coral incluyen la sobrepesca, prácticas pesqueras destructivas, decoloración de corales, acidificación del océano, aumento del nivel del mar, brotes de estrellas de mar, floraciones algales, escorrentías agrícolas, el desarrollo costero y hotelero, contaminación, enfermedades, especies invasoras y huracanes. Utilizamos transectos de cinturón SCUBA para registrar la cobertura de coral y analizar imágenes digitales en el arrecife Dairy Bull, en la costa norte de Jamaica en el Caribe, y encontramos que constituye un ejemplo positivo de cómo los arrecifes pueden recuperarse después de una perturbación ambiental importante. La cobertura de coral vivo aumentó de 13±5% en 2006 a 31±7% en 2008, mientras que *Acropora cervicornis* aumentó de 2±2% en 2006 a 22±7% en 2008. Los niveles de cobertura de coral se mantuvieron hasta el 2012.

Palabras clave: huracanes, blanqueo, amp, el cambio climático global warming, Belice, Jamaica.

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Spearfishing as a potential threat to fishery sustainability in Jamaica: a survey of 23 fishing beaches

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Received 15-VIII-2013 Corrected 05-III-2014 Accepted 24-III-2014

Abstract: Spearfishing was becoming an increasingly important economic activity in the Caribbean as a result of socioeconomic factors related to underemployment and the low capital outlay for equipment. For a year (2011) we surveyed spearfishing in 23 Jamaican beaches. Spearfishing has expanded from approximately 1% of fishers in 1991 to about 10% in 2011. The fishery is larger than expected and probably produced 4 000tons per year. Though reef fishes dominated catches, other resources such as lobsters, conch and octopus were regularly taken. Many small juvenile fishes were observed in catches well below their adult or optimum sizes. A total of 58% of spear-fishers reported they would have significant difficulty finding alternative employment if spearfishing was banned. Spearfishers reported exploiting the entire island shelf and also nearly all the offshore banks, especially Pedro Bank. Night spearfishing was common and targeted sleeping reef fishes. The activity is banned and should be enforced. Our recommendations include: register all spearfishers, actively manage spearfishing, a partial ban for part of the year and a ban on using scuba and hookah gear for spearfishing. Rev. Biol. Trop. 62 (Suppl. 3): 141-149. Epub 2014 September 01.

Key words: Spearfishing, overfishing, management, reef fishery resources, Jamaica.

Jamaica is the third largest island within the Greater Antilles and is situated near the center of the southwestern Caribbean Sea. It lies in the path of the northeasterly trade winds where speeds often exceed 15ms^{-1} and choppy waters are common. Seas are generally calmer between October and February (Aiken, 1993; Munro, 1983). Westerly currents from 0.5-1 kt occur in the vicinity of the island for most of the year with minimal to no tidal effects (Aiken, 1993), although currents over Pedro Bank can reverse at ebb tide (Munro, 1983).

The island shelf and a number of offshore banks constitute the fishing grounds for marine fisheries of Jamaica which are almost all artisanal. Fisheries produce about 12 000tons annually and are conducted by at least 15 000 active (but possibly as many as 20 000) fishers (Aiken, 2008). Most of the seafloor on the island shelf is sea-grass and soft corals over sand and limestone bedrock. Coralline growth is usually concentrated around the shelf edges (Aiken, 1993; Halcrow, 1998). The southern shelf is much larger and wider than the northern shelf, with a maximum distance from the mainland of 24km. The shelf consists of mostly small patches of corals, gorgonians and seaweeds mixed with sandy patches and large reefs on the eastern side. The north shelf is much narrower; with a maximum distance from the mainland of 1.6km (Fig. 1). Fringing reefs with a few gaps (which are virtually continuous with the sill reef) characterize the north shelf. The largest banks that are utilized as fishing grounds are Pedro Bank and Morant Bank. These banks rise abruptly from deeper than 500m to form submerged plateaus with depths averaging between 20-30m (CFRAMP, 2000).

The fishing techniques used in the Jamaican reef fishery are diverse. The most prominent fishing gears are fish traps, beach seine, and tangle and gill nets; followed by hand

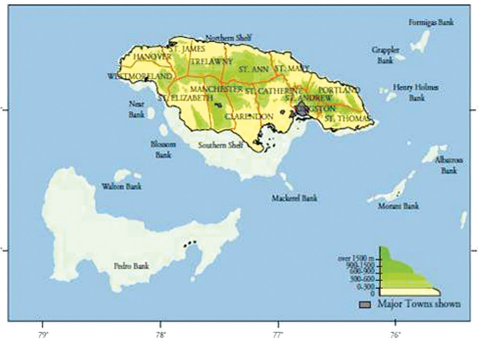

Fig. 1. Major fishing areas of Jamaica. The island shelf consisting of the very narrow northern and much wider southern portions, small nearshore banks, and offshore areas including Pedro Bank (bottom left) and Morant Bank (center right) (Map data from NRCA data unit in CFRAMP, 2000).

Fig. 1. Principales zonas de pesca en Jamaica. La plataforma de la isla consiste de partes muy estrechas al norte y mucho mas amplias al sur, pequeños bancos cercanos a la costa, y las zonas de alta mar, incluyendo el Banco de Pedro (parte inferior izquierda) y el Banco de Morant (centro-derecha) (Datos del mapa son de la unidad de datos NRCA en CFRAMP, 2000).

lines, spearfishing, and some use of illegal explosives. Fishing vessels are mainly small, open, non-motorized wooden canoes (95% of all vessels), with some use of larger, 27 foot motorized fiberglass open canoes (Aiken, 2008; Sary, 2001). The main fisheries resources utilized in Jamaica are coral reef fishes, spiny lobsters, conch, small coastal pelagic finfish and large offshore pelagic finfish. All are targeted by spearfishers (Aiken, 2008).

Spearfishing is defined in this study as "the catching or taking of a fish through the instrumentality of a hand or mechanically propelled, single or multi-pronged spear or lance, barbed or barbless, operated by a person swimming at or below the surface of the water" (FWC, 2011). Types of spearfishing include free diving with snorkel, SCUBA, or hooka.

Munro (1983) noted that spearfishing was becoming an increasingly important economic activity in the Caribbean as a result of socio-economic factors related to underemployment and the low capital outlay for equipment. Spearfishing appeared to be attractive as it offered income earning capacity to otherwise unskilled or impoverished individuals. According to Munro, spearfishing was also attractive in terms of its effect on the natural resources and their management as spearfishing tended to target the oldest, largest and least productive members of the fish community, leaving the younger and more productive members and promoting conservation of the stock (Munro, 1983). He gave an example of the benefits of spearfishing in Belize, stating that about 67% of the production of spiny lobsters at that time was derived from spearfishing and that the spearfishing community appeared to be one of the most prosperous population sectors.

Despite Munro's observations of the benefits of spearfishing in Caribbean countries, some studies have also shown that spearfishing has been implicated in the local extinction of some species. An example is the Goliath grouper (*Epinephelus itajara*) on the Caribbean island of Bonaire (Roberts, 2007). The previous Jamaican study showed that spearfishing accounted for a major portion of the country's annual fisheries production (Passley, 2009; Passley, Aiken & Perry, 2010). That study focused on regular fishermen at beaches around the island and obtained data on the amount, size and type of fish caught, where fishing was most frequently carried out, and how much the fishermen depended on their spearfishing activities. Results showed that spearfishing was much more widely used in Jamaica than expected. The unexpected results from the Passley (2009) study led to the initiation of a second follow-up spearfishing study (the present paper) of commercial spearfishing in Jamaica to confirm the earlier conclusions and to assist the Fisheries Advisory Board in managing commercial spearfishing. Data gathered from this and the previous study were analyzed with the following objectives: 1) to determine the current status of spearfishing in Jamaica, its commercial value, and its contribution to annual fisheries production; 2) to compare the current status of commercial spearfishing in Jamaica with results from the previous study (Passley, 2009; Passley et al., 2010); 3) to determine effective steps that may be taken to conserve the resources of Jamaica's island shelf and determine if commercial spearfishing can continue under regulations, and 4) to conduct a literature Review on commercial spearfishing worldwide.

MATERIALS AND METHODS

Study sites: Survey trips were made to 23 preselected fishing beaches known to have spear-fishers present by the Fisheries Division of the Ministry of Fishing and Agriculture in Jamaica (Fig. 2).

Fig. 2. Fishing beaches visited in Jamaica: 1. Negril Beach, 2. Orange Bay, Hanover 4. Lucea, 5. Sandy Bay, 6. Hopewell, 7. Spring Garden, 8. Whitehouse Beach, St. James 9. Success, 10. Grange Pen, 11. Falmouth Fishing Village, 12. Braco, 13. Rio Bueno, 14. Old Folly, 15. Discovery Bay, 16. Runaway Bay, 17. Swallow Hole, 18. Salem, 19. Priory, 20. St. Ann's Bay, 21. Mammee Bay, 22. White River, 23. Oracabessa, 24. Pagee, 25. Robins Bay, 26. Breakfast Gap, 27. Annotto Bay, 28. Castle Garden, 29. Dover, 30. Buff Bay, 31. Orange Bay, 32. Hope Bay, 33. St. Margaret's Bay, 34. Bryan's Bay. 35. Norwich, 36. Prospect/Port Antonio, 37. Drapers, 38. Fairy Hill, 39. Blue Hole, 40. Preistman's River, 41. Boston Beach, 42. Long Bay, 43. Manchioneal, 44. Innes Bay, 45. Hector's Bay, 46. Holland Bay, 47. Dalvey, 48. Rocky Point, St. Thomas, 49. Port Morant, 50. Leith Hall, 51. Lyssons Beach, 52. Morant Bay, 53. Yallahs, 54. Bull Bay (7 miles), 55. Port Henderson, 56. Hellshire, 57. Old Harbour Bay, 58. Welcome Beach, 59. Barmouth/Portland Cottage, 60. Rocky Point, Clarendon, 61. Alligator Pond, 62. Black River, 63. Long Acre, 64. Whitehouse, Westmoreland, 65. St. Ann's Beach, 66. Smithfield, 67. St. Mary's Beach. Satellite image from Google Earth 2012 ©.

Fig. 2. Playas de pesca visitas en Jamaica. 1. Playa Negril, 2. Bahía Orange, Hanover, 4. Lucea, 5. Bahía Sandy, 6. Hopewell, 7. Spring Garden, 8. Playa Whitehouse, St. James 9. Success, 10. Grange Pen, 11. Villa de pesca Falmouth, 12. Braco, 13. Rio Bueno, 14. Old Folly, 15. Bahía Discovery, 16. Bahía Runaway, 17. Swallow Hole, 18. Salem, 19. Priory, 20. Bahía St. Ann's, 21. Bahía Mammee, 22. Río White, 23. Oracabessa, 24. Pagee, 25. Bahía Robins, 26. Breakfast Gap, 27. Bahía Annotto, 28. Castle Garden, 29. Dover, 30. Bahía Buff, 31. Bahía Orange, 32. Bahía Hope, 33. Bahía St. Margaret's, 34. Bahía de Bryan. 35. Norwich, 36. Prospect/Port Antonio, 37. Drapers, 38. Fairy Hill, 39. Blue Hole, 40. Río de Preistman, 41. Playa Boston, 42. Bahía Long, 43. Manchioneal, 44. Bahía Innes, 45. Bahía de Hector, 46. Bahía Holland, 47. Dalvey, 48. Punta Rocky, St. Thomas, 49. Puerto Morant, 50. Leith Hall, 51. Playa Lyssons, 52. Bahía Morant, 53. Yallahs, 54. Bahía Bull (7 millas), 55. Puerto Henderson, 56. Hellshire, 57. Bahía Old Harbour, 58. Playa Welcome, 59. Barmouth/Portland Cottage, 60. Punta Rocky, Clarendon, 61. Laguna Alligator, 62. Río Black, 63. Long Acre, 64. Whitehouse, Westmoreland, 65. Playa St. Ann, 66. Smithfield, 67. Playa St. Mary. Imagen satelital de Google Earth 2012 ©.

TABLE 1
Main fishing gears reportedly used by 148 spearfishers Islandwide. Four other types of gears were reportedly used by 50% of spearfishers interviewed.

CUADRO 1
Tipos de pesca utilizados principalmente según lo informado por 148 pescadores de arpón en la isla. Según informes, otros cuatro tipos de engranajes fueron utilizados por el 50% de pescadores entrevistados.

Gear used	Percentage of fishers interviewed
Spearfishing only	50
Spearfishing & nets	14
Spearfishing & lines	8
Spearfishing, pots, nets	4
Spearfishing & pots	4
Spearfishing, lines, nets & pots	3
Spearfishing, lines & nets	3
Spearfishing, nets & pots	2
Nets & spearfishing	2
Spearfishing & nets	2
Spearfishing & trawling	1
Spearfishing & 7 other permutations of these gears	1 each

The sites were visited over 9-10 months between January and October 2011. Each trip was made by the researcher and a representative of the Fisheries Division that was well known at the beaches visited. At each site, a questionnaire modified from the original used in the Passley (2009) report was administered to a specified number of spear-fishers. Repeat trips were made when necessary to achieve the desired total sample number. We photographed each spearfisherman interviewed and when available took pictures of spearfishing gear, boats, and catch at the fishing beach. Fifty additional fishing beaches where spearfishing was practiced were also visited to estimate total numbers of spearfishers operating on beaches. Questionnaires were not administered at these additional beaches.

RESULTS

We interviewed a total of 148 spearfishers. The mean age of the spearfishers interviewed on the North Coast was 38±0.5 yrs and 35±0.7 yrs on the South coast. The mean age of all spear-fishers interviewed was 36±0.4 yrs.

The majority of spear-fishers interviewed used spears as their main form of fishing, but some also used hook and line, net, and pot (trap) fishing also (Table 1).

Most (approximately 75%) of the 148 spear-fishers interviewed reported fishing on the island shelf while approximately 25% reported fishing offshore. Among offshore spearfishers, nearly 50% reported fishing Pedro Bank located 160 km southwest of Kingston (Table 2).

This study revealed a new practice of spearfishing at night on reefs. Fully 27% of all spearfishers (29% of south coast and 26% of north coast spearfishers) reported spearfishing at night .

TABLE 2
Reported offshore spearfishing areas by frequency of visit (148 interviews)

CUADRO 2
Zonas informadas de pesca submarina en altamar por frecuencia de visita (148 entrevistas)

Offshore fishing area	Percentage of fishers
Pedro Bank	47.1
Morant Cays	25.5
Formigas Bank	15.7
Colombian Areas	7.8
Grappler Bank	2
Walton Bank	2

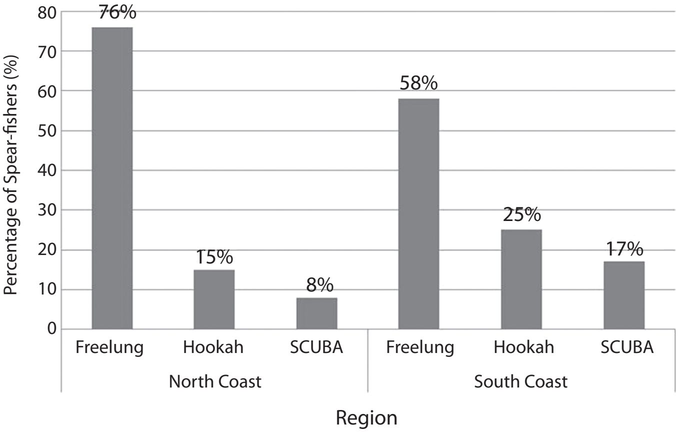

Fig. 3. Distribution of breathing mode used reported by spearfishers by coast. Spearfishing breathing apparatus included hookah, SCUBA, or free-diving ("freelung") while breath holding with snorkel.

Fig. 3. Distribución de modo de respiración utilizado según lo informado por Pescadores de arpón en la costa. Equipo de respiración de pesca submarina incluye hookah, buceo o buceo libre ("freelung"), mientrasse respira con tubo respirador (snorkel).

Spearfishers that reported doing only spearfishing also reported spending an average of 4.4(±0.2) days per week spearfishing Islandwide with slightly more time fishing on the North Coast (4.58±0.1) compared to 4.25 (±0.1) days per week on the South Coast.

Spearfishers interviewed who did only spearfishing (75%) reported that they spent a mean time of 4.5 (±0.16 hours) in the water Islandwide, compared to 4.6 (±0.30) hours on the North Coast and 4.45 (±0.22) hours on the South Coast.

About 75% of all spearfishers reported using commercial spear guns, compared to 25% that used homemade spear guns. More south coast than north coast spearfishers used hookah and scuba gear to spearfish as suggested by Figure 3.

Mean reported daily spearfishing catch islandwide was 18.1±1.8 kg/trip (Fig. 4) were found to be highest on the south coast at 21.3kg/day. Although not a direct objective of the present study, repeated observations of spearfisher catches showed presence of very small and clearly immature reef fishes of several species (Table 1).

All spearfishers interviewed reported taking coral reef fish and that parrotfishes (Scaridae) and Grunts (Haemulidae) dominated catches. Table 3 shows a list of the most commonly landed fishes from spearfishing

Parrotfishes and grunts dominated spearfisher catches around the island and is considered an indicator of an overfished reef

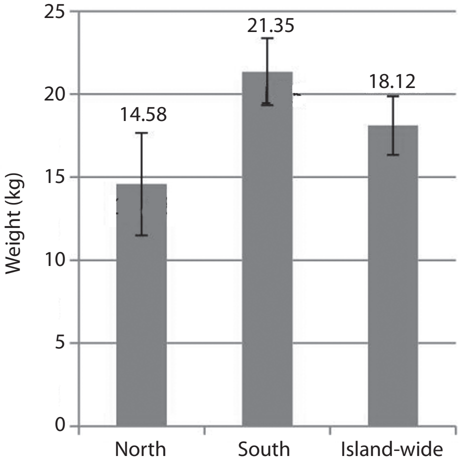

Fig. 4. Reported daily catch rates (kg) by spearfishers by coast and island wide. Numbers show reported average daily catch.

Fig. 4. Tasas diarias de captura(kg) informadas por los pescadores de la costa y en toda la isla. Los numeros muestran el promedio diario de captura.

TABLE 3
Ranking of the eight numerically most abundant fish species caught by spear-fishers by region.

CUADRO 3
Clasificación de las ocho especies de peces más abundantes en las capturas de los pescadores de arpón según la región.

Rank	North Coast (Scientific & common name)	South Coast (Scientific & common name)	Overall (Islandwide)
1	*Sparisoma viride* (stoplight parrot)	*S. aurofrenatum* (redband parrot)	*S. aurofrenatum*
2	*S. aurofrenatum*	*S. viride*	*S. viride*
3	*Acanthurus coeruleus* (tang)	*H. plumieri* (white grunt)	*H. plumieri*
4	*H. sciurus* (bluestripe grunt)	*H. sciurus*	*H. sciurus*
5	*H. flavolineatum* (French grunt*)*	*A. coeruleus*	*H. flavolineatum*
6	*Lutjanus analis* (Mutton snapper)	*Balistes vetula* (queen trigger)	*L. analis*

fish community (Munro, 1983, Aiken, 1993). *Sparisoma viride*, stoplight parrotfish and *S. aurofrenatum*, redband parrotfish, were the two most numerically abundant reef fish species on Jamaican reefs over the last 10 years (Aiken, personal observation). The present study revealed that spearfishing regularly targeted several other species in addition to coral reef fishes including, i) lobsters (mostly *Panulirus argus*, and some *P. guttatus*), ii) octopus (*Octopus vulgaris*), iii) queen conch (*Strombus gigas*) iv) lionfish (*Pterois volitans* and *P. miles*) and great barracuda (*Sphyraena barracuda*).

A total of 74% of all spearfishers reported fishing year round with no special spearfishing “season”. The remaining 26% reported taking a break from spearfishing at some time each year. Spearfishers reported an average of 4.5 hours spent spearfishing per day. Reported perceptions of spearfishers about catch trends are shown in Figure 5. Exactly 64% of spearfishers reported reduced catches on both coasts while approximately 30% reported no change.

Nearly 60% of all interviewed spearfishers expressed the view that they would face unemployment if spearfishing was banned while roughly a quarter reported that they would try another fishing technique for a living.

Mean reported annual income of spearfishers was J$1 992 166.73 (J$480.52/kg * 18.12kg/day *4.4days/week * 52weeks/year = US Exchange Rate = J$100:1 July 2013). Therefore, the mean annual income of spearfishers was the equivalent of US$ 20 000/year. Assuming approximately 1 000 active spearfishers in Jamaica, that total annual production by spearfishers was around 4 145m.

We discovered a new fishing variation involving spear-fishing where a net was used to block off a confined area, then long sticks and

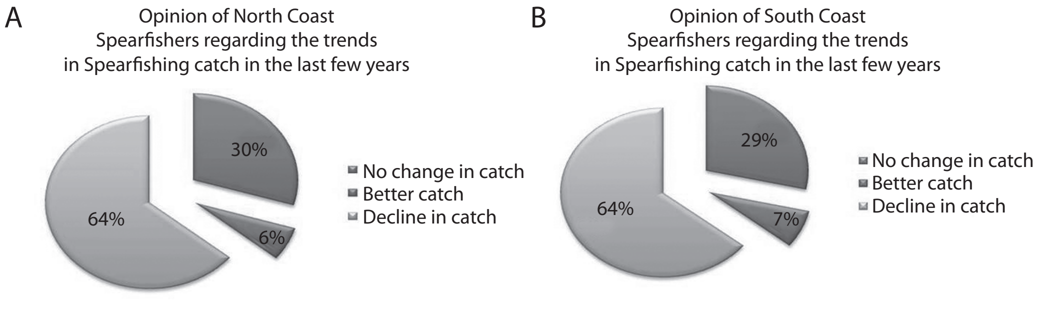

Fig. 5. Reported spearfisher perceptions of catch trends in recent years by coast.
Fig. 5. Percepciones reportadas por los Pescadores de arpón de las tendencias de capturas en los últimas años en la costa.

other scar ing devices were used to strike the water surface in order to make the fish strike the net and become entangled. Those fishes that did not strike the net were speared by swimmers around the net. This method produced very few, if any, escapees.

DISCUSSION

Passley (2009) and Passley et al. (2010) was the first recent study of the state of spearfishing in Jamaica and was considered preliminary in need of supporting data to confirm its findings. It found for example, that 2% of all fishers were found to be spear- fishers as opposed to the 1% in previous estimates (Munro, 1983; Aiken, 1993; Aiken, 2008). About 75% of artisanal spearfishermen in Jamaica used commercially manufactured spearguns and the rest used homemade versions. It was also discovered that spearfishers reported averaging about 4 hour of fishing per day, 5 days a week, which provide an estimated catch of about 3 500 kg/spearfisher/year (Passley, 2009; Passley et al., 2010).

Spearfishing has the potential to be environmentally friendly by being highly selective with no by-catch if participants are educated to target only legally sized fish. However, small fish are continuously being caught and sold in Jamaica, where the reefs are greatly overfished and the fishermen depend on their catch to support their livelihood.

The Jamaica fisheries are considered overfished (Aiken, 1993; Aiken, 2008) based on evidence of observed gradual changes in species composition in catches with time. There has been a great reduction in top carnivorous predatory fish such as the higher-valued snappers and jacks. These species have been replaced by lesser valued herbivorous and omnivorous reef fish such as parrotfishes and doctorfishes (Aiken, 2008). This replacement shows a direct impact of overfishing on reef biodiversity. Other factors affecting the status of fisheries include severe hurricane damage to reefs and the recent introduction to Caribbean waters of the carnivorous lionfish species *Pterois volitan* and *P. miles,* which has no natural predators.

In 2009, a ban was placed on night spearfishing in an attempt to reduce the exploitation of reef fisheries. However, lack of enforcement and an awareness of the ban has somewhat negated its effectiveness. The present study found that night spearfishing was still relatively commonly practiced in 2011 with approximately 27% (nearly one-third) of all spearfishers interviewed reported doing this practice. This violation is one of the most serious conservation and management issues identified in the present study.

The high earnings of the average spearfisher indicates that this occupation is the equivalent to a “middle-class” income for Jamaica (Claremont Kirton, Pers Comm). The estimated annual yield of approximately 4 000t in 2011 is larger than expected and means that spearfishing could be contributing approximately one-third of the total fisheries production of the entire country that was approximately 12 000tons in 2012. This annual production estimate is slightly larger than that 3 500tons estimate for 2009 reported by Passley (2009) and Passley et al. (2010).

Our results showed that many species of coral reef fishes are being removed not only in the day but also at night. This is a serious overall problem for sustainable marine biodiversity. While there is not a problem with the removal of invasive lionfish (*Pterois* sp.), all the other species are removed together, averaging 18.1kg/day. It must be remembered that this sub-sector together with the other activities in the other fishery sub-sectors such as fish trappings, the artisanal and industrial queen conch fisheries, along with spiny lobster harvesting, hook-and-line fishing, and beach seining, comprise a relatively large island fishery. There is therefore tremendous fishing pressure on the already declining fishery resources in Jamaica. This is a serious issue for fisheries management.

Of a total of some 20 000 fishers of all types, spear-fishers now appear to comprise approximately 2 000 or roughly 10%. This proportion is considerably higher than in earlier estimates of roughly 1% of the total fisher numbers (Munro, 1983; Aiken, 1993; Aiken, 2008). The increase in spearfishing may be due to increases in the cost of gear and maintenance for trap and net fishing as well as the apparent success of spearfishing as suggested by Passley et al. (2010).

A total of 33% of spearfishers interviewed by Passley in 2009 reported that they had no replacement skills with which to make a living if spearfishing were to be banned. An equal percentage said that they would attempt to find an alternative means of supporting themselves however 10% said that they would then require government assistance.

In other Caribbean countries, spearfishing is strictly regulated or banned completely. In the Bahamas, the Hawaiian sling is the only approved spearfishing device. Gear such as SCUBA gear or air compressors are not allowed for catching fish, conch, crawfish or other marine animals. Spearfishing is further regulated by location whereby spearfishing is not allowed within one mile of the coast of New Providence, within one mile of the south coast of Freeport, Grand Bahamas and within 200 yards of the coast of all the Out Islands. Spearing or taking marine animals by any means is illegal within national sea parks (The Islands of the Bahamas, 2008-2011).

The present study confirmed that the main types of fish and edible marine life landed by spearfishers were those that had a high sale value, such as parrotfish, snapper and lobster. We also confirmed the finding by Passley (2009, 2010), that night diving was a highly productive fishing activity as sleeping fish presented a stationary target and were easily caught. We support enforceing the night diving ban. Again we confirmed findings by Passley et al. (2010) that most spear-fishers carried out other types of fishing, that a high percentage (58% in this study) were decidedly dependent on their spearfishing activities, and that the number of spear-fishers had steadily increased around the island. If spearfishing were banned, 42% of fishers indicated that they would shift into other types of fishing or other non-fishing activities. The overall sentiment perceived in this study was that spear-fishers agreed that their activities were in need of some sort of regulation and management.

CONCLUSIONS & RECOMMENDATIONS

An awareness of the consequences of taking immature reef fishes during commercial spearfishing was perceived in both spearfishing studies to be lacking. Commercial spearfishing, especially with the aid of compressed air, was banned in many countries, either in an attempt to mitigate or prevent overfishing of those countries' marine resources, but in Jamaica. There is a relatively dire situation with all the fishable marine resources of Jamaica and it our opinion that spearfishing as presently practiced in Jamaica is significantly exacerbating the situation with its high level of fishing effort and large catches of many reef species as shown in this paper.

On the basis of findings from the present 2011 data (supported by the 2009 data), we strongly recommend that the government of Jamaica should, with some urgency, consider doing the following:

- Enforce the ban on night diving declared late 2009.
- Enforce strict spearfishing regulations but not completely ban spearfishing. These regulations should include a minimum size of fish landed and a penalty for possession of undersized catch.
- Publicize the danger of depletion by spearfishing with SCUBA and hookah apparatus. Many fishers are unaware, especially to younger divers.
- Register all spearfishers
- Ban spearfishing with SCUBA & Hookah gears.

ACKNOWLEDGMENTS

Special thanks to Charlene "Nicky" Thomas, Fisheries Instructor, Fisheries Division, Ministry of Agriculture & Fisheries, Kingston, whose invaluable field support facilitated this collaborative project with the UWI. We also thank the Fisheries Division, MAF, for transportation and financial support through the Fisheries Management & Development Fund (Conch Cess Fund).

RESUMEN

Pesca Submarina: una amenaza potencial para la sostenibilidad de la pesca en Jamaica. Un estudio de la pesca submarina en Jamaica durante el 2011 reveló una pesquería mayor que la esperada, que produce aproximadamente 4000 toneladas por año de todos los tipos de recursos pesqueros. Este nivel de producción esta por encima de lo que se pensaba era una actividad pesquera de pequeña escala. Esta pesquería especializada se ha ampliado aproximadamente en 1% de pescadores a al menos el 10%, en un periodo de 20 años (1991 a 2011). Aunque los peces de coral se dominaran como otros recursos tales como langostas, concha y pulpo. Aunque no era un objetivo del censo se observaron muchos peces juveniles en las capturas con tamaños muy por debajo de su tamaño adulto u óptimo. Un total de 58% pescadores informaron que tendrían dificultad para encontrar otra opción de empleo si la pesca submarina se prohibe. Los pescadores explotan recursos en la plataforma de la isla y también en casi todos los bancos de la costa sobre todo en el Banco de Pedro. Este estudio también muestra que comunmente se práctica la pesca submarina durante la noche con el fin de capturar peces de coral durmiendo. A pesar de que esta actividad es prohibida. Se recomienda que los pescadores se registren y que se regule la actividad. Posibles acciones incluyen considerar la prohibición parcial durante el año o prohibir el uso de equipo de buceo y narguile.

Palabras claves: Pesqueria submarina, sobrepesca, manejo, recursos de arrecifes coralinos, Jamaica

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Lionfish abundance, size structure and spatial distribution along the Venezuelan coast (*Pterois volitans*, Pteroinae: Scorpaenidae)

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Received 01-IX-2013. Corrected 23-II-2014. Accepted 24-III-2014.

Abstract: The recent invasion of lionfish (*Pterois volitans)* in the Atlantic is considered a new threat to benthic and fish communities in the Caribbean region. This species was first reported in Venezuela in 2009 at various sites. Increasing reports in the past five years suggest lionfish has expanded its range of distribution and habitats. Nevertheless, this information is mostly anecdotal and extensive surveys aimed to determine its abundance, size structure and other ecological aspects encompassing wider spatial scales are necessary to understand the actual role of this species on sub-tidal marine communities in Venezuela. We determined its density and population size structure through visual census along the Venezuelan coast. Visual censuses were made following strip transects at a depth between 5 and 20m and in daylight time, at 19 sites in five localities. Average density ranged between 7 to 55 individuals per hectare among sites. Most individuals were adults and most were found in caves, coexisting with other lionfish or with different species, while others were actively preying. The fish *Pterois volitans* seems to be well-established along the Venezuelan coast in densities that in some sites appear to be higher than in their Pacific native range but lower than in some invaded localities of the Atlantic. Rev. Biol. Trop. 62 (Suppl. 3): 151-158. Epub 2014 September 01.

Key words: Exotic species, visual census, South Caribbean, *Pterois volitans*.

The introduction of exotic species is considered a major threat to biodiversity because it has produced significant phase shifts in marine ecosystems worldwide (Gurevitch & Padilla, 2004; Ruiz, Carlton, Grosholz & Hines, 1997). Among exotic marine species, *Pterois volitans*, commonly known as lionfish, has recently received special attention. This species is native and widespread in the Indo-pacific but was introduced to the Atlantic probably through numerous releases of ornamental fish since 1985 in Florida (Schofield, 2009). Since then *P. volitans* has invaded from Florida to North Carolina, most of the Caribbean and the Gulf of Mexico (Schofield, 2010). Lionfish was first reported in Venezuelan in 2009, in Cape Bay in the Central Coast of Venezuela and in Morrocoy National Park. After 2010, reports increased in frequency, and it is presumed that *P. volitans* moved from west to east along the coast, according to a database created for divers, fishermen and scientists to report sightings the species (http://pezleon.cbm.usb.ve). Currently, *P. volitans* seems to be well established all along the Venezuelan coast (Lasso-Alcalá & Posada, 2010).

Pterois volitans is a voracious predator feeding from a wide range of fishes and crustaceans (Albins & Hixon, 2008). It has been suggested that the presence of this species in the Atlantic may have negative effects on reef fish communities such as significant reduction in recruitment rates (Albins & Hixon, 2008; 2011). It is also believed that the introduction of lionfish might have indirect effects on the structure of benthic coral communities (Lesser

& Slattery, 2011). Therefore it is necessary first to determine its spatial patterns of distribution. This information will be valuable to help identify the processes that might explain these patterns, and more importantly the spatial scales that are relevant to the design of proper experiments.

We present a preliminary survey of abundance and distribution of lionfish encompassing different sites along the western, central and eastern coast of Venezuela aimed at determining the abundance, size structure and patterns of spatial distribution of lionfish. For this, localities separated by hundreds of kilometers and sites within localities separated by hundreds of meters were sampled along the coast of Venezuela.

MATERIALS AND METHODS

Study sites: The study was conducted at five localities and two to five sites within each locality: (1) Morrocoy National Park (five sites: Caimán, Mero, Boca Seca, Cayo Sombrero and Cayo Norte), (2) Ocumare de la Costa (five sites: Guabinas, Canal de la Ciénaga, Punta de la Ciénaga, Valle Seco and Chuao), (3) Chichirivichi de la Costa (two sites: Punta de Chichirivichi and Bahía de Chichirivichi), (4) Chuspa (two sites: Punta Capino and Quigua), and (5) Mochima National Park (five sites: Punta de Cruces, Tigrillo, Piedra de la Ahogada, Playa Colorada and Burbujas).

Morrocoy national park is located at the western coast of Venezuela (10°51’60”N, 68°14’10”W) it is a marine protected area with major tropical marine communities (seagrass beds, mangrove forest, sandy and rocky shores and coral reefs) occurring in a total area of 320km^2 (López-Ordaz, Ortaz & Rodriguez-Quintal, 2009). Ocumare de la Costa (10°29’20”N, 67°49’21”W) Chichiriviche de la Costa (10°33’15”N, 67°14’20.38”W) and Chuspa (10°38’25”N, 66°17’56”W) are located in the Central Coast of Venezuela. This region in characterized by narrow continental margins and mostly rocky shores. Even thought it has some coral reef developments especially in La Cienaga and Guabinas. Mochima is also a National Park located at the eastern coast of Venezuela (10°23’44”N, 64°22’2”W) dominated by scattered coral communities growing on rocky bottoms, these communities being seasonally exposed to coastal upwelling and is considered the most important coral communities in the eastern of Venezuela (Ruiz et al., 1997).

Lionfish surveys: Visual censuses were made to estimate abundance of lionfish. In each site 7 to 12 belt transects (4m wide and 30m long, 120m^2) were surveyed, according to reef´s size and at depth varying from 20m to 5m. This was made according to the depth in each reef which was a lot deeper in Ocumare and Chichirichi de la Costa. All visual censuses were made by a single diver with special care taken to thoroughly search every cave, crevice and holes inside each transect. The number of lionfish and the size structure were determined using five size categories (0-10cm, 11-20cm, 21-30cm, 31-40cm, more than 40cm). The criteria for selecting these size classes were based following the AGRRA protocol (Ginsburg, R., Kramer, P., Lang, J., Salle, P., & Steneck, R., 1998). Adults and juveniles were identified through determination of total length, considering fish under 10cm as juvenile. To estimate lionfish biomass we used the allometric relationship $W=aL^B$ to convert size to weight, where L=length, a=0.00497 and b=3.201 (Darling, Green, O’Leary & Côté, 2011).

Statistical analysis: A two factor permutation analysis of variance (PERMANOVA), (Anderson, 2005) based on Euclidean distance was used to test the null hypothesis of no differences in lionfish density or biomass between localities (fixed factor with five levels) and across sites (nested factor within localities with 2 to five levels). All analyses were conducted using Primer + Permanova v6.

RESULTS

A total of 62 lionfish were found in 200 belt transects, with significant difference in density observed between localities but not across sites within each locality (Fig. 1). Lionfish were found at all sites except in Playa Colorada and Burbujas in Mochima. Mochima was also the locality with the lowest average density (6ind/ha). Average density across sites showed a high variability ranging from 7ind/ha in Cayo Norte (locality Morrocoy), to 55ind/ha in Punta Capino (Chuspa) (Table 1).

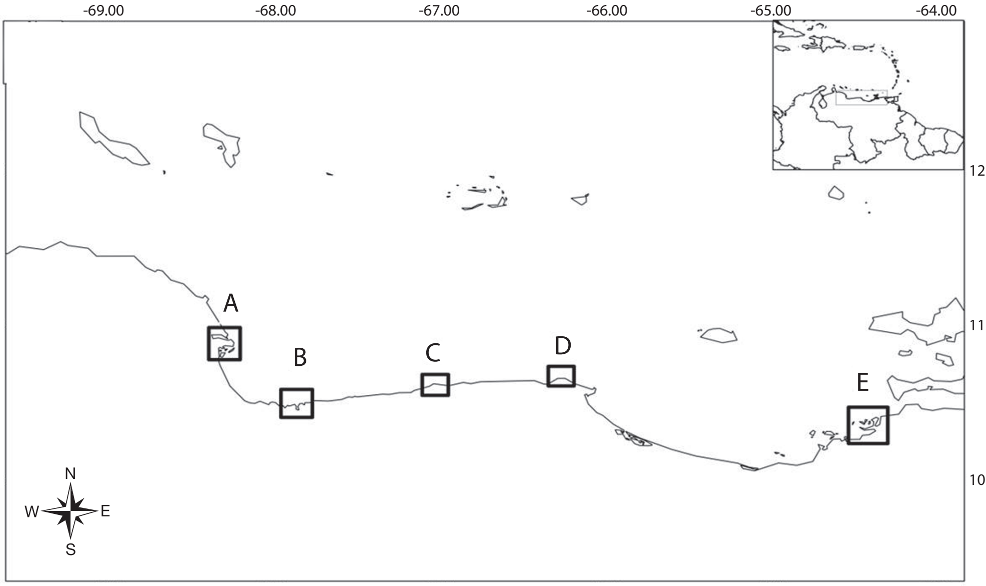

Fig 1. Sampling locations. A) Morrocoy National Park, B) Ocumare de la Costa, C) Chichirivichi de la Costa, D) Chuspa, E) Mochima National Park.

TABLE I

Average density (ind/hectare) with standard deviation in each sampling site

Locality	Site	Average density	St. deviation
Morrocoy	Boca Seca	28	41
	Caiman	12	31
	Mero	38	57
	Cayo Norte	8	25
	Sombrero	7	24
Ocumare	Canal Cienaga	53	101
	Chuao	56	118
	Guabinas	23	54
	Punta Cienaga	53	77
	Valle Seco	21	39
Chichirivichi	Bahía	53	67
	Punta	23	39
Chuspa	Capino	51	162
	Quigua	36	66
Mochima	Ahogada	8	25
	Burbujas	0	0
	Punta Cruz	15	34
	Playa colorada	0	0
	Tigrillo	8	25

Statistical differences were only found between Ocumare and Mochima (PERMANOVA: p = 0.003) and between Chichirivichi and Mochima (PERMANOVA: p= 0.014). The highest component of variation was found at the level of residual, which indicates a higher variability between replicates from the same site. This high variability between replicates may explain the lack of differences found between most localities. Highest density was found in Chuspa, Ocumare de la Costa and Chichirivichi de la Costa and the lowest in Mochima, where only four individuals in total were observed (Fig. 2). The highest biomass was observed in Ocumare de la Costa (Fig. 3), where most individuals belong to the biggest sizes (Fig. 4).

Regarding their behavior, fifty percent of the lionfish were found hiding in caves and crevices. We also observed lionfish floating over the reef (32%) and individuals actively feeding (10%). Many of the lionfish observed were found in groups composed of up to seven individuals hiding in caves (44%). Almost all of the observed lionfish were adults (94%) ranging in size from 15cm to 45cm. Most individuals belonged to the size category between 30 and 40cm. A few juveniles were found in the sites of Cayo Norte in Morrocoy, Tigrillo in Mochima and Guabinas in Ocumare de la Costa, and in both sites of Chichirivichi de la Costa.

DISCUSSION

This study confirmed that lionfish are well-established and widely spread along the coastline of Venezuela. Densities per site range between 6ind/ha to 55ind/ha and the density for Venezuelan Coast was 25.83±66.51. Average density of lionfish for the Venezuelan Coast seems to be lower than those reported for other invaded localities in the Caribbean, like the Bahamas, but is similar to average densities in North Carolina (Whitfield et al., 2002). Density along the Venezuelan Coast was also similar to some parts of the native range, like the density found off Kenya by Darling et al. (2011) of 25.1ind/ha and also to the average density reported in the Indo Pacific of 26.3ind/

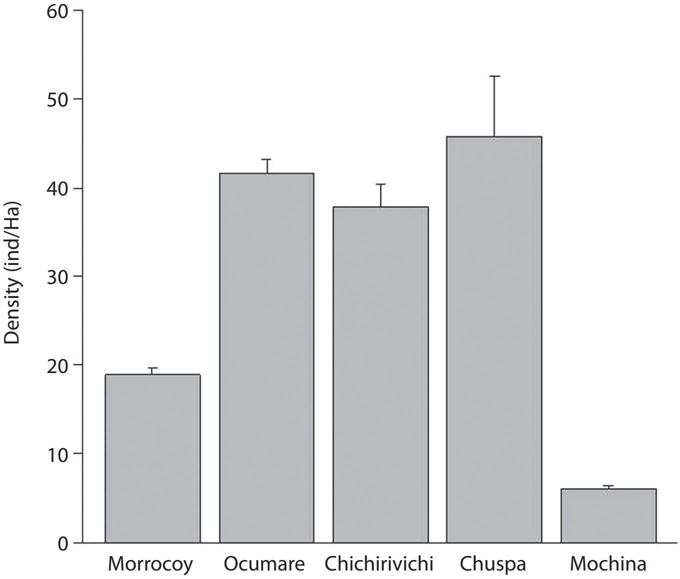

Fig. 2. Average density (ind/ha.) of *P. volitans/miles* in the five sampled localities of the Venezuelan Coast. Localities shown from west to east. Bar: standard error.

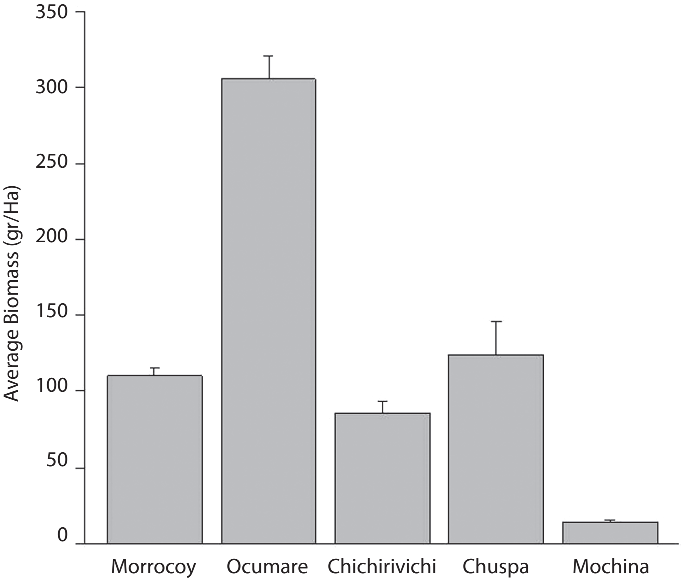

Fig. 3. Average biomass (gr/ha.) of *P. volitans* in the five sampled localities of the Venezuelan Coast. Localities are shown from west to east. Bar: standard error.

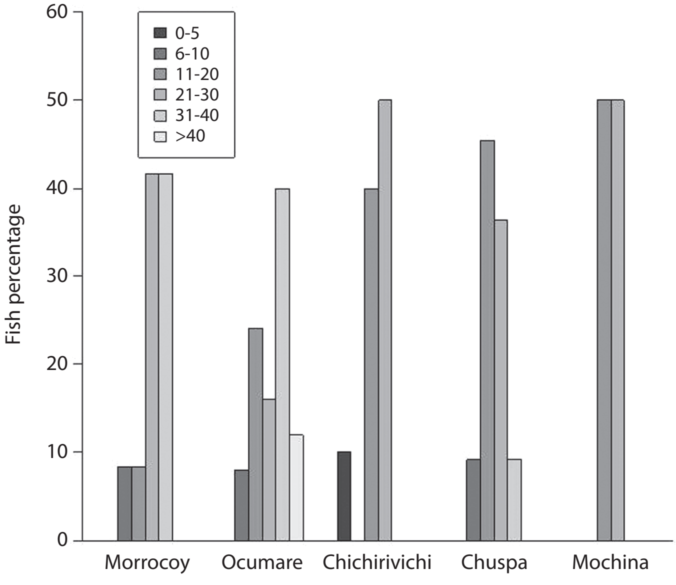

Fig. 4. Percentage of fish corresponding to each of the six size categories founded in each locality. Localities are shown from west to east.

ha (Darling et al., 2011; Kulbicki et al., 2012). This study showed that lionfish abundance is extremely variable at every spatial scale, but particularly among replicates making it difficult to compare its abundance at regional level. High variability among replicates might be explained by patterns of patchy distribution displayed by this species which may clump in few caves and crevices while being absent from most of the reef area.

Chichirivichi de la Costa was one of the first localities were *P. volitans/miles* was reported (January 2010) and the locality with the highest number of reports according to CBM database (http://pezleon.cbm.usb.ve). It was therefore surprising to find only a few lionfish at Punta de Chichiriviche; the majority being of small sizes. This site is a common and popular site for recreational diving where lionfish extraction is practiced. In the second site (Bahia de Chichirivichi), less visited, we found twice the density of individuals, both juveniles and adults. The difference in lionfish abundance between these two sites suggests that regular extraction could maintain low population density of this species and therefore it might be an effective measure of control at a local scale.

Using the CBM database we were able to hypothesize about lionfish dispersion along the Venezuelan coast. We presume it started in the west between November and December of 2009. During 2010 sightings were made in several places of the central coast. We postulate that lionfish did not reach the eastern areas of the Venezuelan coast until the middle of 2011, almost two years after the first report. This may explain why a low average density and so few individuals were found in Mochima National Park during this study. This could also explain the differences in density between Venezuela and other invaded localities like Bahamas, where *P. volitans/miles* has been present since 2004 (Schofield, 2010). This also means there is the possibility of Venezuela having similar densities in the near future. Nevertheless, it has to be considered that the frequency of the reports from this database depends on the popularity of each diving site and so this conclusion must be considered carefully.

High variability in density of lionfish was found between sites at the same localities. Lionfish density may be influenced by factors acting locally like availability of refuges and structural complexity as it know they spend a lot of time hiding in holes and crevice (Fishelson, 1997). Sites in Ocumare de la Costa are coral reefs with low coral cover (less than 25%, *unpublished data*) but with a lot of holes and crevices where lionfish was observed specially in sites like La Cienaga, where mostly of the individuals were seeing hiding in caves. In Chichirivichi de la Costa Bay where also found high density. This site was form by group of rocks mixed with artificial structure made of concrete use by fisherman for anchoring their boats. Sites sampled in Mochima were rocky reef mostly flat with few holes and vertical structures.

The low density of lionfish of small sizes, less than 10cm. (only 6%) may be a consequence of the little power of detecting individuals specially of small sizes (Green et al., 2013). It was reported also a high underestimation of *P. volitans* densities especially in structural complex reef. This suggests that densities reported in this project may by lower than what they actually are, and this could be worse in structural complex reef.

Pterois volitans/miles has been reported as a crepuscular species with nocturnal behavior in its native environment (Fishelson, 1997). In this study, most of the individuals observed were found hiding in caves and crevice. Nevertheless, we observed several individuals actively feeding during the day on juveniles of *Stegastes planifrons* and adults of *Stegastes partitus*. We observed a fishing behavior similar to those described by Côté and Maljkovic (2010) wherein lionfish remain motionless and only move to strike and eat prey passing nearby. They are also considered as solitary individuals (Fishelson, 1997), which is contrary to our observation of groups of up to seven individuals of different sizes inhabiting a cave.

In conclusion, this study provides the first baseline of lionfish distribution and abundance based on wide-scale standardized surveys encompassing sites and localities along the coast of Venezuela, southern Caribbean. The results corroborate anecdotal information suggesting that the invasive species had become established invading rocky reef, coral reefs and coral communities on scales that vary from several hundred of meters to hundred of kilometers. Differences in density and biomass at localities suggest that habitat quality (e.g. food resources, environmental setting, etc) for this species might also be variable. The high variability among replicates might suggest a patchy distribution for this species. Future studies must focus in determining the underlying processes that explain these spatial patterns like structural complexity, availability of refuges and abundance of prey.

ACKNOWLEDGMENTS

We are thankful to Cesar Herrera and Aldo Croquer for critically reviewing the manuscript and to Luis Miguel Montilla, Jose Cappeletto and Alejandra Hernandez for provide valuable help during dives and visual census. We also thank Juan Jose Cruz-Motta for his contribution in the design of the project. This project was financed by SARCE (South American Research on Coastal Ecosystem).

RESUMEN

Abundancia, estructura de tamaños y distribución espacial a lo largo de la costa venezolana del pez león (*Pterois volitans*, Pteroinae: Scorpaenidae). La reciente invasión del pez león (*Pterois volitans*) en el Atlántico se considera una nueva amenaza para bentónicos y peces de las comunidades en la región del Caribe. Esta especie fue informada por primera vez en varios sitios de Venezuela en 2009. El aumento de informes en los últimos cinco años sugiere que ha ampliado su distribución y hábitats. Sin embargo, esta información es principalmente anecdótica por lo que son necesarios estudios dirigidos a determinar su abundancia, estructura de tallas y otros aspectos ecológicos que abarquen más escalas espaciales para entender el papel real de esta especie en comunidades marinas en Venezuela. Determinamos la densidad y estructura del tamaño poblacional del pez león a través de censos visuales en la costa venezolana. Realizamos censos visuales siguiendo transectos lineales a una profundidad entre 5 y 20m durante el día, en 19 sitios de cinco localidades. La densidad media varia entre 7 y 55 individuos por hectárea entre sitios. La mayoría de los individuos eran adultos que se encontraban en cuevas, coexistiendo con otro peces león o con diferentes especies; mientras que otros estaban forrajeando activamente. El pez *Pterois volitans* esta bien establecido a lo largo de la costa venezolana y sus densidades en algunos sitios parecen exceder lo informado para su distribución nativa en el Pacífico pero son densidades menores que las informadas en localidades del Atlántico.

Palabras clave: Las especies exóticas, censos visuales, volitans del Sur del Caribe, Pterois

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Breeding success of the masked booby (*Sula dactylatra dactylatra*, Pelecaniformes:Sulidae) at Middle Cay, Pedro Bank, Jamaica

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Received 17-X-2013 Corrected 13-III-2014 Accepted 24-III-2014

Abstract: The masked booby (*Sula dactylatra dactylatra)* colony at Middle Cay, Pedro Bank, 60 miles south of Jamaica, has been affected by challenges resulting from anthropogenic disturbances. Despite habitat degradation, the colony displays resilience by remaining extant on the cay. Between June 2008 and June 2009 we investigated the colony's health (mainly breeding success). Data were collected once per month for twelve months and included one day, seven day and 24 hour (day and night continuous observational) sojourns. Forty-four nests were marked and monitored using a novel method for marking seabird nests based on painted seashells. Data collected from the colony included: the presence/absence/number of egg(s)/chick(s) in nests, offspring maturity, adult attendance at nests and the time of data collection. An average of 227 adult birds constituted the colony. Using the Mayfield Method and the "Naïve Estimator" for comparison, the colony's breeding success was determined to be 37.20% despite a hatching success of 40% and a fledgling success of 93%. This is less than the estimated 45.77% success typical of healthy colonies of sulids such as the masked booby elsewhere. Based on the breeding success calculations the long term survival of this colony is at risk and needs active conservation. Rev. Biol. Trop. 62 (Suppl. 3): 159-167. Epub 2014 September 01.

Key words: masked booby, Middle Cay, Pedro Bank, Jamaica, breeding success, sea bird, Mayfield Method.

The Caribbean with its tropical environment provides a variety of unique habitats for avian species which survive with other organisms within undisturbed ecosystems. While information is available on the population dynamics for some avian species within the region, little information exist for others. This may be so since Caribbean ornithology is often focused on birds with direct economic importance, eye-catching appearances or those that exist within habitats which are conveniently accessible. One such avian species within Jamaica for which limited information is available is the seabird *Sula dactylatra dactylatra* (Lesson, 1931); the masked booby (Atlantic). This seabird species is extant in separate colonies on two of three inhabitable cays located at Pedro Bank Jamaica. The cays with established masked booby colonies are known as Middle and Bird Cay. Though historical reports have indicated that the third cay known as Top Cay also served as a masked booby habitat, there has been no recent observation to substantiate the reports.

By serving as a habitat for more than five seabird species, Pedro Bank's Cays (Pedro Cays) are of importance to Jamaica's seabird diversity and also to Neotropical migrants that stopover to rest during their yearly southward journey. The Bank's submerged environment also provides good habitat for a variety of organisms and represents one of Jamaica's last remaining healthy marine ecosystems, supporting c*oral reefs, sea grass beds and coral cays* (Levy & Koenig, 2009). This healthy marine ecosystem makes Pedro Bank an ideal location for subsistence fishing which is the main economic activity practiced at the location. Fishermen from mainland Jamaica and other Caribbean islands have been reported to reside on Top Cay and Middle Cay instead of returning to their mainland home between fishing bouts (Allen & Webber, 2013). The presence of fisher folk on Top and Middle Cay has resulted in severe disturbances to those cays' environments thus subjecting native species to direct and indirect anthropogenic influences which may affect their fecundity.

This study was designed to provide information on the Middle Cay masked booby colony's health or resilience within its disturbed habitat through the determination of its breeding success and comparisons between the colony's observed success and that of healthy colonies in relatively undisturbed habitats.

MATERIALS & METHODS

Study Area: The Pedro Bank is a seamount which rises abruptly from about 500m and extends more than 160.93km east to west. Located 80km south of Jamaica, with its area of 8 040km^2, the bank is one of the largest offshore banks in the Caribbean Basin (The Nature Conservancy, 2007). Pedro bank is composed of a variety of marine habitats such as sand, coral reefs, deep reefs, sea grass beds and is one of Jamaica's last remaining healthy marine ecosystems (The Nature Conservancy, 2007). The seamount breaks the sea's surface in eight places, four of which are craggy rocks – Portland Rock, Blower Rock, Southwest Rock and the Shannon Rocks – inhabited only by seabirds; the other four form the Pedro Cays (Espeut, 2006).

The Pedro Cays are a group of three small low-lying coralline cays, located on the southeastern margins of the Pedro Bank between 16˚57' and 17˚03'N and 77˚46' and 77˚51'W. Historical reports mention a fourth Cay, the South Cay, however it has been eroded and now exists as a shallow shoal with a very small sandy beach (Hay, 2006). Humans reside on only two of the three inhabitable cays, namely, Top Cay and Middle Cay (Zenny, 2005). The situation on the inhabited cays is complex and challenging for management and conservation purposes. An estimated 150 to 1 200 fishers have been reported to operate from the cays (Allen & Webber, 2013). There are no proper toilet facilities or running water and solid waste is burnt, buried or dumped. No masked boobies were observed to nest on Top Cay however masked boobies nest on Middle Cay. According to Zans (1958) seabirds originally nested on all three cays.

Middle Cay located at 17˚1'N and 77˚46'W houses a base for the Jamaica Defense Force Coast Guard and is normally inhabited by hundreds of Jamaican fishermen (Espeut, 2006). Middle Cay, though the smallest of the three cays with an area of 40 000m^2 (Zans, 1958), has been reported to experience a rapid increase in human inhabitants since the 1990s (Hay, 2006). Middle Cay is densely populated and consists mainly of corrugated zinc and wooden shacks (Zenny, 2005). More than 50% of the surface area of the cay is occupied by squatter housings (Hay, 2006).

Sampling: The site was sampled at least once per month between June 2008 and June 2009 with and exception of May 2009 during which no sampling was conducted. Two types of sampling visits were done: day visits and weeklong visits.

Nests were selected for monitoring upon the detection of a laid egg in a nest. Once a nest was selected for monitoring, a conch shell was placed adjacent to that nest with its convoluted tip pointing in the direction of that nest. However before a shell was placed, its convoluted tip was spray-painted in a colour that contrasted with the cay environment and a number depicting the sequence in which the nest was detected and selected written on the inside and outside of the shell using a permanent marker. A map of the colony area showing the general layout of the habitat and the relative locations of each monitored nest was also created and updated each time a new nest was selected for monitoring. Adult masked boobies from monitored nests were banded with metal bands while their offspring, once at the downy chick stage of development, were temporarily banded with cable ties. All cable ties were removed at the end of the study.

Based on the size of the colony (approximately 227 birds) and a formula from Zar (1999) a sample size of 16 breeding pairs was determined to be a sufficient to obtain statistically sound breeding success values for the colony. Nonetheless twenty-seven nests were monitored through to the offspring's fledgling stage and forty-four nests were monitored through to their offspring's hatchling stage. A core set of data were collected during each visit to Middle Cay, which comprised of the following: nest number, presence or absence of (an) egg(s) in nest, the presence or absence and number of chicks in nests, the monitored offspring's stage of development, the presence or absence of adult(s) at nest, the date and time of data collection. Following each colony visit the data collected were brought back to a lab where they were reviewed and entered into a spread sheet for later analysis.

The hatching and fledgling success of a colony can provide valuable information about that colony's health within its breeding habitat. Hatching success indicates the proportion of that colony with the ability to hatch viable offspring from a set of eggs laid. While on the other hand, the fledgling success of a colony indicates the proportion of that colony with the ability to raise chicks to the point at which they achieve flight. The product of the hatching and fledgling successes of a colony will provide the breeding success of that colony (Priddel, Hutton, Olson & Wheeler, 2005). The breeding success of a colony indicates the proportion of that colony that is able to produce viable offspring which survive to achieve flight. By comparing the breeding success of a colony to the typical level of success obtained from healthy colonies of masked boobies, one can receive an indication of the health or resilience of the colony under investigation. The methods used to calculate hatching, fledging and breeding success are described below.

Two methods were used to determine the proportion of hatching and fledgling success observed for Middle Cay's masked booby colony; they are:

1. The Mayfield Method (Mayfield, 1961; Johnson, 1979)
2. A "Naive Estimator" (Frank Rivera pers. comm., 2009)

The results obtained from the application of the above methods to the data for hatching success were compared to assess the significance of any difference between the results. The same procedure was then followed for the determination of fledgling success. The result obtained from the Mayfield Method for the hatching success was then compared to the range of hatching successes (53% - 60%) reported by Anderson (1990) from his study on a healthy masked booby colony. For the fledging success, the result obtained from the application of the Mayfield Method to respective data was compared to the average fledgling success (81%) obtained from previous studies done on a healthy colony masked boobies by Kepler (1969).

The breeding success (the product of the hatching success and fledgling success, Priddel et al., 2005) of Middle Cay's masked booby colony was calculated at first using the results from the Mayfield Method and then those from the "Naïve estimator". The breeding successes obtained from both methods were then compared to see if the deviated from each other. Next, the breeding success obtained from the Mayfield Method was compared to the breeding success obtained from the product of the average hatching and fledgling successes observed from healthy colonies in other locations. If the breeding success of Middle Cay's masked booby colony was found to be greater than or equal to that obtained from healthy colonies at other locations, then the Middle Cay colony could be assumed to be in good condition at the time of the study. However, if the breeding success of the Middle Cay colony was found to be below that of healthy colonies that would suggest that the colony was failing at the time of the study.

In Mayfield (1961) analysis of Kirtland's Warbler (*Dendroica kirtlandii*) he encountered various discrepancies in his data that could not be rectified using customary methods. One of his most serious problems came from the fact that many of the nests used in his sample had not been detected until after incubation had begun. In his attempt to make his results more accurate Harold Mayfield proposed a new method to analyse this type of data. The new method became known as the Mayfield Method (Mayfield 1961, 1975).

For the Mayfield Method the following information must be known:

- The sample size (number of nests being monitored).
- The stage of development of the offspring within each nest.
- The time taken for the species to hatch, fledge or successfully breed must be known.
- The fate of each monitored offspring.
- Days between visits to sample site.
- Exposure time of offspring in each monitored nest (Following Johnson (1979) that when days between visits are > 15 days, 40% of exposure time must be used instead of 50%)
- Total exposure time of monitored offspring within the sample.

The method incorporates the exposure time of sample nests in its determination of success and thus is believed to be more accurate than other methods. To use this method the daily mortality (dmr) rate of the colony must be determined. This is done by dividing the number of nests to fail at hatching (fh) by the total exposure time (tet) of the sample nests within the colony (summation of the exposure time of all sample nests). The daily survival rate (dsr) may then be determined by subtracting the dmr from 1. The Mayfield Method allows for the calculation of the amount of variance contained in the data with the use of the following formula:

$$v = (1)/(((tet)^3)/((tet-fh)fh))$$

Where "v" is the variance. The standard error (SE) many now be determined by finding the square root of the variance: $SE=\sqrt{v}$

In the context of this research, hatching or fledgling success (S) of the colony may now be determined by raising the daily survival rate to the power of the total time taken by the species to hatch or fledge respectively, so S=(tth): dsr^{tth}. The resulting success (S) may be reported as a percentage ranging from 0% to 100%. The upper and lower limits of success may also be calculated from the results and reported with the proportion of observed success. This is done for the upper limit by using the formula: $(dsr + (2SE))^{tth}$. And for the lower limit using the formula: $(dsr - (2SE))^{tth}$.

"**Naïve Estimator**"**:** This method was dubbed the "Naïve estimator" by Rivera (pers comm., 2009). This was done because unlike the Mayfield Method that used exposure time to calculate its results thus making them more accurate, the "Naïve Estimator" does not. Due to this the results obtained by the "Naïve Estimator" may be considered as less accurate since it does not consider variation in its calculation. The information needed for the use of the "Naïve estimator" is as follows:

- The number of nests in the sample
- The number of failed nests.

Using the "Naïve Estimator" hatching mortality (hm) would be calculated by dividing the number of nests that failed to hatch (fn) by the number of monitored nests (n), as shown in the formula: hm=fn/n. The hatching success (hs) could then be calculated by subtracting the hatching mortality from 1, as shown in the formula: hs=1-hm. Because the results of the "Naïve Estimator" are not corrected for errors, its results were only used in comparisons with the results of the Mayfield method and not to draw conclusions from this study.

RESULTS

The results of the one year field assessment are reported as observations, in tables and as calculated hatching success, fledgling success and breeding success. Population counts revealed an estimate of 227 total boobies forming the colony from which 44 nests were monitored to provide the below results.

Hatching success: Two nests within the colony received eggs during the June 2008 to August 2008 period. These two nests were monitored and labelled sample Nests 1 and 2. However both nests failed to produce a hatchling. A third nest (Nest 3) received eggs in August 2008 and was monitored (Table 1). Sample Nest 3 also failed to produce a hatchling. In September of the same year there was a 100% increase in the number of eggs laid in nests over previous nest monitoring months; three nests became active in September 2008. Of the three nests two were successful in producing hatchlings. Most colony nests received eggs in October 2008 (Table 1). Twenty-one nests with eggs were marked and monitored from October 2008. These nests were monitored to their offspring's fledgling developmental stage, at which point the fate of a monitored offspring could be determined. Of the twenty-one nests, nine failed to produce a hatchling while 12 were successful. In April 2009 a second mass laying of eggs at the colony was observed. Seventeen of the nests from the second colony breeding attempt were monitored. These seventeen nests were monitored to determine their hatching success. Of the seventeen nests two successfully produced hatchlings; Nests 28 and 39 (Table 1). Therefore, of the forty-four monitored nests, sixteen successfully produced hatchlings. Despite the size of a nests' clutch only one chick was raised by the adults of successful nests. No dead chicks were observed in failed monitored nests where un-hatched eggs were absent.

The results obtained by using the "Naïve Estimator" and the Mayfield Method are presented in Tables 2 and 3 respectively. While the "Naïve Estimator" produced a proportion hatchling success of 0.36/36%; corrected to 2 decimal places (Table 2) the more reliable Mayfield Method produced a hatchling success of 0.4/40% (Table 3). The Mayfield Method also provided lower and upper 95% confidence interval spread of 0.29/29% at minimum and 0.57/57% at maximum.

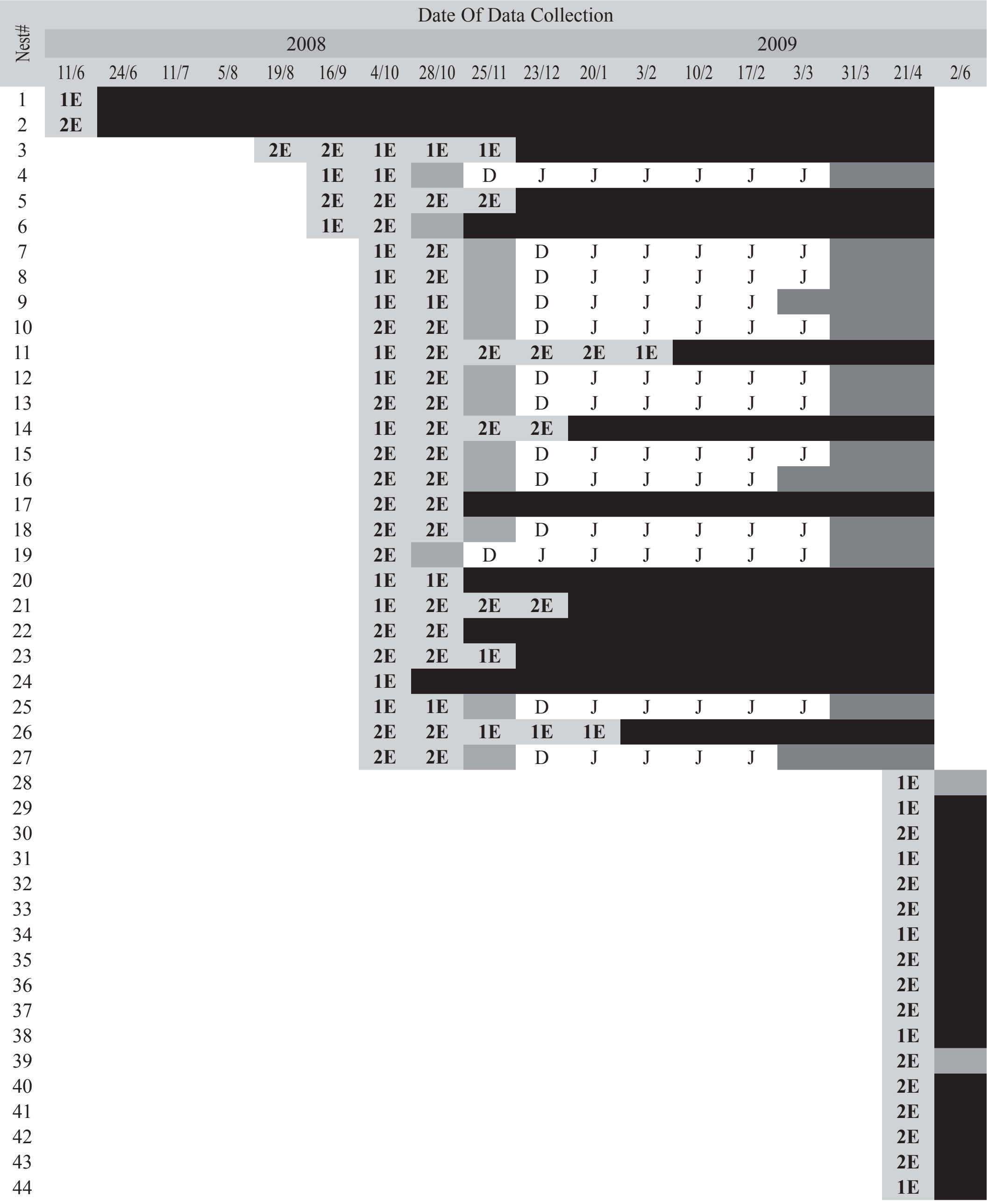
Fledgling success: Data were collected from twenty-seven nests (Nests 1 to 27) for the determination of the colony's fledgling success. Of the 14 nests that successfully produced a hatchling, 13 were successful at producing a fledgling (Table 1). According to the "Naïve Estimator" the fledgling success was found to be 0.93 (Table 4); corrected to 2 decimal places, which was the same as the result produced by the Mayfield Method (Table 5). The lower 95% confidence interval spread was found to be 0.79 while the upper 95% confidence interval spread was 1.0. The daily survival rate was found to be 0.99936 thus indicating that almost no fledgling mortality occurred on a day to day basis.

Breeding success: The breeding successes obtained from the two methods employed (Table 6). to determine the breeding success of Middle Cay's masked booby colony the product of the observed hatching and fledgling successes was found. The colony's breeding success was determined to be 37.20% according to the Mayfield Method and 33.81% according to the "Naïve Estimator". These two successes were determined to be significantly similar ($p=0.05$) according to the 95% confidence intervals produced by the Mayfield Method. Both methods produced slightly different results but with the same implication.

DISCUSSION

Ultimately, breeding success is the product of hatching and fledgling successes and these

TABLE 1
Data collected for the determination of the Middle Cay masked booby colony's breeding success



Nest#	Date Of Data Collection																	
	2008									2009								
	11/6	24/6	11/7	5/8	19/8	16/9	4/10	28/10	25/11	23/12	20/1	3/2	10/2	17/2	3/3	31/3	21/4	2/6
1	**1E**	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
2	**2E**	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
3					**2E**	**2E**	**1E**	**1E**	**1E**	■	■	■	■	■	■	■	■	
4						**1E**	**1E**	▩	D	J	J	J	J	J	J	▓	▓	
5						**2E**	**2E**	**2E**	**2E**	■	■	■	■	■	■	■	■	
6						**1E**	**2E**	▩	■	■	■	■	■	■	■	■	■	
7							**1E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
8							**1E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
9							**1E**	**1E**	▩	D	J	J	J	J	▓	▓	▓	
10							**2E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
11							**1E**	**2E**	**2E**	**2E**	**2E**	**1E**	■	■	■	■	■	
12							**1E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
13							**2E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
14							**1E**	**2E**	**2E**	**2E**	■	■	■	■	■	■	■	
15							**2E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
16							**2E**	**2E**	▩	D	J	J	J	J	▓	▓	▓	
17							**2E**	**2E**	■	■	■	■	■	■	■	■	■	
18							**2E**	**2E**	▩	D	J	J	J	J	J	▓	▓	
19							**2E**	▩	D	J	J	J	J	J	J	▓	▓	
20							**1E**	**1E**	■	■	■	■	■	■	■	■	■	
21							**1E**	**2E**	**2E**	**2E**	■	■	■	■	■	■	■	
22							**2E**	**2E**	■	■	■	■	■	■	■	■	■	
23							**2E**	**2E**	**1E**	■	■	■	■	■	■	■	■	
24							**1E**	■	■	■	■	■	■	■	■	■	■	
25							**1E**	**1E**	▩	D	J	J	J	J	J	▓	▓	
26							**2E**	**2E**	**1E**	**1E**	**1E**	■	■	■	■	■	■	
27							**2E**	**2E**	▩	D	J	J	J	J	▓	▓	▓	
28																	**1E**	▩
29																	**1E**	■
30																	**2E**	■
31																	**1E**	■
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36																	**2E**	■
37																	**2E**	■
38																	**1E**	■
39																	**2E**	▩
40																	**2E**	■
41																	**2E**	■
42																	**2E**	■
43																	**2E**	■
44																	**1E**	■

Lettering Key	
D	Downy Chick
J	Juvenile
1E/2E	Number of Eggs

Shade/Pattern Key	
■	Failed Nest
▩	Hatching Success
░	Incubating nest
▓	Nest with Fledgling

TABLE 2

Results of calculations done on the data to determine the colony's hatching success using the "Naïve Estimator"

Hatchling survival (success)	0.364
Hatchling mortality (failure)	0.636
Number failed hatching	28
Number survived to fledge	16
Number monitored nest (n)	44

TABLE 3

Results of calculations done on the data to determine the colony's hatching success using the Mayfield Method

Daily mortality rate	0.02083
Daily survival rate	0.97917
Variance	1.5178E-05
Standard error	0.00390
Hatching survival (success)	0.40
Number survived hatching	16
Number monitored nests (n)	44
Lower 95% confidence interval	0.29
Upper 95% confidence interval	0.57

TABLE 4

Results of calculations done on the data to determine the colony's Fledging success using the "Naïve Estimator"

Fledging survival (success)	0.928571429
Proportion of chicks that died	0.071428571
Number failed hatching	1
Number survived to fledge	13
Number monitored nest (n)	14

TABLE 5

Results of calculations done on the data to determine the colony's Fledging success using the Mayfield Method

Daily mortality rate	0.00064
Daily survival rate	0.99936
Variance	4.1065E-07
Standard error	0.00064
Fledging survival (success)	0.93
Number survived to fledge	13
Number of monitored nests (n)	14
Lower 95% confidence interval	0.79
Upper 95% confidence interval	1.08

are calculated estimates which account for a researcher's observations at the nests as well as a researcher's time away from the nests with no observations. The three successes therefore need to be considered in the final analysis.

Hatching success is a potentially important fitness component for avian species (Knape et al., 2008). Due to this, the determination of a colony's hatching success may provide critical information about a bird colony's resilience within its habitat. Table 2 shows that successful sample nests produced only one offspring despite the observation that a maximum of two eggs were laid in nests. This observation is characteristic of the species and is due to the persecution of the younger chick by its older sibling; a process known as siblicide (Nelson, 1978). Consistent with the biology of the species, each monitored nest which produced one chick was reported as being successful at its attempt. According to the Mayfield Method, the colony was determined to have a hatching success of 40%, while the "Naïve Estimator" suggested a success of 36.4%. The confidence limits produced by the Mayfield Method indicated that the two results were not significantly different when tested at the 90% Confidence Interval.

According to Anderson (1990) the proportion of the hatching success observed from obligately siblicidal species, such as the masked booby, should fall within the range of 53% to 60%. By comparing the hatching success observed for the colony, which was 40%, to the range of successes presented by Anderson (1990) it is evident that the observed success did not fall within the range of successes

TABLE 6

Calculated breeding success of the masked booby colony nesting on Middle Cay, Pedro Bank, Jamaica

Method	Hatching	Fledging	Breeding	% Breeding Success (2d.p.)
"Naïve Estimator"	0.364	0.93	0.338	33.81
Mayfield Method	0.4	0.93	0.372	37.20

expected. It was therefore deduced that at the time of the study, middle cay's colony was not achieving a level of success which is associated with that of a healthy masked booby colony. Despite this, the upper 95% confidence limit determined for the colony's hatching success fell within the range of successes representative of healthy colonies and so the success, at the upper limit, obtained for the Middle Cay colony was not significantly different from that of fit colonies. Though a significant difference was not detected between the previously mentioned statistics, the results still suggest that the colony would benefit from scientific intervention to increase its hatching success. The range of hatching successes observed by Anderson (1990) for siblicidal Sulids was a good statistic to use for this analysis since hatching success tends to vary between colonies of Sulids found in different locations.

The fledging success of Middle Cay's masked booby colony was determined to be 93% by both the Mayfield Method and "Naïve Estimator". Kelper (1969) observed a fledging success of 79% from a study done on 43 boobies in 1964 and a success of 83% from a study done on 30 boobies the following year (1965) at Green Island, Kure. The results from Kelper's 1969 study were used in the analysis because the Green Island colony was not exposed to adverse disturbances such as that of the Middle Cay colony. Using the average of the fledging successes obtained by Kelper, an average expected fledging success of 81% was obtained. From a comparison between the observed fledgling success of 93%, and the average "expected" success of 81%, it was deduced that Middle Cay's masked booby colony was experiencing a more than satisfactory level of fledgling success and so the colony was in no need of scientific intervention in the area of fledgling success.

The acceptable breeding success for siblicidal masked booby colonies was determined to be 45.77%, which is the product of the average "expected" range for the hatching success from Anderson's data (56.5%) and that of the fledgling successes obtained by Kelper (81%). A comparison of the two results (37.20% according to the Mayfield Method and 33.81% according to the "Naïve Estimator") revealed that at the time of the study, the colony obtained a success which was less than that characteristic of healthy colonies. Due to this it may be concluded that the Middle Cay's masked booby colony would benefit from intervention to improve its breeding success.

Greatest error in this calculation of breeding success may be attributable to the hatching success calculation but confidence in the data surrounding fledging success and observations of activities in the colony especially over the 24 hour period support the finding of a colony whose breeding success is less than acceptable for this species. Conservation interventions if considered should surround the improvement of the hatching success by reduction of the environmental pressures observed at Pedro Cays but only after more detailed data collection and analysis. The presence of large and apparently increasing number of fisher folk on Middle Cay has resulted in severe reduction in physical space and modifications of the environments available to the birds. Hourly counts of adult masked boobies at the colony during a one week period, reveled the colony's attendance to peak at an estimated 227 individuals by dawn which left little room for the arrival or departure of colony members. Being now more densely populated, the Sulids at Middle Cay's are encountering species specific triggered habitat reduction as well as intense disturbances from fisher folk. These factors appear to be important contributors to the recorded low breeding success of these sea birds in their natural environment.

ACKNOWLEDGMENTS

The completion of this research would not have been possible without assistance from the Jamaica Defence Force Coast Guard, The Nature Conservancy (TNC), E.A. Schreiber and Brandon Hay.

RESUMEN

Determinación del éxito reproductivo del alcatraz enmascarado (*Sula dactylatra dactylatra,* Pelecaniformes:Sulidae) en Cayo Middle, Banco de Pedro Jamaica. La colonis del alcatraz enmascarado (*Sula dactylatra dactylatra)* en Cayo Middle, Banco de Pedro, 60 millas al sur de Jamaica, ha sido afectada por una serie de desafíos resultantes de disturbios antropogénicos a su hábitat. A pesar de la degradación excesiva del hábitat, la colonia muestra resiliencia al permanecer en el cayo. Entre junio de 2008 y junio de 2009 realizamos una investigación de la salud de la colonia (principalmente éxito reproductivo). Los datos fueron recogidos una vez al mes durante doce meses e incluyó un día, siete días y 24 horas (día y noche de continua observación). Cuarenta y cuatro nidos fueron marcados y monitoreados utilizando un método novedoso para marcar nidos de aves marinas. Los datos recogidos de la colonia incluyen: presencia/ausencia/número de óvulos/polluelos en nidos, madurez de crías, asistencia de adultos en los nidos y el tiempo de recolección de datos. Un promedio de 227 aves adultas constituían la colonia. Usando el método de Mayfield para analizar los datos y el "estimador Naïve" para la comparación, el éxito reproductivo de la colonia se determinó de un 37.20% a pesar de un 40% de éxito de eclosión y un éxito de pichones del 93%. Esto es menos que el éxito estimado de 45.77% en colonias saludables como la del alcatraz enmascarado en todo el mundo. Basado en los cálculos de éxito la supervivencia a largo plazo de esta colonia está en riesgo y necesita se ejecute conservación activa.

Palabras clave: enmascarados Piquero, medio Cay, Pedro Bank, Jamaica, cría éxito, aves marinas, método Mayfield

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Fish assemblages on fringing reefs in the southern Caribbean: biodiversity, biomass and feeding types

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Received 22-VIII-2013 Corrected 18-II-2014 Accepted 24-III-2014

Abstract: Reef fish assemblages in the Caribbean are under increasing pressure from human activities. Inadequate enforcement of legislation coupled with unreliable and data-poor landings in Tobago have led to the unregulated exploitation of reef fish for decades. This study addresses the lack of data on major reefs. Visual observations of fish fauna were conducted from November 2011-May 2013 at open access reef sites (Speyside, Charlotteville, Culloden, Arnos Vale, Mt. Irvine, La Guira, Kilgwyn, Plymouth and Black Rock) and one protected area (Buccoo Reef Marine Park). Belt transects surveys were used to determine fish density, species diversity and abundance at the 10-15m depth contour. Fish sizes were converted to biomass using the length-weight relationship of fish $W=aL^b$. Most fish assemblages were dominated by small herbivores (<15cm), in particular Pomacentridae and Scaridae. Few large predators (>40cm) e.g. Serranidae, were noted, which is indicative of fishing pressure. MDS ordination identified three fish assemblages: i) northeastern, ii) southwestern and iii) intermediate. The northwestern cluster (Speyside and Charlotteville) were most representative of reef fish assemblages across the entire island, and exhibited the highest species richness, diversity and biomass. However, the southwestern cluster the highest numerical abundance. The marine protected area contained higher fish biomass, abundance, diversity and richness, but it was only representative of reef fish assemblages on the southwest of the island and not the entire Tobago. Research on the reef fishery, particularly spear fishing, is recommended to determine impact. Rev. Biol. Trop. 62 (Suppl. 3): 169-181. Epub 2014 September 01.

Key words: coral reef fish, Tobago, trophism, underwater visual surveys.

Coral reef fishes are the most diverse vertebrate communities on Earth (Jones, 1991) and their spatio-temporal distribution is influenced by a combination of complex biological and physical factors. These factors include larval supply (Doherty, 1991), competition (Munday, Jones & Caley, 2001; Holbrook & Schmit, 2002), wave exposure (Fulton, Bellwood & Wainwright, 2005), depth (Srinivasan, 2003) and habitat complexity (Friedlander, Sandin, DeMartini & Sala, 2010). Reef fishes, as predators or herbivores, play an important role in the community dynamics of coral reefs through their interactions with corals, algae, other herbivores and other predators. Disruption in the balance of reef fish assemblages can decrease coral cover and increase algal abundances (Roberts, 1995). Because of this importance, fishes are often a focus of monitoring and management programmes to evaluate the condition of reef communities (Green, Bellwood & Choat, 2009). Historically coral reef fish have been difficult to manage, in part, because different species often have different habitat requirements (Sale, 2002), life history patterns (Appeldoorn, Recksiek, Hill, Pagan & Dennis, 2003) and feeding regimes (Holland, Peterson, Lowe & Wetherbee, 1993).

Reef fish communities around Tobago exist on the margin of coral reefs in the southern Caribbean, and play a critical role in maintaining reef integrity. However, declining reef fish (abundance and biomass) as told in the oral history of Tobago, threatens the mainstay of the local diet and dependent economies. Further, the recent invasion of the lionfish onto Tobago's reefs poses a real threat to juvenile and small reef fish communities. The purpose of this study is to a) establish some baseline data on the abundance and species richness of reef fishes around Tobago and b) assess any spatial variation in these assemblages.

MATERIALS AND METHODS

Study site: This study was conducted over an eighteen month period October 2011 to March 2013 on the reefs surrounding Tobago (10°2' to 11°12'N and 60°30' to 61°56'W) (Fig. 1), located 7km east off the Paria Peninsula. Study reefs (n=23) were of comparable size(~4ha) and represented the variability of the major reef systems. Tobago's underwater topography is characterized by two distinct topographic regimes, a shallow limestone gently sloping shelf on the southwest side of the island, and a narrow, rocky, steeply sloping shelf on the northeastern side, upon which a variety of coral have been established (Snake, Rowe, Yule & Wadge, 1986). In this study, the southwest reefs are considered true coral reef (CR) formations consisting of corals colonies built upon a carbonate substrate with distinct reef zonation. Whereas the northeast reefs are considered coral associations (CA) consisting of coral-sponge co-dominated reefs established on rocky non-carbonate based substrata. Reefs along the northeast of Tobago are more exposed

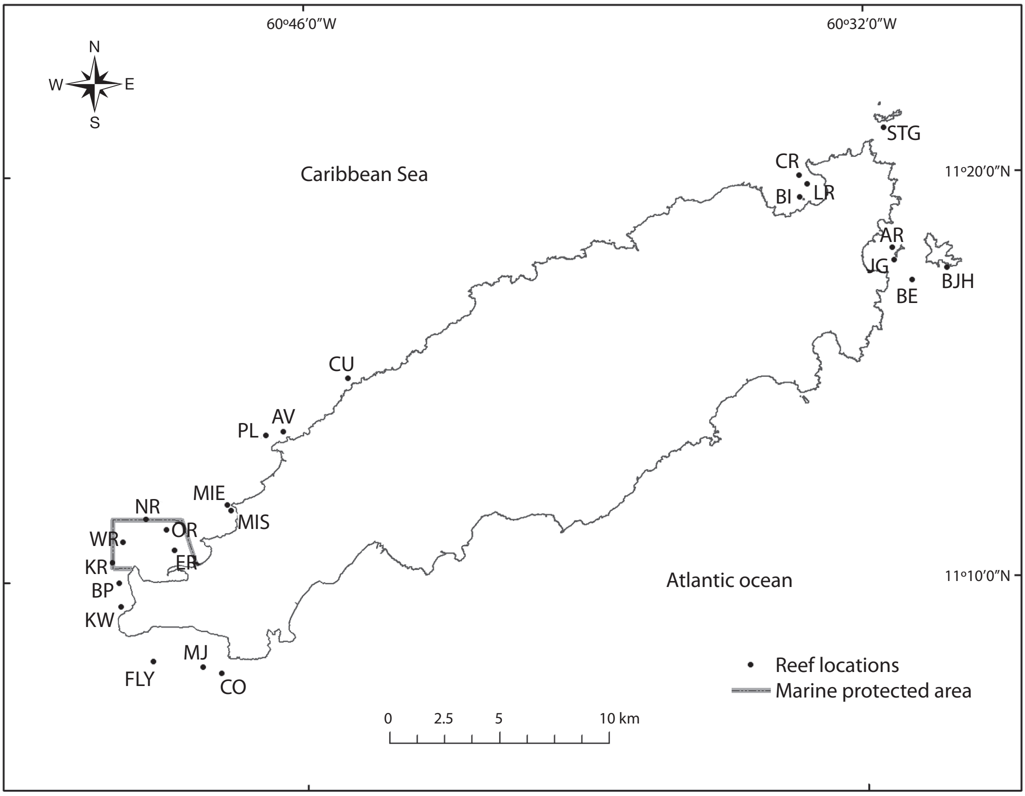

Fig. 1. Study sites in Tobago. Outer Reef (OR), Western Reef (WR), Northern Reef (NR), Eastern Reef (ER), Ketchup Reef (KR), BoPez (BP), Flying Reef (FLY), Cove (CO), Kariwak Reef (KW), Majeston Reef (MJ), Arnos Vale Reef (AV), Culloden Reef (CU), Plymouth Reef (PL), Mt. Irvine Extension (MIE), Mt. Irvine Reef (MIS), Landslide Reef (LS), St. Giles Island (STG), Booby Island (BI), Corner Rock (CR), Book Ends (BE), Angel Reef (AR), Black Jack Hole (BJH) and Japanese Garden (JG).

to the northeast trade winds and occur in a high energy environment due to the convergence of the Atlantic Ocean and Caribbean Sea. All study reefs were dominated by coral taxa such as *Montastraea faveolata*, *Siderastrea siderea*, *Diploria strigosa* and *Colpophyllia natans*.

Reef fish census: Reef fish surveys were conducted to estimate abundance, richness and to determine spatial distribution. Surveys were conducted along three 25x5m belttransects along the outer reef slope between 10-15m depth. Along each transect the number of individuals of each species was estimated and the total length of each fish was visually estimated and classified into 10cm classes (<10cm, 10–20cm, >20–30cm, >30–40cm and >40cm). Blennids and gobiids were excluded for this assessment, due to their cryptic nature, difficulty in field identification and field time constraints. Shannon-Weaver diversity indices (H’) [$H' = -\sum i\, p_i (\log p_i)$], species richness (S), fish density/100m^2 (D) and species abundance (N), were determined for all reefs.

Fish biomass was estimated using the length-weight relationship of fish, $W = aL^b$. The most suitable “a” and “b” constants were acquired from Froese and Pauly (2013), and where no relationship was available for species, that of a closely related species as applied. Trophic guilds were classified according to Froese and Pauly (2013), however in many cases there was no definitive consensus as to the trophism of several species. As a result trophic groups were consolidated and presented as planktivores, primary consumers (herbivores and detritivores), secondary consumer (omnivores and benthivores) and piscivores.

Benthic cover and vertical relief was also measured along benthic transects. Benthic cover was estimated using six 10 x 1m belt transects at each site as described by (Hill & Wilkinson, 2004). Ten non-overlapping 1m^2 photos were taken along each transect and analysed using the Coral Point Count with Excel (CPCe) programme (Kohler & Gill, 2006). Sixty random points were overlaid onto each photoquadrat, and the benthos under each point was identified to the lowest taxonomic level, for a total of 3 600 points per site. Only hard coral cover is presented. Vertical relief was measured as the distance between the lowest point and highest point on the substrate along that transect (Luckhurst & Luckhurst, 1978). Low relief was considered to be areas of between 0–1.5m and high relief to be >1.5m.

Bray-Curtis similarity on fourth-root transformed abundance and biomass was calculated, and analysis of similarities (ANOSIM) was conducted to test for differences in similarity between reefs and reef types. The ANOSIM results in a global R statistic that reflects the differences in variability between groups and within groups, and checks for significance of R were performed using permutation tests (Clarke & Warwick, 2001). Two dimensional ordinations were created using non-metric multidimensional scaling (MDS), which was used to generate plots in which the distance between points is proportional to their degree of dissimilarity, so closer points are more similar than points farther away (Clarke & Warwick, 2001). MDS plots were generated using entire assemblage level parameters, mean abundances and species biomass. A low stress value is an indicator of low error, similar to a measure of standard deviation (Clarke & Warwick, 2001). The species predominantly responsible for discriminating between assemblages were identified by the similarity percentage (SIMPER).

RESULTS

A total of 15 576 fish, representing 96 species and 23 families were recorded around Tobago, with an average of 677.2±376.3 individuals/site. The most abundant species were *Stegastes partitus*, *Chromis miltilineata* and *Clepticus parrae* which collectively represented approximately 45.0% of the total number of fish observed. The least abundant species were *Balistes vetula*, *Mycteroperca bonaci*, *Bothus lunatus*, *Scarus coelestinus*, *Lutjanus cyanopterus*, *Lactophyrs quadricornis*, *M. tigris*, *Sphyraena barracuda* and *Abudefdub taurus*, with each being only observed once.

Over 80.0% of the fish observed belonged to the families Pomacentridae (39.2%), Labridae (25.6%) and Scaridae (15.4%) (Table 1). Species from the families Pomacentridae, Labridae, Scaridae, Haemulidae, Acanthuridae and Serranidae were found at all locations, and together with Pomacentridae accounted for 90% of fish observed. Chaetontidae was observed in all but one site. Together, these seven families accounted for ~70.0% of the total biomass, with the highest biomass (21.0%) provided by Pomacentridae (56kg/100m^2). Other major contributors to overall biomass included Scaridae (11.4%), Lutjanidae (8.2%), Acanthuridae (6.4%) and Haemulidae (6.2%), with all other noted families contributing <5% each to overall biomass (Table 2).

The most abundant trophic group was the primary consumer (herbivores and detritivores) which accounted for 43.2% of all fish recorded,

TABLE 1
Abundance, biomass and trophism of surveyed reef fishes at 23 sites in Tobago

Trophic Level	Family/Scientific Name	Biomass (g/100m^2)				Density (fish/100m^2)			
		SA	I	O	NE	SA	I	O	NE
	Acanthuridae								
Pr	*Acanthurus coeruleus* (Bloch & Schneider, 1801)	270.8	405.5	673.7	1442.7	6.9	5.1	1.4	12.6
Pr	*Acanthurus chirurgus* (Bloch, 1787)	384.4	319.9	3 051.0	2 145.7	5.1	3.5	11.4	11.2
Pr	*Acanthurus bahianus* (Castelnau, 1855)	286.6	1 306.0	1 461.4	3 901.1	14.7	15.2	8.3	35.4
	Aulostomidae	131.5	90.0	216.9	51.2				
P	*Aulostomus maculatus* (Valenciennes, 1841)					2.1	1.6	1.9	1.4
	Balistidae								
Pr	*Melichthys niger* (Bloch, 1786)					1.6		16.6	7.0
S	*Balistes vetula* (Linnaeus, 1758)				142.7				0.2
Pr	*Cantherhines pullus* (Ranzani, 1842)	96.8	315.1	199.7	746.0	1.1	1.9	1.8	2.8
S	*Cantherhines macrocerus* (Hollard, 1853)		64.6	560.9	646.4		0.8	3.4	1.6
S	*Aluterus scriptus* (Osbeck, 1765)		31.7	118.8	2 257.7		0.3	0.8	6.0
	Bothidae								
Pl	*Bothus lunatus* (Linnaeus, 1758)				15.3				0.2
	Carangidae								
P	*Caranx ruber* (Bloch, 1793)	2 030.8	111.3		3 099.6	4.3			15.0
P	*Seriola rivoliana* (Valenciennes, 1833)		3 662.7						
P	*Caranx latus* (Agassiz, 1831)				967.3				4.0
P	*Caranx crysos* (Mitchill, 1815)			209.0				2.0	
P	*Elegatis bipinnulata* (Quoy & Gaimard, 1825)			1 493.0				24.0	
	Chaetontidae								
S	*Chaetodon striatus* (Linnaeus, 1758)	6 495.6	1 730.4	1820.1	933.5	3.5	2.9	1.2	1.0
S	*Chaetodon capistratus* (Linnaeus, 1758)	14 798.9	800.2	346.4	3 417.9	8.3	3.2	0.9	4.0
S	*Chaetodon sedentarius* (Poey, 1860)		1 245.5	890.7	14 001.5		0.8	1.0	7.6
S	*Chaetodon ocellatus* (Bloch, 1787)	5.5	6.9	30.9	177.7	1.1	0.5	0.6	2.4
	Engraulidae								
S	*Lycengraulis grossidens* (Spix & Agassiz, 1829)			30.6				26.7	
	Haemulidae								
S	*Haemulon sciurus* (Shaw, 1803)	47.6	156.2	147.1	251.4	0.8	0.3	0.6	1.0
S	*Haemulon carbonarium* (Poey, 1860)	293.7	121.5	85.6	201.3	4.5	1.1	2.7	1.6
S	*Haemulon flavolineatum* (Desmarest, 1823)	85.5	152.6	461.6	706.9	7.7	4.3	9.5	6.6
S	*Haemulon chrysargyreum* (Günther, 1859)	4.3	386.7	509.9	1 905.1	1.3	1.9	7.6	10.4
S	*Haemulon plumierii* (Lacepède, 1801)		220.2	16.3	322.0		0.5	0.3	1.2

TABLE 1 (Continued)

Trophic Level	Family/Scientific Name	Biomass (g/100m^2)				Density (fish/100m^2)			
		SA	I	O	NE	SA	I	O	NE
S	*Haemulon macrostomum* (Günther, 1859)	160.9	308.6	321.8	11.7	0.3	0.5	0.5	0.2
S	*Anisotremus virginicus* (Linnaeus, 1758)	86.0	96.9			0.3	1.3		
S	*Anisotremus surinamensis* (Bloch, 1791)		106.4		2 216.6		0.3		17.8
S	*Haemulon melanurum* (Linnaeus, 1758)	37.6	74.3	56.4	558.7	0.5	0.3	0.6	5.4
Pl	*Haemulon aurolineatum* (Cuvier, 1830)			54.4	93.9			0.2	1.6
S	*Haemulon steindachneri* (Jordan & Gilbert, 1882)				4767.4				31.0
	Holocentridae								
S	*Myripristis jacobus* (Cuvier, 1829)	457.3	1 201.3	2 053.9	978.6	2.4	2.9	13.5	1.8
S	*Holocentrus adscensionis* (Osbeck, 1765)	388.3	645.8	1 568.4	399.3	2.7	2.1	9.1	2.2
S	*Holocentrus coruscum* (Poey, 1860)			150.0				1.2	
	Kyphosidae								
Pr	*Kyphosus vaigiensis* (Quoy & Gaimard, 1825)				2173.0				7.8
	Labridae								
Pl	*Thalassoma bifasciatum* (Bloch, 1791)	220.9	230.2	281.9	572.9	106.4	94.9	65.6	64.8
Pl	*Clepticus parrae* (Bloch & Schneider, 1801)					190.1	54.4	31.9	108.8
S	*Lachnolaimus maximus* (Walbaum, 1792)		298.0		910.0		0.3		2.4
S	*Bodianus rufus* (Linnaeus, 1758)	66.1	194.8	663.8	127.9	1.1	3.7	4.4	2.8
S	*Halichoeres garnoti* (Valenciennes, 1839)	272.4	283.0	230.9	1 345.3	35.7	13.6	10.3	32.2
S	*Halichoeres maculipinna* (Müller & Troschel, 1848)	0.4	111.9	2.7	397.5	0.3	1.9	1.4	53.2
S	*Halichoeres radiatus* (Linnaeus, 1758)	15.9	0.6		1 895.0	1.3	0.3		48.6
S	*Halichoeres bivittatus* (Bloch, 1791)	88.0	10.4	75.9	249.6	11.5	10.9	6.0	12.4
	Lutjanidae								
P	*Lutjanus apodus* (Walbaum, 1792)	230.8		675.3		2.9	1.3	1.1	
P	*Ocyurus chrysurus* (Bloch, 1791)	81.4	15.7	8 726.5	266.7	0.5	0.3	9.6	0.8
P	*Lutjanus cyanopterus* (Cuvier, 1828)	10 151.1				0.3			
	Mullidae								
S	*Mulloidichtys martinicus* (Cuvier, 1829)	2 434.3	44.4	45.2	144.0	17.6	0.5	0.6	2.8
S	*Pseudupeneus maculatus* (Bloch, 1793)	27.1	15.2	691.4	148.6	0.5	0.8	1.3	0.6
	Ostraciidae								
S	*Lactophrys polygonia* (Poey, 1876)	21.3	80.8	231.4	115.7	0.3	0.3	1.2	0.6
S	*Lactophyrs quadricornis* (Linnaeus, 1758)			55.9				0.2	
	Pomacanthidae								
S	*Pomacanthus paru* (Bloch, 1787)	2 650.0	1 802.3	3645.4	1 401.5	1.3	0.8	1.7	1.4
S	*Holacanthus ciliaris* (Linnaeus, 1758)	258.8	121.3	0.4	250.2	1.1	0.3	0.3	0.6
S	*Pomacanthus arcuatus* (Linnaeus, 1758)				125.3				0.4
S	*Holacanthus tricolor* (Bloch, 1795)			558.9	1 005.5			2.0	1.2
	Pomacentridae								
Pr	*Stegastes leucostictus* (Müller & Troschel, 1848)	41.4	37.5		128.6	11.2	19.2		1.8
Pr	*Stegastes partitus* (Poey, 1868)	7 632.9	12 057.8	11 588.6	13 399.4	195.5	151.7	79.0	273.2
Pl	*Stegastes fuscus* (Cuvier, 1830)	27.2	100.1	10.4	150.6	0.8	3.2	2.1	5.4
S	*Abudefduf saxatilis* (Linnaeus, 1758)	123.9	146.3	1 059.5	635.2	11.7	1.6	7.4	6.4
Pr	*Microspathodon chrysurus* (Cuvier, 1830)	378.7	186.4	759.8	2 247.4	14.9	8.3	8.1	15.8
Pl	*Chromis multilineata* (Guichenot, 1853)					81.9	161.3	179.9	118.2
Pl	*Chromis cyanea* (Poey, 1860)						4.3	11.2	18.6
Pr	*Stegastes diencaeus* (Jordan & Rutter, 1897)						0.3		1.6
S	*Stegastes planifrons* (Cuvier, 1830)				28.8	4.3			1.0

TABLE 1 (Continued)

Trophic Level	Family/Scientific Name	Biomass (g/100m^2)				Density (fish/100m^2)			
		SA	I	O	NE	SA	I	O	NE
Pr	*Abudefduf taurus* (Müller and Troschel, 1848)								0.2
	Priacanthidae								
Pl	*Pricanthus cruentatus* (Lacepède, 1801)			7 456.5				12.8	
	Scaridae								
Pr	*Scarus taeniopterus* (Lesson, 1829)	961.1	623.6	960.6	643.9	124.8	49.3	19.4	15.2
Pr	*Scarus vetula* (Bloch & Schneider, 1801)					23.2	3.5	1.1	15.4
Pr	*Sparisoma aurofrenatum* (Valenciennes, 1840)	670.7	561.0	1 669.8	1 112.3	16.3	15.2	9.9	5.6
Pr	*Sparisoma viride* (Bonnaterre, 1788)	3 215.1	1 936.7	1 186.8	4 895.1	36.5	21.9	4.9	23.6
Pr	*Scarus iseri* (Bloch, 1789)	1 363.2	1 831.8	163.1	3 394.6	171.2	40.3	9.5	18.2
Pr	*Sparisoma atomarium* (Poey, 1861)	2.8	3.4			1.3	1.6		
Pr	*Sparisoma chrysopterum* (Bloch & Schneider, 1801)	32.8	0.6		1 493.5	0.5	0.3		11.8
Pr	*Scarus coelestinus* (Valenciennes, 1840)	257.5				0.3			
Pr	*Scarus guacamaia* (Cuvier, 1829)	659.5			197.9	0.5			0.4
Pr	*Scarus coeruleus* (Edwards, 1771)				147.3				0.4
	Sciaenidae								
S	*Paraques acuminatus* (Bloch & Schneider, 1801)		45.6	1.6				0.8	
S	*Equatus punctatus* (Bloch & Schneider, 1801)								0.2
	Serranidae								
P	*Cephalopholis fulva* (Linnaeus, 1758)		94.2	473.6	461.4		0.5	1.1	0.6
P	*Cephalopholis cruentata* (Lacepède, 1802)	372.1	87.2	1 031.2	835.8	2.7	1.6	2.9	4.0
P	*Mycteroperca bonaci* (Poey, 1860)	54.8				0.3			
S	*Epinephelus adscensionis* (Osbeck, 1765)	171.1		2.5	301.0	0.3		0.8	15.0
S	*Serranus tigrinus* (Bloch, 1790)	349.3	182.4	284.6	158.9	9.3	8.8	6.1	8.0
S	*Hypoplectus puella* (Cuvier, 1828)	897.2	3.0	0.4	38.2	5.9	1.9	0.3	1.2
S	*Hypoplectrus gummigutta* (Poey, 1851)					1.3	0.5	0.3	0.8
S	*Hypoplectrus nigricans* (Poey, 1852)					0.3	0.5		
P	*Mycteroperca tigris* (Valenciennes, 1833)			234.2				0.2	
P	*Epinephelus striatus* (Bloch, 1792)				24.3				0.4
P	*Rypticus saponaceus* (Bloch & Schneider, 1801)								1.4
Pl	*Paranthias furcifer* (Valenciennes, 1828)				142.8				0.6
S	*Epinephelus guttatus* (Linnaeus, 1758)								0.4
	Sphyraenidae								
P	*Sphyraena barracuda* (Edwards, 1771)			100.8				0.2	
	Synodontidae								
P	*Synodus saurus* (Linnaeus, 1758)	86.5	509.2		345.0	0.5	1.1		1.4
	Tetraodontidae								
S	*Monacanthus tuckeri* (Bean, 1906)	2.6	1 012.3	379.2		0.8	3.2	0.9	
S	*Diodon hystrix* (Linnaeus, 1758)			478.9	68.1			0.3	0.2
S	*Canthigaster rostrata* (Bloch, 1786)					7.2	0.5	1.0	1.4

Pl=Planktivores, Pr=Primary consumers, S=Secondary consumers, P=Piscivores. SA=Southwestern assemblage, I=intermediate assemblage, O=Outliers, NE=Northeastern Assemblage.

followed by planktivores (36.5%), secondary consumers (17.8%) and piscivores (2.5%). The primary consumer, *Stegastes partitus* contributed the most towards total biomass across sites, 19.2% of the total fish biomass. Other major contributors to the overall fish biomass included *Chromis multilineata* (14.8%), *Clepticus parrae* (10.6%) and *Thalassoma bifasciatum*

TABLE 2

Characteristics of benthic habitats at reef fish surveys sites in Tobago

	% Coral cover	% Sponge cover	% Algae	Bare substrate	Relief (m)	Depth (m)	Species Richness (S)	Species Diversity (H’)	Density (fish/100m^2)	Total biomass (g/100m^2)
OR	17.7	0.3	69.2	0.0	1.3	10-12	27	2.641	111.5	2 763.1
WR	13.0	1.3	57.0	3.2	1.5	10-13	32	2.383	159.2	3 623.9
NR	10.0	5.7	82.7	0.0	1.3	10-14	30	2.165	188.5	6 272.1
ER	20.5	4.5	64.2	6.7	0.9	8-10	35	2.251	185.9	8 398.2
KR	7.5	0.6	24.2	54.2	1.0	8-10	20	1.959	190.9	721.7
BP	17.7	1.0	43.5	23.6	0.1	11-13	29	2.263	124.5	32 751.6
FLY	11.9	7.6	55.7	12.9	3.0	10-14	20	1.959	190.9	12 996.5
CO	4.7	15.1	31.4	35.6	1.5	10-15	41	2.557	170.7	12 398.8
KW	15.7	3.5	13.0	38.7	2.0	11-14	25	2.39	88.5	1 795.1
MJ	7.8	3.2	32.2	21.6	1.1	10-13	17	1.636	110.1	2 448.8
AV	14.0	5.4	52.7	22.2	1.8	11-15	17	1.234	114.4	3 555.4
CU	16.3	3.8	59.9	1.8	0.5	10-12	23	2.6	43.7	1 687.4
PL	8.7	2.9	29.7	40.0	1.9	10-16	40	2.547	112.5	5 600.5
MIE	11.1	3.0	34.8	13.5	2.5	10-17	37	2.61	149.6	4 462.5
MIS	9.1	1.8	40.5	41.8	1.0	10-18	27	2.249	108.0	2 185.8
LS	6.5	3.0	65.7	1.5	4.0	10-14	35	3.003	71.2	3 172.5
STG	42.8	0.8	41.7	0.0	6.0	12-15	30	2.989	50.8	6 729.5
BI	16.1	1.4	68.2	2.3	3.4	10-19	38	2.203	305.6	39 544.8
CR	17.5	1.5	36.7	3.2	3.5	10-12	39	2.362	219.6	13 070.4
BE	12.7	14.0	45.0	0.0	2.4	10-13	46	2.373	272.0	14 168.3
AR	20.5	21.5	48.1	0.3	3.0	12-14	46	2.951	190.2	16 248.7
BJH	16.9	15.0	25.0	4.0	4.5	10-15	45	2.721	241.0	18 611.3
JG	8.5	28.0	27.5	3.5	3.5	10-16	42	2.342	248.4	32 585.9

Outer Reef (OR), Western Reef (WR), Northern Reef (NR), Eastern Reef (ER), Ketchup Reef (KR), BoPez (BP), Flying Reef (FLY), Cove (CO), Kariwak Reef (KW), Majeston Reef (MJ), Arnos Vale Reef (AV), Culloden Reef (CU), Plymouth Reef (PL), Mt. Irvine Extension (MIE), Mt. Irvine Reef (MIS), Landslide Reef (LS), St. Giles Island (STG), Booby Island (BI), Corner Rock (CR), Book Ends (BE), Angel Reef (AR), Black Jack Hole (BJH) and Japanese Garden (JG).

(9.1%). All other species each contributed <7% to overall fish biomass.

Fish assemblages at all locations were dominated by fish ≤10cm in size, probably as a result of the numerical abundance of the inherently small-sized pomacentrids. Fish ≤10cm in size accounted for 71.1% of all fish recorded. The 11-20 and 20-30cm size classes held 22.6% and 4.5% respectively.Very few fish were larger than 30cm. Those recorded larger than 30cm included *Sparisoma viridae*, *Pomacanthus arcuatus, Scarus vetula* and *Hypoplectrus nigricans*.

MDS ordination identified three main assemblages of fish based on reef type (ANOSIM, R=0.281, P<0.001), with three outlier groups at LS, BI and MIE based on the numerical abundance of fish (Fig. 2). These assemblages were well separated from the other reefs in ordination space (Stress=0.2). Sites grouped into a northeast Tobago high relief assemblage (CR, STG, JG, BJH and BE),a southwest Tobago low relief assemblage (OR, BP, WR, NR, ER, CU, AV and KR) and an intermediate relief low coral cover assemblage (KW, AR, FLY, MIS, PL, MJ and CO) (Fig 2).Species richness and diversity were generally higher at the northeastern Tobago reefs, particularly at BI (S=38, H'=2.989), STG (S=46, H'=2.95) and BJH (S=45, H'=2.72). The overall highest diversity was occurred at AR (3.003) in the southwest and the lowest H' occurred at CO (H'=1.234) in the intermediate cluster (Table 2).

Similarly, there was also a significant difference in family composition with reef type (ANOSIM, R=0.263, P<0.002). The northeast assemblage accounted for 55.9% of the total fish biomass and 42.4% of the total fish abundance and the southwest assemblage accounted for 32.5% of total biomass and 36.2% of total abundance. The special interest area, Buccoo Reef Marine Park (BRMP) within the southwestern cluster accounted for 23% of total fish abundance but only 8.8% biomass. This separation in assemblages underlinesthe differences in geomorphologic characteristics on either side of the island, high relief rock-based coral reefs occurring in northeast Tobago and low relief limestone-based coral reefs occurring in southwest Tobago.

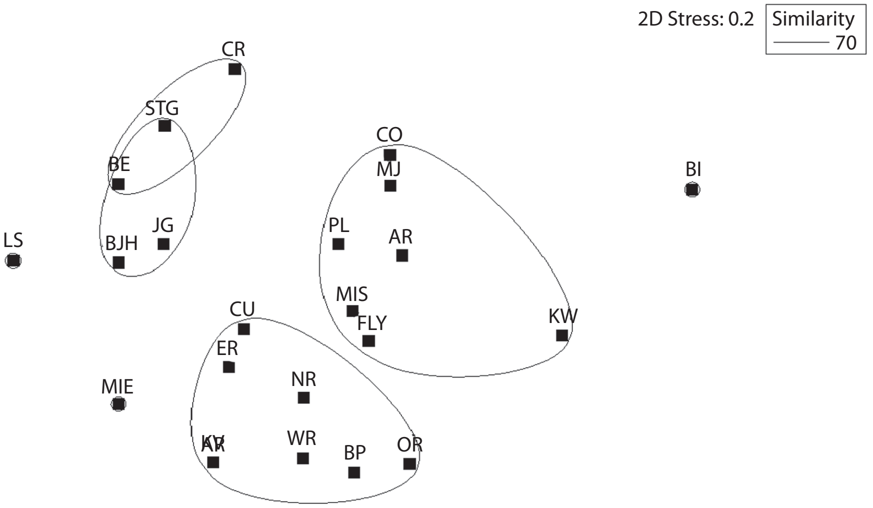

Fig. 2. Non-metric multidimensional scaling plots based on Bray-Curtis similarity on forth root transformed abundance data of all fishes. Outer Reef (OR), Western Reef (WR), Northern Reef (NR), Eastern Reef (ER), Ketchup Reef (KR), BoPez (BP), Flying Reef (FLY), Cove (CO), Kariwak Reef (KW), Majeston Reef (MJ), Arnos Vale Reef (AV), Culloden Reef (CU), Plymouth Reef (PL), Mt. Irvine Extension (MIE), Mt. Irvine Reef (MIS), Landslide Reef (LS), St. Giles Island (STG), Booby Island (BI), Corner Rock (CR), Book Ends (BE), Angel Reef (AR), Black Jack Hole (BJH) and Japanese Garden (JG).

With regards to fish biomass, while the general separation of clusters between northeastern and southwestern reefs was maintained in ordination space, there was no significantly relationship with reef type (ANOSIM, R=0.036, P=0.226). In fact the low R values indicate the three groups were not well separated. Non parametric MDS ordination plots based on size class and trophism did not provide distinct fish assemblages, even when reef type was considered.

Overall, the variation in abundance of Acanthuridae, Serranidae, Scaridae, Pomacentridae and Labridae was responsible for most of the dissimilarity among sites and assemblages. In particular, 16 species were responsible for most of the dissimilarity between northeastern, southwestern and intermediate assemblages (SIMPER, average dissimilarity=52.6%). Acanthuridae (particularly *Acanthurus bahianus*), Serranidae (particularly *Serranus tigrinus* and *Epinephelus adscensionis*), Pomacentridae (particularly *Chromis multilineata*, *Stegastes partitus*, *Microspathodon chrysurus*) and Balistidae (particularly *Melichthys niger*) were mostly found on the northeastern reef cluster, whereas Scaridae (particularly*Scarus iseri, S. taeniopteus, Sparisoma viride, S. aurofrenatus*) and Labridae (particularly *Thalassoma bifasciatum*, *Clepticus parrae*) were dominant in the southern and intermediate reef clusters.

Most top predators/piscivores (primarily Serranidae, Carangidae and Lutjanidae) were noted in the southwesterncohort of fish, which accounted for 45.8% of the total piscivores biomass. It should be noted that ~29.0% of piscivores biomass was detected at a single site in the southwest (BP) which were mainly represented by *Ocyurus chrysurus* and *Lutjanus cyanopterus*. The only site where no piscivores were observed was MJ. LS, the northeastern and intermediate assemblages accounted for 24.9%, 19.3% and 5.7% of total piscivores biomass respectively. Sixty five percent of all planktivores were recorded at LS which represented 38.8% of planktivore biomass. These were dominated by small bodied fish such as *Chromis multilineata* and *Thalassoma bifasciatum*. Primary consumers were most dominant within the northeast cluster and secondary consumers were most dominant within the southwest cluster (Table 1).

Few fish >40cm were recorded, and where they were noted densities were quite low. The highest densities of large fish occurred at AV (3.5 individuals/100m^2), ER (2.7 individuals/100m^2) and BP (1.6 individuals/100m^2). Overall most fish (93.7%) were <20cm in size. Fish <10cm were similarly distributed among reefs, with the highest densities occurring at LS (7.4 individuals/100m^2) in the northeast and KR (7.3 individuals/100m^2) in the southwest. The highest densities of fish 11–20cm, 21–30cm and 31–40cm were all noted in the northeastern reefs. Medium sized fish (20-30cm) within southwest cluster and intermediate cluster consisted mainly of *Scarus* spp, *Sparisoma* spp, *Pomacanthus paru*, *Mulloidichtys martinicus, Acanthurus* spp and *Stegastes* spp. Whereas, the northeast assemblage displayed a wider range of medium sized such as *Thalassoma* spp, *Halichores* spp, *Chromis* spp, *Clepticus* sp., *Haemulon* spp, *Mycteroperca tigris, Cephalopholis cruentata*, *Cephalopholis fulva*, *Ocyurus chrysurus*, *Aulostomus maculates* and s *Scarus* spp.

Within the 23 reefs, live coral cover ranged from 4.6% at CO to 42.8% at STG. Macroalgae (including erect coralline algae, turf algae and fleshy macroalgae) was the dominant feature on most reefs, with only four reefs (KW, KR, BJH and JG) having <30% algal cover. Sponge cover ranged from 0.3%28.0%, and together with hard corals was responsible for much of the habitat complexity observed on the reef. The northeastern and southwestern clusters of reefs showed similar coral cover, whereas the lowest coral cover was noted among the intermediate reef cluster. Sponge cover was highest five reefs (CO, BE, AR, BJH and JG), mainly within the northwestern reef cluster, but generally most sites exhibited <6% sponge. Thirteen to eighty three percent (13–82.6%) of reefs were bare substrate (crustose coralline algae, dead coral, rubble and sand) (Table 2). Overall, the northeastern reefs were mostly high relief reefs, with STG exhibiting the highest relief. Mean relief among the southwestern and intermediate reefs was 1.3±1.2m and 1.9±0.7m.

DISCUSSION

This study examined variation in reef fish community structure (diversity, trophism, biomass and richness) across major reef systems in Tobago with the greatest differences occurring between reefs located in the northeastern and southwestern side of the island. The results identify distinct reef fish assemblages, associated with differences in reef type and morphology. Biomass, abundance, diversity and richness of reef fish, varied widely among reefs from northeast to southwest, as a result of shifts in dominance of functional groups and among reefs such as scarids. Overall, fish densities were between 44-306 individuals/100m^2 and were dominated by small-bodied fishes of low commercial value (such as pomacentrids and labrids) and few highly valuable commercial species such as serranids and lutjanids. This is similar to other reefs in the Caribbean that have been overfished or highly impacted (Hughes, 1994; Mallela, Roberts, Harrod & Goldspink, 2007; Aguilar-Perera & Appledoorn, 2008). Reef fish biomass in Tobago was low compared to other islands in the region. Newman, Gustavo, Sala & Jackson, (2006) estimated fish biomass in a range of coral reef habitats in the Caribbean and found average biomass estimates to range between 15 and 60g/m^2, whereas in Tobago mean biomass 10.7±11.0g/m^2.

MDS ordination separated fish populations in three distinct assemblages with three outlier groups. Mean fish density, species richness, and diversity were higher at the northeastern rocky reefs relative to coralline reefs found on the intermediate and southwestern reef cluster. Some taxa exhibited densities several fold higher in northeastern reefs (e.g. pomacentrids and haemulids), than on the intermediate or southwestern reefs and vice versa (e.g. scarids). The differences in densities may be due to the northeastern sites offering greater structural complexity for exploitation by reef fish (Hixon & Beets, 1989; Caley & St. John, 1996; Friedlander, Brown, Jokiel, Smith & Rodgers, 2003; Graham, McClanahan, Letourneur & Galzin, 2007; Benfield, Baxter, Guzman & Mair, 2008; Friedlander et al., 2010). Additionally, the paucity of reef development in Tobago (Spalding, Ravilious & Green, 2001) would force principally reef-associated species exploit less-preferred habitats (e.g. rocky reefs) (Sandin, Vermeij & Hurlbert, 2008) around the island, such as those found on the northeastern reefs.

Structurally complex habitats fragment the area, resulting in numerous microhabitats being formed and encouraging heterogeneous fish assemblages (Gratwicke & Speight, 2005), and this appears to be the case in this study. The gently sloping coralline reefs in the southwest of the island contrast with the steeply sloping rocky reefs and overhangs that characterise the other reefs on the island. The intermediate cluster possesses both coralline reef and rocky reef features, but is also popular recreational fishing areas (spear, fishpot and handline) for coastal communities. We conjecture that the regular removal of fish from these sites and low coral cover are responsible for the paucity of fish. It should be noted, that not all reefs fish assemblages in the southwest or northeast clustered together into an overall southwest assemblage and northeast assemblage, possibly as a result of the differences in the biological and physical character of neighbouring sites (Curley, Kingsford & Gillander, 2002).

The differences in spatial variability of piscivores (Table 1) could be due to spatial differences in habitat availability and food availability. Generally, piscivore density was highest in the northeastern reefs, although most of the piscivore biomass was found at BP in the southwestern cluster. It is plausible that the higher biomass of piscivores such as serranids and lutjanids (Table 1) in the northeastern reefs could be a direct result of the food availability and an indirect result of habitat availability for prey items (Stewart & Jones, 2011). Serranids and lutjanids are roving predators that feed mostly on fish and are associated with coral reefs (Ferreira, Floeter, Gasparini, Ferreira & Joyeux, 2004). Beukers & Jones (1997) however, suggest that habitat availability is a stronger factor than food availability on influencing piscivore abundance on a coral reef. The effect of habitat complexity could either be direct, where it provides fish habitat, or indirect where it influences the distribution of the food source of these species.

Marine protected areas enclosing coral reefs have had a broad range of positive effects such as increased biomass, abundance, average size and diversity of fish and invertebrates (Russ & Alcala, 2011). In this study similar results were observed, supporting previous small scale studies on the impact of MPAs on increasing reef fish populations and biomass (Polunin & Roberts, 1993; Rakitin & Kramer, 1996). It should be noted that connectivity of the MPA to nearby mangrove and seagrass habitats which are suitable for some reef-associated fishes, might contribute to the higher abundance and biomass observed. In fact, the biomass of important herbivores within the MPA such as parrotfish (scarids: ~12.0g/100m^2) was almost twice the scarid biomass of nearby reefs (~6.8g/100m^2) (Table 1). When compared to other well protected MPA in the region such Los Roques (scarid biomass 60.7g/m^2) and Flower Garden Banks (scarid biomass 35.8g/m^2) (Posada, Villamizar & Alvarado, 2003), the MPA's scarid biomass is quite low. On the non-protected fishes reefs of Curacao scarid biomass is approximately 15.2g/m^2 and as low as 4.6 on the overfished Montego Bay reefs (J. Jackson et al., unpublished).

This study represents a comprehensive baseline assessment of the reef fish fauna of Tobago and is instructive as to where efforts should be prioritised to conserve reef fish populations from human threats (fishing) and alien invasive threats (*Pterois* sp.). Additionally, future research on the reef fishery, particularly spears fishing, to determine impacts by these activities on fish populations.

ACKNOWLEDGMENTS

I would like to thank Stefan Lue Chin, Sherron Barker, Jonathan Gomez and Addison Titus who assisted in data collection and analysis. Special thanks to Rahanna Juman, Anika Gellineau, Dawn A.T. Phillip and Michelle Cazabon-Mannette for reviewing and commenting. This research was conducted as part of the Project for Ecosystem Services (www.proecoserv.org) while the author was a graduate student at the University of the West Indies. Financial support from the Global Environment Facility (GEF) and UNEP is gratefully acknowledged.

RESUMEN

Ensambles de peces en los arrecifes de franja en el Caribe sur: biodiversidad, biomada y tipos de alimentación. Los ensamblajes de peces de arrecife en el Caribe están bajo una creciente presión de las actividades humanas. La ejecución inadecuada de la legislación, junto con los desembarques poco fiables y con escasez de datos en Tobago han llevado a una explotación sin reglas durante décadas. Este estudio aborda la falta de datos sobre las comunidades de peces de arrecife en los principales arrecifes. Las observaciones visuales se llevaron a cabo desde noviembre 2011 hasta mayo 2013 en sitios de acceso a los arrecifes abiertos (Speyside, Charlotteville, Culloden, Arnos Vale, el monte Irvine, La Guira, Kilgwyn, Plymouth y Negro Rock) y un área protegida (El parque Buccoo Marine Reef). Se utilizaron encuestas para determinar la densidad de peces, la diversidad y abundancia de especies a 10-15m de profundidad del contorno. El tamaño de los peces se convirtió a biomasa utilizando la relación talla-peso de los peces $W=aL^b$. La mayoría de las comunidades de peces son dominadas por pequeños herbívoros (<15cm), en particular Pomacentridae y Scaridae. Pocos depredadores grandes (>40cm), por ejemplo Serranidae, se observó, lo que es indicativo de la presión de pesca. El análisis de escala multidimensional identificó tres conjuntos distintos de peces indicados como i) del noreste, ii) al suroeste y iii) grupos intermedios. El grupo del noroeste (Speyside y Charlotteville) es más representativo de comunidades de peces de arrecife en toda la isla, y mostró la mayor riqueza de especies, diversidad y biomasa. Sin embargo, se observó la abundancia más alta de peces en el grupo del suroeste. El área marina protegida contenia mayor biomasa, abundancia, diversidad y riqueza de peces, pero era el único representante de las asociaciones de peces arrecifales en el suroeste de la isla y no de todo Tobago. Se recomienda

determinar los impactos de la pesca en los arrecifes, particularmente con el uso de arpón.

Palabras clave: trofismo, Tobago, peces de arrecife de coral, encuestas submarinas visuales.

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Bomb-cratered coral reefs in Puerto Rico, the untold story about a novel habitat: from reef destruction to community-based ecological rehabilitation

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Received 23-VIII-2013   Corrected 21-II-2014   Accepted 24-III-2014

Abstract: Ecological impacts of military bombing activities in Puerto Rico have often been described as minimal, with recurrent allegations of confounding effects by hurricanes, coral diseases and local anthropogenic stressors. Reef craters, though isolated, are associated with major colony fragmentation and framework pulverization, with a net permanent loss of reef bio-construction. In contrast, adjacent non-bombarded reef sections have significantly higher benthic spatial relief and biodiversity. We compared benthic communities on 35-50 year-old bomb-cratered coral reefs at Culebra and Vieques Islands, with adjacent non-impacted sites; 2) coral recruit density and fish community structure within and outside craters; and 3) early effects of a rehabilitation effort using low-tech Staghorn coral *Acropora cervicornis* farming. Reef craters ranged in size from approximately 50 to 400m^2 and were largely dominated by heavily fragmented, flattened benthos, with coral cover usually below 2% and dominance by non-reef building taxa (i.e., filamentous algal turfs, macroalgae). Benthic spatial heterogeneity was lower within craters which also resulted in a lowered functional value as fish nursery ground. Fish species richness, abundance and biomass, and coral recruit density were lower within craters. Low-tech, community-based approaches to culture, harvest and transplant *A. cervicornis* into formerly bombarded grounds have proved successful in increasing percent coral cover, benthic spatial heterogeneity, and helping rehabilitate nursery ground functions. Rev. Biol. Trop. 62 (Suppl. 3): 183-200. Epub 2014 September 01.

Key words: Benthic community structure, bombing impacts, community-based ecological rehabilitation, coral reefs, fish community structure, military activities, novel habitats.

Long-term adverse ecological impacts of military maneuvers on coral reef ecosystems have remained as a concern as there is still limited information in the literature about impacts across multiple spatial and temporal scales. Most studies have often focused on very large spatial scale assessments, which have by default often overlooked some of the acute impacts on bomb-cratered coral reefs at smaller (i.e., fringing reef) spatial scales. Most published accounts were from studies conducted at Vieques Island, Puerto Rico (Raymond, 1978; DON 1979; DON 1980; DON 1986, Raymond & Dodge, 1980; Antonius & Weiner, 1982; GMI, 2003; GMI, 2005, Deslarzes, Nawojchik, Evans, McGarrity & Gehring, 2006; Evans, Nawojchik & Deslarzes, 2006; Hernández-Cruz, Purkis & Riegl, 2006; Kendall & Eschelbach, 2006; McGarrity & Deslarzes, 2006; Riegl, Moyer, Walker, kohler, Gilliam & Dodge, 2008; Bauer, Menza, Foley & Kendall, 2008; Bauer & Kendall, 2010) which were conducted over island wide spatial scales and found minimal destructive ecological impacts of bombing activities at such large scales, concluding that hurricanes and multiple localized human stressors (i.e., sedimentation, fishing) caused significant confounding effects. Even studies which have documented critical acute impacts of bombing and sedimentation across military-impacted coral reefs (IDEA, 1970; Carrera-Rodríguez, 1978; Rogers, Cintrón & Goenaga, 1978; Goenaga, 1986; Goenaga, 1991) did not provide a full quantitative characterization of the localized impacts on bomb-cratered reefs at reef-level spatial scales. None of these studies had either the temporal resolution to address long-term recovery of impacted sites. Therefore, the impacts of habitat fragmentation at across reef spatial scales associated to military activities and its long-term consequences on the recovery ability of local community structure and ecosystem resilience have still been poorly addressed.

Localized bombing impacts on coral reefs still remain controversial, and most of the literature has focused on blast fishing. This is known to cause extensive reef framework destruction across Indo-Pacific (McManus, Reyes & Nañola, 1997; Pet-Soede & Erdmann, 1998) and Red Sea coral reefs (Riegl, 2001), besides its concomitant overexploitation of fishery resources. Blast fishing impacts have caused significant loss of coral cover, an increase in the amount of bare substrate and rubble, and a decline in fish species richness and abundance (Riegl & Luke, 1999). These authors suggested that natural regeneration of impacted reef communities is likely to be very slow, possibly taking several hundred years, and that rehabilitation would be difficult since coral transplants would have to mimic the previously existing community. The frequency and magnitude of military bombing activities in Vieques Island showed a steady significant increase during the cold war years. Rosa-Serrano (1996) documented increasing crater abundance within bombarded areas between 1964 and 1988 using GIS-based analysis, suggesting a long-term increase of physical impacts of bombing. Porter (2000) found unexploded ordnance, leaking toxic 2-4-6-Trinitrotoluene (TNT) on and around reefs, and over 1,000 deteriorating barrels of unknown chemicals on the sunken military vessel *USS Killen* off southeast Vieques. Porter, Barton and Torres (2011) also found a statistically significant inverse correlation between the coral species richness, colony abundance and species diversity, and the density of military ordnance across reef scales in Vieques. There were also multiple animals across the reef food web polluted with toxic compounds similar to those present in unexploded ordnance. Chromium in sediments, and TNT in both, water and sediments, exponentially increased within areas still littered with unexploded ordnance.

Reef craters present in both, Culebra and Vieques Islands coral reefs are often very small in comparison to the scale of each island, each ranging in size from approximately 50 to 400m^2. But these are largely dominated by heavily fragmented flattened benthos, with % coral cover usually below 2% and dominance by non-reef building taxa (i.e., filamentous algal turfs, macroalgae) (Fig. 1a-c). In contrast, adjacent non-bombarded reef zones are still dominated by consolidated benthos, with higher percent living coral cover and larger abundance of reef building species (Fig. 1d-f). Benthic spatial heterogeneity is also significantly lower within crater scales which also results in a lowered functional value as fish nursery ground. The fact that physical disturbance within bombarded grounds was so locally extensive resulted in a mosaic of habitat patches with permanent loss of reef framework and in potentially declining multiple ecosystem functions and services. Therefore, reef craters have become a *de facto* novel habitat, and as such, there is a need to address the ecological status of benthic and fish communities, as well as their recovery state three to five decades after bombing.

This study was aimed at: 1) documenting the condition of benthic communities within 35-50 year-old reef craters at Culebra and Vieques Islands, Puerto Rico, in comparison to adjacent non-bombarded sites within former military maneuver sites; 2) comparing coral recruit density and fish community structure within and outside reef craters; and

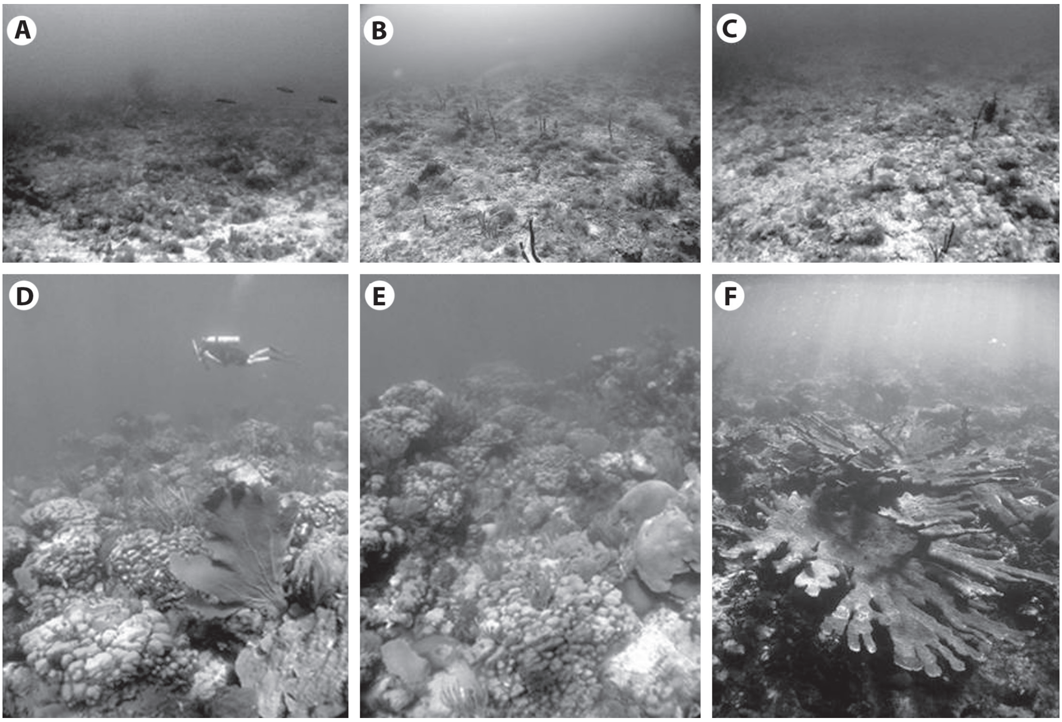

Fig. 1. Benthic community structure within bomb-cratered and non-impacted reefs. A-B) Reef craters dominated by low spatial relief and brown macroalgae *Dictyota* spp.; C) Reef crater dominated by filamentous algal turf; D-E) Non-impacted forereef terrace dominated by *Montastraea* (=*Orbicella*) *annularis* species complex; F) Shallow non-impacted reef with remnant patch of *Acropora palmata*.

3) addressing the preliminary impacts of a community-based bombarded coral reef rehabilitation effort using low-tech approaches to cultivate threatened staghorn coral, *Acropora cervicornis* (Lamarck, 1816), and rehabilitate bombarded coral reefs.

MATERIALS AND METHODS

Study sites: Studies were conducted across 15 fringing reef sites, 11 at Culebra Island (located between 18°19.791’N, 65°19.943’W and 18°20.776’N, 65°20.498’W) and 4 at Vieques Island (located between 18°08.784’N, 65°18.482’W and 18°09.698’N, 65°25.073’W), off eastern Puerto Rico (State Plane, NAD83, FIPS PR5200, Fig. 2). Reef craters examined in this study ranged between 50 and 400m^2. Sites were selected based on their representativeness of typical reef segments impacted by framework destruction as our aim was documenting what is the status of severely impacted reef sites 35-50 years after bombing impacts. Crater age was estimated from aerial photography and from anecdotal accounts from older fisher folks from both islands, and was a key factor for selecting impacted study sites to have a more accurate estimate of reef recovery trends through time. Control sites were selected on adjacent (usually <250m) sites not directly impacted by bombs. Reefs were subdivided by treatment (impacted-craters [n=7], non-impacted controls [n=8]), and depth (shallow, 1-3m [n=9]; deep, 6-10m [n=6]). In Culebra, sampling was conducted in 6 shallow (3 impacted, 3 controls) and 5 deep (2 impacted, 3 controls) reefs. In Vieques sampling was conducted in 2 shallow (1 impacted, 1 control) and 2 deep (1 impacted, 1 control) reefs. All benthic surveys in Culebra were conducted

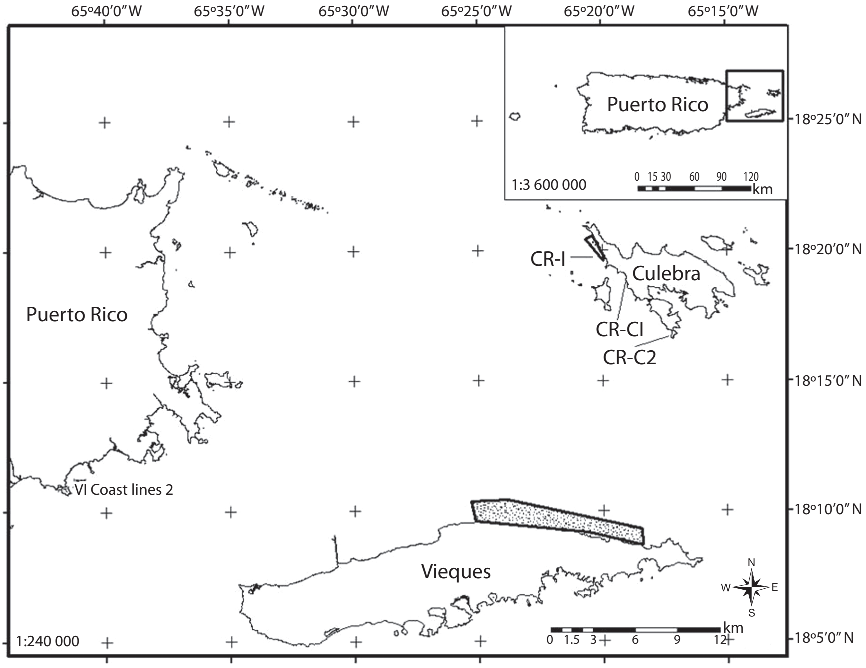

Fig. 2. Study sites in Culebra and Vieques Islands, Puerto Rico. Acronyms are described in the Methods section.

within the Canal Luis Peña no-take Natural Reserve (CLPNR) where all fishing is prohibited. Fish studies were conducted only in Culebra within the CLPNR to reduce confounding factors with fishing impacts elsewhere. Coral recruitment and reef rehabilitation studies were conducted in Culebra at the bombarded area described above (CR-I1, CR-I2), at Bahía Tamarindo (CR-C1, 18°18.877'N, 65°19.093'W), and at Punta Soldado (CR-C2, 18°16.846'N, 65°17.192'W). Bahía Tamarindo is also located within CLPNR and was used for artillery training activities and amphibious vehicle landing practices between 1920s and 1950s, but was never bombarded. Punta Soldado is located outside CLPNR and was used as a target site during the 1920s but never thereafter. These were used as control sites which underwent different levels of military activities, across different temporal scales, in comparison to direct recent bombing within reef cratered areas at impacted sites until 1970s. Also, these sites are part of a network of coral recruitment monitoring sites.

Benthic community: Benthic habitats were characterized across all sites through 3-6 replicate ten m-long digital video-transects. Number of replicates varied as a function of crater size and covered at least 50-75% of the impacted area within each crater. Transect deployment within each crater was haphazard, often separated by at least 5m. A total of six random, non-overlapping still images/transect were obtained and analyzed with Coral Point Count with excel extensions (v3.6) (Kohler & Gill, 2006) to address percent cover of all benthic components, including coral, algal functional groups (macroalgae, turf, crustose coralline algae [CCA], erect calcareous algae [ECA], *Halimeda* spp.), cyanobacteria, other components, sand, rubble, and bare substrate. A total of 20 random dots per image were used. Coral species richness, species diversity index (H'n) (Shannon & Weaver, 1948), and evenness (J'n) (Pielou, 1966) were also calculated.

Coral recruits: Coral recruit densities were addressed only in Culebra using triplicate

2.25 x 2m quadrat grids subdivided in 12 replicate 0.75 x 0.50m quadrats/grid from one shallow (CR-IS) and one deep crater (CR-ID), and from two control non-impacted sites at Bahía Tamarindo (CR-C1), and Punta Soldado (CR-C2). High-resolution digital images were collected and all hydrocoral/scleractinian recruits with a diameter below 5cm were counted and identified to the lowest taxon possible.

Fish community structure: Fish communities were characterized only in Culebra using stationary visual censuses within craters (impacted) and adjacent (control) locations following a slight modification from Bohnsack and Bannerot, (1986). Data was collected within a 5 m-radius imaginary cylinder during a period of 15min. All individuals were counted, identified to the lowest taxon possible, and standard fork length was estimated. Size data were used to estimate biomass. Weight-length relationships were calculated following Bohnsack and Harper (1988). Basic information of the fish community structure reported in this study included species richness, abundance, H'n, J'n, total biomass, and piscivore biomass. Reef structural complexity is known to have an important influence on fish community structure (Roberts & Ormond, 1987). A 6-point scale was used to characterize a reef structural heterogeneity index (RSHI) as follows: 0= no vertical relief; 1= low and sparse relief; 2= low but widespread relief; 3= moderately complex; 4= very complex with numerous caves and fissures; 5= exceptionally complex with high coral cover and numerous caves and overhangs (Hawkins et al., 1999).

Statistical analyses: A three-way permutational analysis of variance (PERMANOVA) was used to test the null hypothesis of no significant difference in benthic biodiversity parameters and community structure between sites (Culebra, Vieques), treatment level (bombarded areas, non-impacted controls), and depth (1-3m, 6-9m) using PRIMER-e v.6.1.14 (Anderson, Gorley & Clarke, 2008). Principal component ordination (PCO) was used to determine which benthic taxa explained spatial clustering patterns of benthic communities. Proportional data on percent benthic components cover were √-transformed prior to analysis. A one-way PERMANOVA was used to test spatial patterns of coral recruits between bombarded and non-impacted sites in Culebra, followed by PCO. A one-way analysis of similarity (ANOSIM) was used to test spatial patterns of fish communities between bombarded and non-impacted sites in Culebra, followed by a multi-dimensional scaling (MDS) analysis (Clarke & Warwick, 2001). Data were also √-transformed prior to analysis. All tests were based in 10 000 permutations. Fish community data also were correlated (Spearman) with RSHI.

Coral reef rehabilitation: A total of 2 000 corals were harvested from existing low-tech coral farms through the *Community-Based Coral Aquaculture and Reef Rehabilitation Project* and outplanted to adjacent coral reefs within former military maneuver ranges at two sites in Culebra Island, Bahía Tamarindo and Punta Soldado. Sites selected for outplanting were located within a flat shallow reef (<2.5m) used as artillery maneuver areas at Bahía Tamarindo (impacted site) and at a reef segment at Punta Soldado non-impacted by bombing or artillery maneuvers since 1920s (control site). Corals were attached to masonry nails driven to reef bottom, outplanted in patches of densities ranging from 80 to 120 per 25m^2. Survival rates and growth were addressed following two representative patches located at elevated rocky outcrops and two patches adjacent to reef sand pockets at increasing time intervals during a year. A two-way ANOSIM was used to test the null hypotheses of no significant change in coral survival rates, skeletal extension, and branch production through time and between sites.

RESULTS

Benthic community: Coral reef benthic communities across bombarded areas showed

TABLE 1
PERMANOVA results of coral reef benthic biodiversity and community structure

Variable	d.f.	Species richness Pseudo-F (*p*)	H'n Pseudo-F (*p*)	J'n Pseudo-F (*p*)	Community structure Pseudo-F (*p*)
Site	1,13	0.0060 (0.8179)ns*	0.39 (0.5426)ns	2.36 (0.1555)ns	2.18 (0.0473)
Treatment	1,13	11.60 (0.0071)	19.49 (0.0014)	7.24 (0.0252)	2.47 (0.0348)
Depth	1,13	2.33 (0.1432)ns	1.93 (0.1925)ns	0.0061 (0.8079)ns	2.12 (0.0583)ns
Site x Treatment	3,11	3.66 (0.0452)	6.11 (0.0107)	5.24 (0.0174)	1.96 (0.0221)
Treatment x Depth	3,11	6.80 (0.0133)	9.81 (0.0033)	2.31 (0.1366)ns	2.41 (0.0054)
Site x Treatment x Depth	6,8	6.75 (0.0123)	8.32 (0.0044)	2.13 (0.1519)ns	1.95 (0.0122)

*ns= not significant.

significantly more physical destruction and an altered coral assemblage in comparison to control non-impacted sites (Table 1). There was a significantly different benthic community structure between sites (*p*=0.0473) and treatments (*p*=0.0348). Also, interactions between site and treatment, treatment and depth, and among site, treatment and depth were highly significant. Bombarded sites were characterized by having significantly lower coral species richness (*p*=0.0452), percent coral cover (*p*=0.0025), H'n (*p*=0.0107), and J'n (*p*=0.0174) (Fig. 3a-d). Mean coral species richness within bombarded bottoms was 2.2/transect, while mean value at adjacent non-impacted control sites was 8.8/transect. Mean living coral cover within bombarded bottoms was 1.9% and 15.7% at control sites. Coral cover was also higher at deeper (13%) than at shallower sites (6.5%). Mean H'n within bombarded bottoms was 0.4912 and 1.6101 at control sites, while mean J'n within bombarded bottoms was 0.4169 and 0.7834 at control sites. Species richness and H'n also had significant treatment x depth, and site x treatment x depth interactions. Macroalgal cover was higher on control sites (47%), in comparison to bombarded areas (29%), while algal turf was higher within bombarded grounds (26%), in comparison to control sites (16%) (Fig. 1e-f). But none of these differences were significant.

The percent relative cover of the most important reef building coral species was significantly lower within bombarded areas (Fig. 4). *Montastraea (=Orbicella) annularis* (Ellis & Solander, 1786) averaged 0.05% within bombarded areas and 4.1% at control sites, while *O. faveolata* (Ellis & Solander, 1786), *O. franksi* (Gregory, 1895), and *M. cavernosa* Linnaeus, 1767 averaged 1.3, 0.5, and 1.0%, respectively, at control sites. None of these species were present within bombarded areas. *Colpophyllia natans* (Houttuyn, 1772) averaged 0.01% within bombarded grounds and 0.38% in control sites. *Diploria strigosa* (Dana, 1846) averaged 0.7% at control sites and was absent within bombarded areas, and *Siderastrea siderea* (Ellis & Solander, 1786) had a mean 0.14% cover within bombarded areas and 1.8% in control sites.

Principal component ordination (PCO) analysis showed two larger clusters of reef communities, and 5 individual sites (Fig. 5). Impacted sites at Culebra were dominated by open substrates composed by a mixture of bare bedrock, rubble and sand pockets (SPR), algal turf, brown macroalgal patches (e.g., *Dictyota* spp.), and sporadic colonies of octocoral *Pseudopterogorgia* spp. (Fig. 1a-b). Vieques impacted sites were dominated by algal turfs (Fig. 1c). Culebra control site showed a higher spatial heterogeneity mostly dominated by macroalgae, *M. annularis*, and *P. astreoides* (Fig. 1c-d). Control sites at Vieques were also dominated by turf, and in a lesser degree a mixed octocoral community. The proposed PCO solution explained 57% of the observed spatial variation.

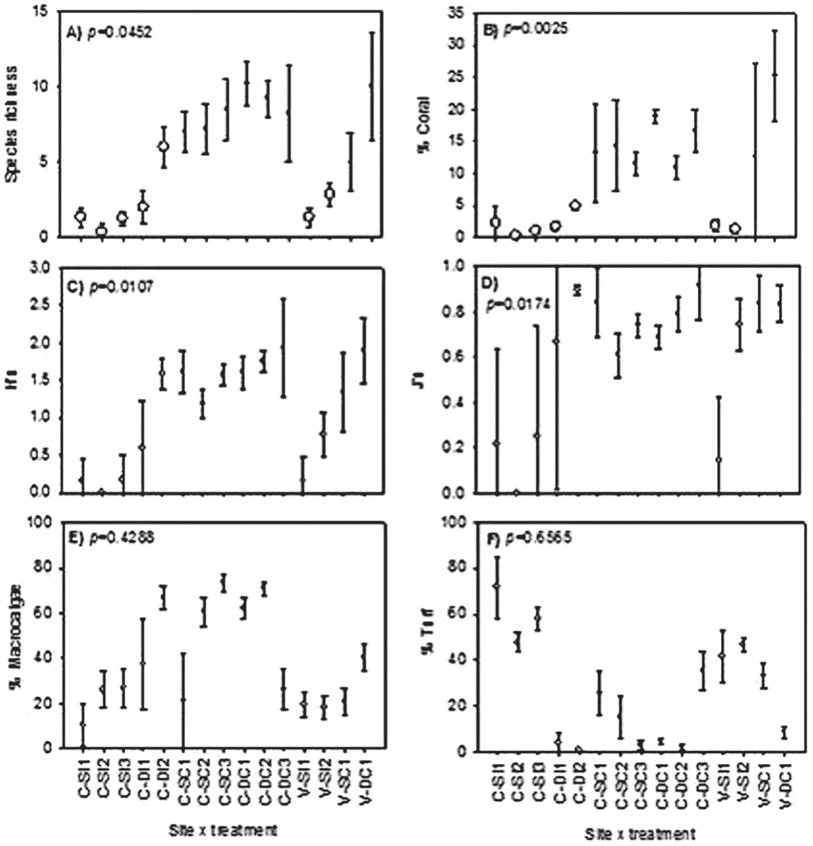

Fig. 3. Benthic community characterization within impacted (open dots) and control sites (black dots) (mean±95% confidence intervals): A) Coral species richness, B) Percent coral cover, C) H'n, D) J'n, E) Percent macroalgae, and F) Percent algal turf. *P* values derived from two-way PERMANOVA (site x treatment effects).

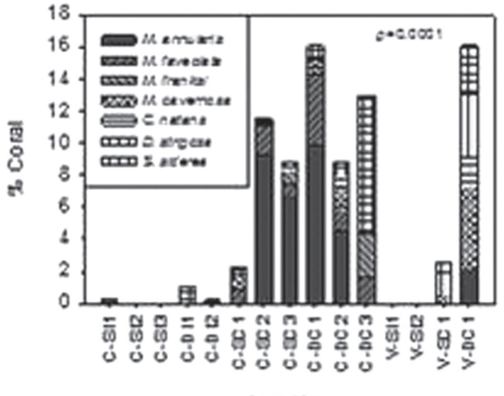

Fig. 4. Percent relative cover of the principal reef-building coral species.

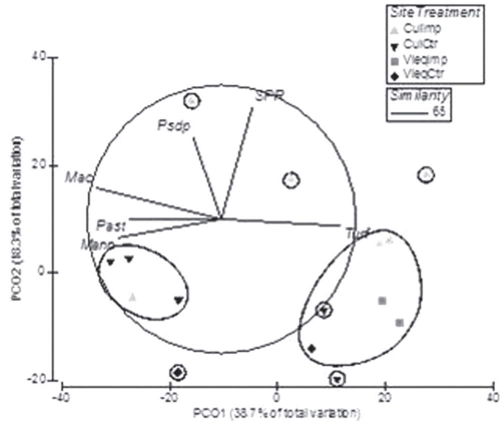

Fig. 5. Principal component ordination (PCO) plot of coral reef benthic communities within bombarded and control reefs. Spatial resolution= 57%. Correlation level of vector selection= 0.65. Similarity cutoff level= 65%.

Coral recruits: Coral recruit density was significantly higher (PERMANOVA, Pseudo-F=6.55, p=0.0001) within non-impacted control sites in comparison to bombarded areas. Control site CR-C1 located within CLPNR averaged 51 colonies/30m^2, while CR-C2 outside CLPNR averaged 21 colonies/30m^2 (Fig. 6). Impacted site CR-I1 averaged 8 colonies/30m^2, while CR-I2 averaged less than 3 colonies/30m^2. Both impacted sites were also located within CLPNR. ANOSIM analysis showed that coral recruit community structure was significantly different between treatments (R=0.830, p=0.0001). Also, species richness (R=0.736, p=0.0006), and H'n (R=0.747, p=0.0006) were significantly higher at control sites than at bombarded areas. No significant difference in J'n was documented. Brooder species such as *Favia fragum* (Esper, 1795), *Siderastrea radians* (Pallas, 1766), and *Porites astreoides* (Lamarck, 1816) were dominant at control sites, while lower abundances of *S. radians* and *P. astreoides* characterized bombarded sites, particularly, at deeper impacted areas. PCO analysis showed five different clusters of reef communities, and five individual sites (Fig. 7). The three clusters composed of control non-impacted sites were explained by *P. astreoides*, *P. porites*, *F. fragum*, and *Millepora striata* (Lamarck, 1816). Bombarded sites clusters were determined by *S. radians*. The proposed solution by PCO explained 71.1% of the observed spatial variation.

Fish community: Fish community structure also showed significant difference (p<0.0001) between treatment levels that were mostly related to a highly significant decline (p=0.0030) observed in the reef structural heterogeneity index (RSHI) within bombarded sites (Fig. 8a). RSHI had a mean value of 0.69 within bombarded areas and 2.72 within control sites. Fish species richness was significantly higher (23.4 per count) at control sites (p=0.0020) than at bombarded areas (12.6) (Fig. 8b). Fish abundance was also significantly higher (p=0.0002) at control sites (491) versus bombarded sites (108) (Fig. 8c). Also, H'n was significantly higher (p=0.0020) within control areas (1.6744) in comparison to bombarded

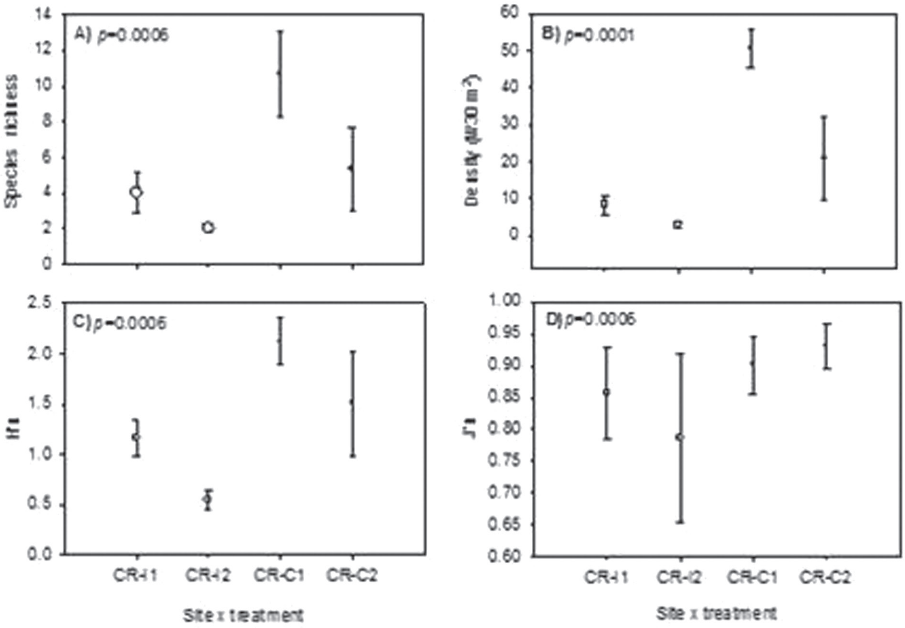

Fig. 6. Coral recruit community parameters at bombarded (open dots) and control non-impacted (black dots) sites in Culebra (mean±95% confidence intervals): A) Species richness, B) Recruit density, C) H'n, and D) J'n.

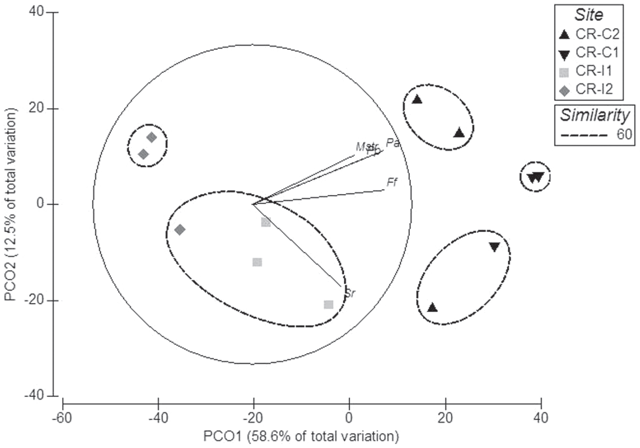

Fig. 7. Principal component ordination (PCO) plot of coral recruit communities within bombarded and control reefs. Spatial resolution= 71.1%. Correlation level of vector selection= 0.60. Similarity cutoff level= 60%.

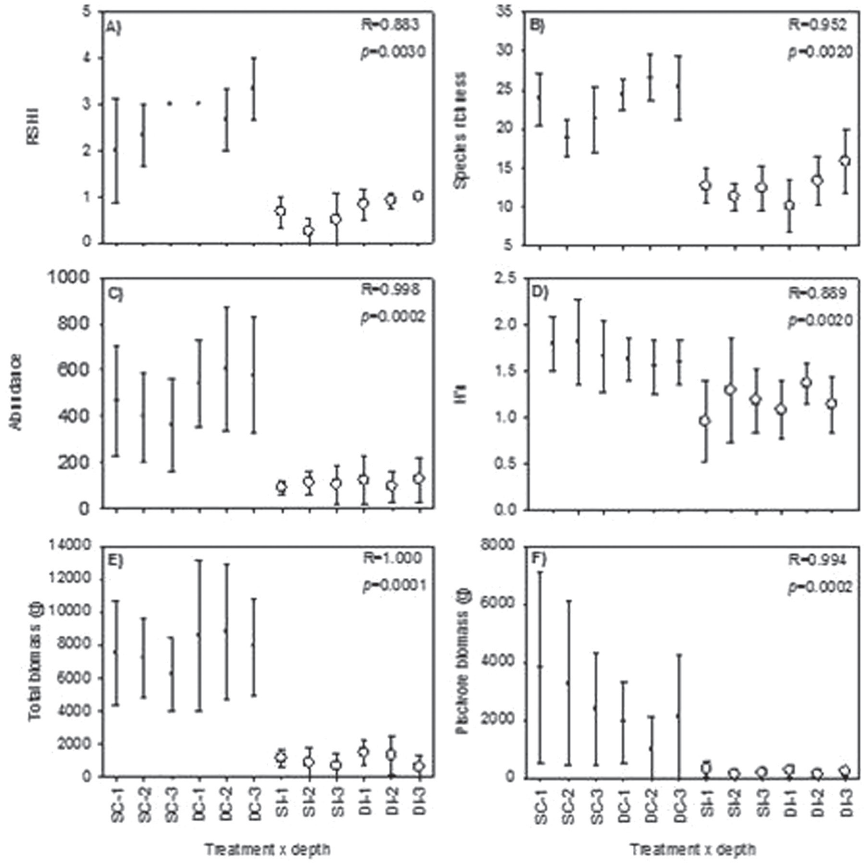

Fig. 8. Fish communities within and outside bombarded grounds (mean±95% confidence intervals): A) Reef structural heterogeneity index (RSHI), B) Species richness, C) Abundance, D) Species diversity index (H'n), E) Total biomass (g), and F) Piscivore biomass (g). Black dots= bombarded grounds, Hollow dots= non-impacted control sites. *P* values derived from one-way ANOSIM tests. SC= Shallow control, DC= Deep control, SI= Shallow impacted, DI= Deep impacted.

grounds (1.1716) (Fig. 8d). Total fish biomass was significantly higher (p=0.0001) at control sites (7 697g) than at bombarded areas (999g) (Fig. 8e). Similarly, piscivore biomass was significantly higher (p=0.0002) at control sites (2,406 g) than at bombarded areas (206g) (Fig. 8f). All fish community parameters showed a highly significant linear regression (p<0.0088) with RSHI (Table 2), suggesting the strong permanent negative impacts of bombing activities on the demolition of reef framework and the net decline in fish communities associated to losing spatial benthic heterogeneity. Significant reef functional herbivore guilds such as scrapers, including *Scaru*s *iserti* Bloch, 1790, *S. vetula* Schneider, 1801, *Sparisomq viride* (Bonnaterre, 1788), *S. rubiprinne* (Valenciennes, 1839), and *S. radians* (Valenciennes, 1839), and browsers such as *Acanthurus coeruleus* Schneider, 1801 were largely absent from reef craters, in comparison to adjacent non-bombarded sites. Also, important piscivore guilds such as groupers, including *Epinephelus guttatus* (Linnaeus, 1758), *E. adscensionis* (Osbeck, 1765), *Cephalopholis fulva* (Linnaeus, 1758), and *C. cruentata* (Lacepède, 1802), and snappers *Lutjanus jocu* (Schneider, 1801), *L. analis* (Cuvier, 1828), and *L. apodus* (Walbaum, 1892) were also absent from reef craters. Fishing impacts was not a factor influencing observed differences in fish community structure within and outside craters as fish data were collected from sites located within the no-take CLPNR.

Coral reef rehabilitation: Mean percent colony survival rates of *Acropora cervicornis* outplants was 81% at impacted sites and 86% at control sites after one year, with a mean survival of 88% at impacted sites and 70% at impacted sites on low-relief reef patches adjacent to sand (Fig. 9). Percent survival at elevated rocky outcrops reached 92% at impacted sites and 84% at control sites. Percent

TABLE 2
Linear regression of fish community parameters with the reef structural heterogeneity index (RSHI)

Variable	R	*p*	Regression equation
Species richness	0.9155	<0.0001	y= 9.515 + 4.958x
Abundance	0.9238	<0.0001	y= 3.401 + 173.2x
H’n	0.7896	0.0023	y= 1.075 + 0.2034x
Total biomass	0.9311	<0.0001	y= -689.4 + 2949x
Piscivore biomass	0.7158	0.0088	y= -142.9 + 848.3x

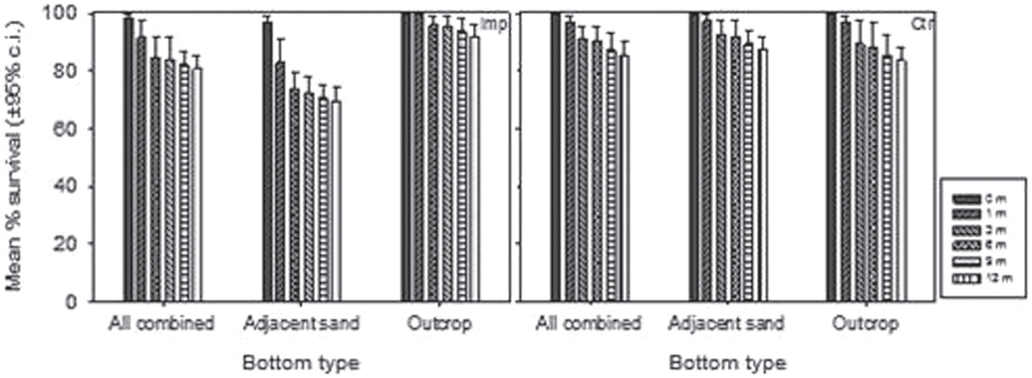

Fig. 9. Mean percent colony survival rate (±95% confidence intervals) of *Acropora cervicornis* outplants within impacted (Imp) and control (Ctr) sites after one year.

live coral tissue cover on outplanted colonies averaged 85% at both, impacted and control sites after one year (Figure 10a), ranging from 82 to 88% within impacted sites in low-relief patches adjacent to sand and in elevated outcrops, respectively. Mean % live tissue cover ranged from 82 to 89% within impacted sites in low-relief patches adjacent to sand and in elevated outcrops, respectively. Total outplanted colony linear length showed a mean overall increase from 41 to 129cm across impacted sites, and from 32 to 81cm across control sites after one year (Figure 10b). Total outplanted colony branch abundance/colony showed a mean overall increase from 4.5 to 14.4 cm across impacted sites, and from 3.4 to 8.3cm across control sites after one year (Figure 10c). Temporal effects were significant for all variables, but treatment and position effects were not (Table 3).

DISCUSSION

Profound, acute and persistent negative impacts of historical bombing activities were documented in Culebra and Vieques Islands, Puerto Rico, across coral reef craters spatial scales. Severely impacted reef segments were characterized by having significantly lower spatial relief, bedrock exposure and

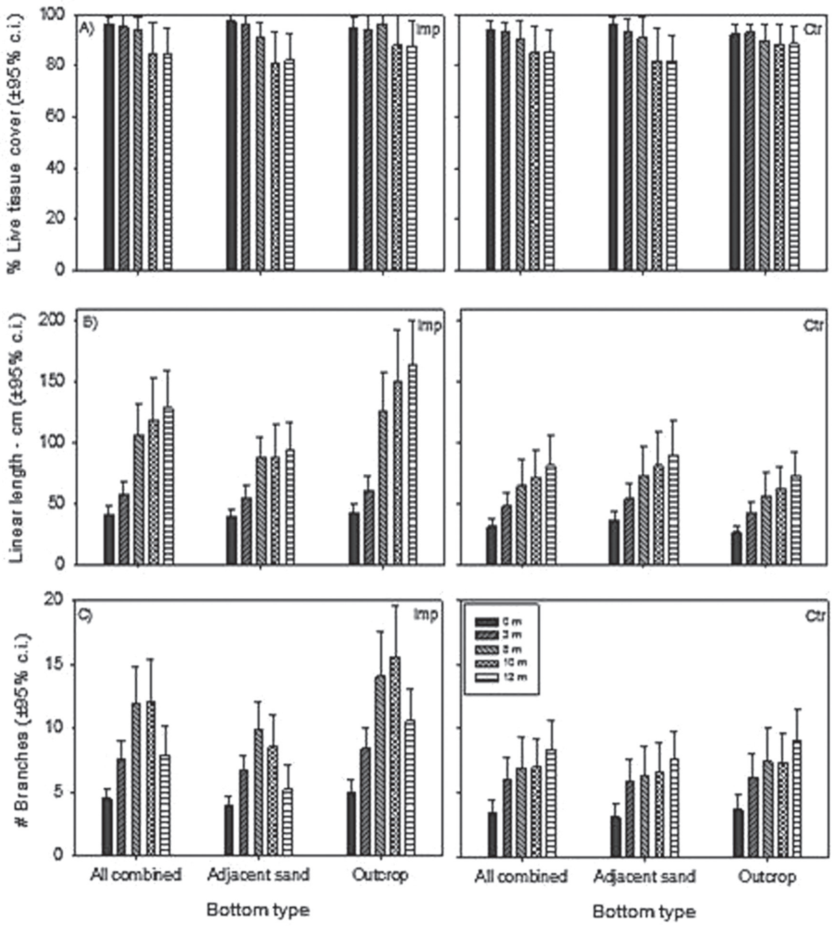

Fig. 10. Outcome of *Acropora cervicornis* outplanting within impacted (Imp) and control (Ctr) sites after one year (mean±95% confidence intervals): A) Percent live coral tissue cover; B) Total linear colony length (cm); C) Branch abundance per colony.

TABLE 3
ANOSIM results of *Acropora cervicornis* outplanting

Variable	Survival	% Cover	Linear length	# Branches
Treatment	R=-0.081	R=0.016	R=0.011	R=0.117
(0.8630)ns*	(0.5260)ns	(0.3460)ns	(0.0890)ns	
Time	R=0.625	R=0.576	R=0.405	R=0.308
(0.0020)	(0.0030)	(0.0020)	(0.0060)	
Position	R=0.003	R=0.001	R=-0.024	R=-0.046
(0.3220)ns	(0.1240)ns	(0.5270)ns	(0.6670)ns	
Treatment x Time	R=0.445	R=0.565	R=0.491	R=0.475
(0.0150)	(0.0060)	(0.0060)	(0.0060)	
Treatment x Position	R=-0.139	R=0.006	R=-0.058	R=0.020
	(0.9020)ns	(0.6100)ns	(0.6690)ns	(0.3720)ns
Time x Position	R=0.733	R=0.821	R=0.290	R=0.134
	(0.0010)	(0.0006)	(0.0540)ns	(0.1980)ns

*ns= Not significant.

an abundant mixture of unstable turf-covered rubble and bedrock boulders demolished by explosions. These substrates were also characterized by low coral colony abundance, low percent living coral cover, low coral species richness and H’n, when compared to adjacent control sites. Similarly, coral recruit communities were significantly more depauperate within impacted grounds than in control sites, either within or outside the no-take CLPNR, which suggest the persistent inability of coral recruits to survive the natural oceanographic dynamics of unstable substrates within bombarded sites. This is consistent with severe impacts by blast fishing documented elsewhere (Riegl & Luke, 1999; Riegl, 2001). The permanent lack of natural recovery ability of 35-50 years old bomb-cratered coral reef segments, when compared to adjacent non-bombarded control sites dominated by massive reef-building species such as *M. annularis* species complex, implies that at the local ecosystem scale, bombarded coral reefs have shown a permanent shift in composition and functions, that full recovery of previously existing benthic community structure and spatial heterogeneity may take centuries. Coral recruitment rates of critical reef-building species across the northeast Caribbean region are increasingly low (Rogers, Fitz, III, Gilnack, Beets & Hardin, 1984; Edmunds & Elahi, 2007; Edmunds, Ross & Didden, 2011), suggesting that habitat fragmentation by bombing has resulted in a permanent localized loss of coral reproductive stock and that in combination with natural low recruitment rates of most reef-building species, natural recovery of composition and functions is very unlikely.

Bombarded areas were also characterized by sustaining lower fish species richness, H’n, abundance, and biomass, as a result of the permanent loss and lack of recovery of reef benthic spatial relief. They also had a very low abundance or absence of significant fish functional groups of herbivores and carnivores, including multiple commercially-important species. These findings are consistent with IDEA (1970) which estimated at least 10 times higher fish densities outside cratered reefs in Culebra Island, though no quantitative parameters were provided. Riegl (2001) found that coral cover decreased, bare substratum and rubble increased, and fish communities changed within areas impacted by blast fishing in Egypt. Depauperate fish assemblages within bombarded reef segments were also consistent with declining fish communities documented on reefs that have already shown rapid benthic community decline as a result of climate change impacts (Jones, McCormick, Srinivasan & Eagle, 2004, Graham et al., 2006; Pratchett et al., 2008). Such changes may become more pronounced as coral cover continues to decline and as fishing pressure continues to increase (Pratchett, Hoey & Wilson, 2014). Fishing impacts were not a factor in this study as all fish data collection was conducted within the no-take CLPNR. Status of more diverse and rich fish communities across control sites is consistent with previous accounts across similar spatial scales for the site (Hernández-Delgado, Rosado-Matías & Sabat, 2006). Therefore, differences in fish community structure were presumed to occur at the studied spatial scales as the result of altered benthic community structure and spatial heterogeneity due to bombing activities.

Individual reef craters are often small in size (50-400m^2) and isolated in space, which render them as very small spatial units generally disregarded as having low ecological significance as they may represent a small geographical proportion of reef surface area in comparison to island wide spatial scales. Studies of bombing impacts at small spatial scales are still very limited. Dodge (1981) found no significant impacts of military bombing on *M. annularis* growth rates on individual coral core samples from Vieques, but Macintyre, Raymond & Stuckenrath (1983) found significant destruction by bombing of shallow *Acropora palmata* (Lamarck, 1816) and *Porites porites* (Pallas, 1766) frameworks. Porter et al. (2011) also found a statistically significant inverse correlation between the coral species richness, colony abundance and species diversity, and the density of military ordnance across reef scales in Vieques. Nonetheless, at smaller ecological scales (e.g., fringing reef unit), reef craters represent localized mosaics of reef segments that were severely reduced to a flattened, unstable, demolished reef bottom, with depauperate biodiversity, that have shown little or no recovery even after three to five decade temporal scales. Placed within the context of current sea surface warming trends, recurrent massive bleaching events, and documented decline of northeastern Caribbean coral reefs (Miller et al., 2009; Hernández-Pacheco, Hernández-Delgado & Sabat, 2011; Edmunds, 2013), net recovery of ecosystem structure and functions within bombarded grounds is unlikely to occur, rendering them as novel habitats (*sensu* Graham, Cinner, Norström & Nyström, 2014). This suggests that future trajectories of dramatically changed reef communities constituting novel habitats will be quite different from the past, and embracing novel futures may enable more pragmatic approaches (e.g., rehabilitating ecological functions instead of restoring original diversity) to maintaining or re-building the dominance of massive reef-building corals from the past.

The lack of meaningful natural coral reef recovery within 35-50 year-old reef craters from Culebra is alarming, but surprisingly, still poorly addressed. Our study suggests that coral community recovery is minimal within reef craters and limited to sporadic ephemeral species such as *S. radians* and *P. astreoides*. There is increasing evidence that natural coral reef recovery ability from blasting even across small spatial scales can become severely limited with increasing spatial and temporal scale of destruction. Extensively blasted areas for fishing in Indonesia showed no significant recovery within a period of six years despite adequate coral larval supply from adjacent reefs (Fox & Caldwell, 2006). Extensive bombing can result in the formation of unstable coral rubble fields that can move with ocean currents and storm swells, causing extended mortality on adjacent remnant patches of living corals and that can also prevent successful coral larval recruitment over unstable bottoms (Fox, Pet, Dahuri & Caldwell, 2002; 2003; Lindhal, 2003; Raymundo, Maypa, Gomez & Cadiz, 2007). Therefore, reef natural recovery ability within directly bombarded grounds seems poorly probable and will require assisted coral reef rehabilitation methods (Bowden-Kerby, 1997; Raymundo et al., 2007; Hernández-Delgado, Suleimán, Olivo, Fonseca & Lucking, 2011). This can be feasible across small spatial scales similar to those of reef craters. Nonetheless, human intervention is unlikely to be effective on large spatial scales due to prohibitive costs, highlighting the need for a combination of effective management approaches to foster the rehabilitation of reef ecological functions and ecosystem resilience.

A particular concern is that a habitat once dominated by a *M. annularis* species complex framework has not shown any sign of recovery over the course of several decades through sexual coral larval recruitment. Though coral larval settlement do occur within the crater, coral spat mortality appears to be high largely due to the unstable fragmented nature of the bottom. Considering the significant decline of *M. annularis* species complex percent living cover across the region (Miller et al., 2009; Hernández-Pacheco et al., 2011, Edmunds, 2013), recovering benthic spatial heterogeneity ecological functions is largely improbable. Therefore, an alternative strategy that can potentially achieve rapid results in rehabilitating shallow reef ecological functions as juvenile fish nursery grounds is the use of community-based, low-tech farming and outplanting of rapid-growing *Acropora cervicornis*. Low-tech, community-based approaches to culture, harvest and transplant *A. cervicornis* into formerly bombarded grounds proved highly successful in fomenting increasing benthic spatial heterogeneity, while fostering meaningful community-based participation. Outplanted colonies showed outstanding survival and growth rates. Observed decline occurred as a result of partial coral mortality associated to massive runoff events from deforested steep slopes adjacent to the coastline following heavy rainfall. Higher percent survival rate observed on rocky outcrops at impacted sites (within no-take CLPNR) was the result of lower predation impacts by corallivore gastropod *Coralliophila abbreviata* Lamarck, 1816 and *C. caribaea* Abbott, 1958, and by fireworm *Hermodice carunculata* Pallas, 1766; in comparison to adjacent controls outside the reserve. This could be the result of lack of invertebrate predators across control non-reserve sites, which is consistent with previous accounts of fish community structure from the site (Hernández-Delgado et al., 2006). This suggests that *A. cervicornis* farming and outplanting is a key successful tool to help rehabilitate shallow reef nursery grounds. But further, it also showed that reef trophic condition is a key element in determining reef rehabilitation success. Therefore, the combination of a no-take marine protected area designation and low-tech coral farming and outplanting are key management tools to foster the rehabilitation of reef ecological functions and ecosystem resilience of impacted sites across reef spatial scales. History has shown that introducing and fostering compliance with coral reef conservation measures in a small island community still traumatized by historical military practices and by past actions by the government perceived by local communities as serious violation of trust has become a paramount challenge. Nonetheless, community-based participatory management approaches have proved to be a highly successful and empowering strategy to rehabilitate impacted coral reefs ecosystems and to educate base communities through hands-on experience on the significance of reef conservation and rehabilitation.

There is also a concern that military impacts on coral reef are ecologically persistent and that they may still represent a risk of toxic pollution further threatening reef recovery. Goenaga (1986, 1991) suggested that the large abundance of unexploded ordnance and the potential leaching of pollutants from bombs in coral reefs may significantly impair their future recreational and fishing value. Porter (2000) found evidence of abundant "unexploded bombs, artillery shells, and shell casings on the coral reef and in adjacent seagrass beds; burial and shading of coral reef organisms by unexploded ordnance and ordnance debris; fracturing of the coral reef framework and the underlying coral bed rock, and the existence of bombs and bomb fragments impregnated into the reef; the existence of parachutes from flares and cluster bomb fragments draped over corals and other coral reef flora and fauna; and the existence of unexploded bombs leaking materials into coral reef environment and creating a limited "dead zone" around the bombs". Porter et al. (2011) also found a statistically significant inverse correlation between the density of unexploded ordnance and coral species richness, coral colony abundance, and coral species diversity, with reefs with the highest concentrations of bombs and bomb fragments having the lowest health indices and the lowest species diversity. Further, evidence of leaking toxics from unexploded ordnance has also been documented in reef demersal fauna from Vieques (Porter et al., 2011). These factors, in combination with the long-term impacts of uncontrolled, poorly planned land uses in the post-military land development boom in Culebra and Vieques has also resulted in the implementation of a non-sustainable development model with paramount adverse ecological and socio-economic implications to environmental and socio-economic sustainability of the islands (Hernández-Delgado et al., 2012; Ramos-Scharrón, Amador & Hernández-Delgado, 2012). This is an aspect that deserves further research.

Our findings showed that there was still an untold story about bombing impacts across small reef spatial scales, that benthic habitat destruction is ecologically long-lasting (over decadal scales) and that lack of net recovery has resulted in converting impacted reefs in a *de facto* novel habitat. Natural reef recovery abilities within bombarded reefs need to be continuously monitored. Targeted monitoring efforts will become critical in the context of increasing sea surface temperature and its long-term impacts on coral reefs. Declining reefs across the region due to climate change impacts may aggravate the ability of bombarded reefs to show at least a modest degree of recovery. The lack of natural recovery ability coupled with a declining social-ecological system significantly reduces the probability of ecosystem and socio-economic recovery. A major community-based effort should be launched to foster improved coral reef ecosystem and socio-economic resilience rehabilitation. Integration of local stakeholders should help improve efforts by local natural resource managers and decision-makers to accelerate recovery of ecological functions of degraded reef ecosystems and socio-economic systems, but also to repair communication and trust.

ACKNOWLEDGMENTS

This study was possible thanks to the support provided to E.A. Hernández-Delgado by the National Science Foundation HRD #0734826 through the Center for Applied Tropical Ecology and Conservation. We also thank the partial support from the Caribbean Coral Reef Institute of the University of Puerto Rico (NA04NOS4260206, NA05NOS4261159, and NA07NOS4000192) to E.A. Hernández-Delgado, and the partial support provided by NOAA and The Nature Conservancy (MAR-SAM-110110) through Sociedad Ambiente Marino to S. Suleimán-Ramos and E.A. Hernández-Delgado.

RESUMEN

Los arrecifes de coral con craters-bomba en Puerto Rico, la historia no contada sobre un hábitat inusual: desde la destrucción de arrecifes hasta la rehabilitación ecológica basada en la comunidad. Los impactos ecológicos de las actividades militares de bombardeos en Puerto Rico se han descrito a menudo como mínimos, con recurrentes denuncias al confundir efectos por huracanes, enfermedades de corales y estresores antropogénicos locales. Los cráteres de arrecife, aunque aislados, están relacionados con una alta fragmentación de la colonia y pulverización del contorno, con una pérdida neta permanente de arrecife en bio-construcción. En contraste, secciones adyacentes de arrecife no bombardeado tienen mayor biodiversidad y mayor relieve espacial bentónico. Comparamos las comunidades bentónicas en cráteres-bomba de arrecifes de coral con 35-50 años de antigüedad en las islas de Vieques, Puerto Rico, en comparación con los sitios adyacentes no impactados; 2) la densidad de reclutamiento de coral y estructura de la comunidad de peces dentro y fuera de los cráteres; y 3) impactos preliminares de un esfuerzo de rehabilitación basado en la comunidad arrecifal usando tecnología simple con el cultivo del coral Staghorn *Acropora cervicornis*. Los cráteres de arrecife se distancian en tamaño de aproximadamente 50 a 400m^2 y fueron dominados ampliamente por fragmentos de bentos aplanado, con una cubierta de coral generalmente por debajo de 2% y el predominio de taxones no constructores de arrecifes (es decir, tapetes de algas filamentosas, macroalgas). La heterogeneidad espacial bentónica fue significativamente menor dentro de cráteres que también resultaron en un reducido valor funcional como tierra de vivero de peces. La riqueza de especies de peces, abundancia y biomasa y densidad coral recluta fueron significativamente menores dentro de cráteres. Tecnología simple, basada en los enfoques de cultivo de comunidad, la cosecha y transplante de *A. cervicornis* en terrenos anteriormente bombardeados han demostrado un éxito al aumentar el porcentaje de cobertura de coral, la heterogeneidad espacial bentónica y ayudando a rehabilitar funcionalmente la tierra para vivero.

Palabras clave: estructura de la comunidad bentónica, impactos de bombardeo, rehabilitación ecológica basada en la comunidad, arrecifes de coral, estructura de la comunidad de peces, actividades militares, hábitat inusual

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Variación del ciclo gonádico del ostión americano, *Crassostrea virginica* (Ostreoida: Ostreidae) en función de su talla en la laguna de Tamiahua, Veracruz, México

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Received 24-VIII-2013 Corrected 12-III-2014 Accepted 24-III-2014

Abstract: Variation of gonadal cycle of the american oyster, *Crassostrea virginica* **(Ostreoida: Ostreidae) as a function of height in Tamiahua Lagoon, Veracruz, Mexico.** The American oyster, *Crassostrea virginica* is one of the most important fishery resources of the Gulf of Mexico, where it has been classified as "resource exploited at maximum". Since 1994 state authorities set a minimum extraction shell length of 70 mm (adult size); this was based on population studies alone. We compare the gonadal cycle of subadults oysters with adult organisms. From January to December 2011, 90 oysters were collected monthly in Tamiahua Lagoon, Veracruz and classified as subadults (50-69mm; 75% of sample) and adults (≥70mm). Histological gonad sections were classified in four categories: rest, gametogenesis, maturation and release of gametes. In subadults, the rest stage had two peaks (January 22% and June 13%), and gametogenesis between January and July (22-74%). Maturation was observed in July, August and September (40, 64 and 41% respectively) and release in October (66%) and November (45%). Correspondingly, adults were resting in January and June (17 and 13%), and January-July gametogenesis (56-88%), matured in August and September (64 and 42%) and released gametes in September and October (54 and 70%). The gametogenic cycle was similar in subadults and adults: the species breeds from sizes equal or smaller than 50 mm and this should be considered by authorities. Rev. Biol. Trop. 62 (Suppl. 3): 201-206. Epub 2014 September 01.

Key words: minimum size of extraction, gametogenic cycle, *Crassostrea virginica*, Tamiahua Lagoon, histology.

El ostión americano, *Crassostrea virginica* (Gmelin, 1791) es un miembro prolífico de los estuarios en la costa oriental de América (Meyer & Townsend, 2000), localizado desde el Golfo de San Lorenzo en Canadá hasta la península de Yucatán en el Golfo de México (Buroker, 1983).

La pesquería del ostión es considerada la más importante por volumen de captura en todo el Golfo de México. En 2012, se encontraban registradas 61 sociedades cooperativas, que incluyen 8 685 socios agremiados, que se dedican a la extracción de ostión en el Golfo de México (DOF, 2012).

Debido a la intensa explotación que se ha ejercido sobre este recurso, las poblaciones silvestres de *C. virginica* poseen el estatus de "recurso aprovechado al máximo sustentable" en los estados de Veracruz, Tabasco y Campeche (DOF, 2012). Como medida de protección de la pesquería se formuló la NOM-015-PESC-1994 (DOF, 1995) en la cual se regula la extracción de las existencias naturales de ostión y establece los programas de aprovechamiento y manejo en los que quedan obligados a participar concesionarios y titulares de permisos, dentro de los sistemas lagunarios-estuarinos del Estado de Tabasco.

Los ostiones son categorizados de acuerdo a la longitud de su concha en subadultos (50-69 mm) y adultos (≥70 mm). Se considera que los ejemplares con tallas de subadultos apenas han iniciado su actividad reproductiva, mientras que los ostiones con tallas adultas han alcanzado el óptimo reproductivo de la especie (SEPESCA, 1994). Considerando lo anterior, la NOM-015-PESC-1994 establece la talla mínima de extracción (TME) en 70 mm de longitud de concha.

Debido a que el estado de Veracruz no posee una norma oficial que regule la pesquería del ostión, toma como referencia la TME propuesta para el estado de Tabasco. En este trabajo se describió y comparó el ciclo reproductivo de ostiones subadultos y adultos de la laguna de Tamiahua, Veracruz, para evaluar si existe mayor actividad reproductiva entre los ostiones considerados adultos con respecto a los subadultos y de esta manera probar la veracidad de la TME propuesta en la NOM-015-PESC-1994.

MATERIALES Y MÉTODOS

Área de estudio. La laguna de Tamiahua se encuentra en la porción occidental del Golfo de México, en el estado de Veracruz entre las coordenadas 97°23’ y 97°46’W y entre 21°06’ y 22°05’N. Es la laguna costera más grande del estado de Veracruz, con una superficie aproximada de 880km^2, longitud de 100km y ancho de 25km (Contreras, 1993). Su clima es cálido húmedo con lluvias en verano. En ella descargan numerosos esteros, entre los que destacan La Laja, Cucharas y Tancochín que reciben los aportes de agua residual de las poblaciones de La Laja, Cucharas y Naranjos respectivamente. Cuenta con dos bocas: Tampachiche al norte y Corazones al sur, está última se encuentra frente a la ciudad de Tamiahua. Su profundidad promedio es de 2.2m (De la Lanza & Cáceres, 1994).

Recolección de muestras. Se colectaron 90 organismos mensualmente de enero a diciembre de 2011. Los ostiones eran medidos para ser catalogados como subadultos (50-69mm) o adultos (≥70mm). De cada organismo se tomó una muestra transversal de la región media del complejo gónada-glándula digestiva.

Procesamiento histológico. Los tejidos extraídos fueron fijados en formol al 10% en agua filtrada de la misma laguna durante un lapso de 72 horas. Posteriormente se deshidrataron en una serie creciente de alcohol de 70°, 90° y 100° para después pasar por solvente UltraClear®. Los tejidos preparados fueron embebidos en bloques de parafina Paraplast®. Se realizaron los cortes de 6μm de cada bloque empleando un micrótomo Microm®. Dichos cortes, fueron montados sobre portaobjetos y teñidos con la tinción Hematoxilina-Eosina (H-E). Las preparaciones histológicas teñidas fueron observadas al microscopio para reconocer el estadio gonadal de cada ejemplar.

Índices reproductivos. Una vez que se determinó el estadio gonadal, se calculó la actividad reproductiva, el índice de maduración y el de liberación utilizando las siguientes ecuaciones:

Actividad Reproductiva $AR = \frac{(G+M+L)}{N}$

Índice de maduración $IM = \frac{M}{N}$

Índice de liberación $IL = \frac{L}{N}$

Dónde:
N: número total de ostiones
G: número de organismos en gametogénesis
M: número de organismos en maduración
L: número de organismos en liberación

Análisis estadístico. Se realizó una prueba de t ($p<0.05$) para contrastar la variación entre el ciclo reproductivo de subadultos y adultos; y para comparar los índices reproductivos en ambas tallas.

RESULTADOS

Se consideraron cuatro fases o estadios gonadales para describir el ciclo reproductivo de *C. virginica* éstas fueron: I) Reposo, II) Gametogénesis, III) Maduros y IV) Liberación. Los estadios fueron tomados y modificados de la escala propuesta por Baqueiro, Aldana, Sevilla y Rodríguez (2007). Para la determinación del estadio de madurez sexual que presentó cada ostión, se consideró la relación entre la cantidad de tejido conjuntivo y la de tejido gonádico, la cantidad de túbulos seminíferos u ovígeros y la cantidad y tipo de células sexuales.

Reposo. El tejido conjuntivo ocupa todo el espacio entre la glándula digestiva y el tejido gonádico. No se observan vestigios de gametos que permitan la identificación del sexo. El tejido germinal está limitado a cordones gruesos de células altamente acidófilas de color morado.

Gametogénesis. Los gametos empiezan a diferenciarse entre machos y hembras. Entre el tejido conjuntivo se empiezan a formar folículos que en los que se presentan gametos con tallas diferentes. En hembras, la cromatina es laxa y pueden o no observarse los nucléolos

Maduros. El tejido conjuntivo es muy escaso. Los túbulos ovígeros y seminíferos según sea el caso, ocupan casi todo el espacio del tejido gonadal. En hembras, se presentan ovocitos de talla uniforme en los que el núcleo se encuentra bien definido. En los machos los gametos dominantes fueron las espermátidas y espermatozoides orientados hacia la luz de los túbulos.

Liberación. Los túbulos ovígeros y seminíferos no están bien definidos y se encuentran pocos gametos que muestran forma indefinida.

Proporción de tallas. La muestra obtenida para este trabajo presentó 731 ostiones subadultos y 332 ostiones adultos. La proporción de tallas fue de 2.97 subadultos por cada adulto.

Ciclo reproductivo. La figura 1 presenta la evolución anual de los estadios gonadales para establecer el ciclo reproductor. El estadio de reposo fue constante y de baja intensidad tanto en subadultos como en adultos, presentando el mayor pico de abundancia en el mes de enero (22% en subadultos y 17% en adultos). La fase de gametogénesis fue la más abundante de todos los estadios; en subadultos, los mayores porcentajes de presencia se ubicaron de febrero a julio (47-74%), mientras que en los adultos los meses más importantes fueron de enero a julio (52-88%). Los meses de la estación lluviosa, julio-septiembre, presentaron el mayor porcentaje de organismos en maduración, tanto para subadultos (40-64%), como para adultos (36-61%). Por último, el porcentaje de liberación fue importante para los dos grupos de tallas, entre septiembre y noviembre teniendo el mayor pico en octubre (subadultos 66%, adultos 75%).

De acuerdo a los resultados de la prueba de t (cuadro 1), ninguno de los estadios gonadales presentaron diferencia significativa (α=0.05) entre ostiones subadultos y adultos.

Índices reproductivos. El cuadro 2 muestra los valores obtenidos para los índices de actividad reproductiva, maduración y liberación. No existe diferencia (α=0.05) en ninguno de los índices entre ostiones subadultos y adultos.

DISCUSIÓN

En *C. virginica* los eventos reproductivos se encuentran ligados a cambios en los

CUADRO 1
Prueba de t para los estadios de madurez gonadal entre ostiones subadultos y adultos de la laguna de Tamiahua, Veracruz

TABLE 1
T test for gonadal maturity stages between young and adult oysters from Tamiahua lagoon, Veracruz

	Valor de t	Valor de p
Reposo	0.75	0.46
Gametogénesis	0.88	0.38
Maduros	0.60	0.54
Liberación	0.39	0.69

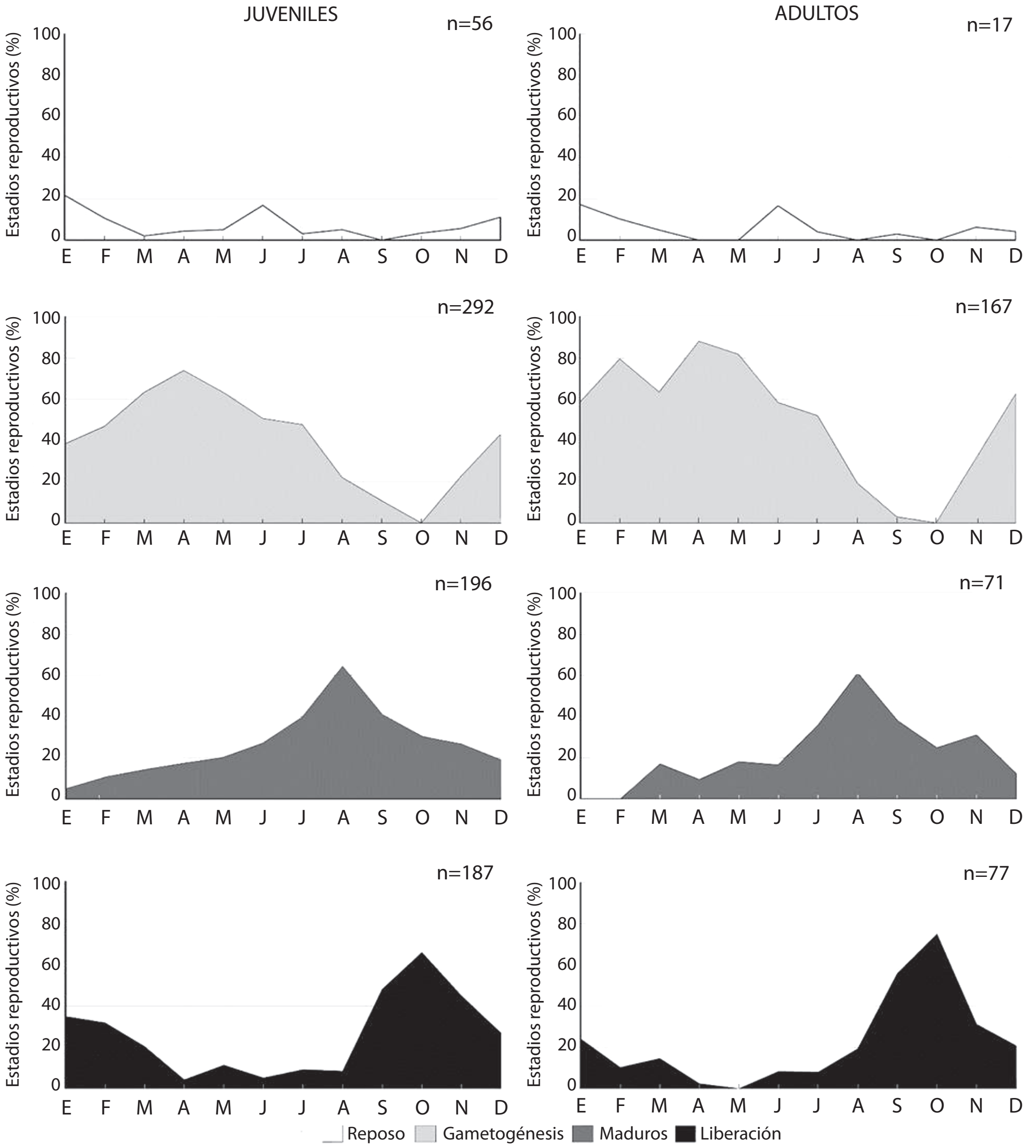

Fig. 1. Ciclo reproductivo de subadultos y adultos de *Crassostrea virginica* de la laguna de Tamiahua, Veracruz.
Fig. 1. Reproductive cycle of sub-adults and adults of *Crassostrea virginica* from Tamiahua Lagoon, Veracruz.

factores ambientales tales como temperatura, salinidad, pluviometría, corrientes, alimento disponible entre otros (Martínez, Aldana, Brule & Cabrera, 1995; George-Zamora, Sevilla & Aldana, 2003; Mazón-Suástegui et al., 2011). Sin embargo, no existe ningún trabajo que haya demostrado experimentalmente la relación entre la talla de concha de *C. virginica* con su desarrollo gonadal.

En el trabajo de Pazos, Román, Acosta, Abad & Sánchez (1996) se evaluó el efecto de la talla *Mytilus edulis* sobre sus estadios gonádicos, reportando que los individuos juveniles mostraron un solo periodo de liberación

CUADRO 2
Índices reproductivos para los ostiones de la laguna de Tamiahua. AR, Actividad reproductiva. IM, Índice de maduración. IL, Índice de liberación

TABLE 2
Reproductive index for oysters from Tamiahua lagoon. AR, reproductive activity. IM, maturation index. IL, Index release

	AR	IM	IL
Subadultos	92.34	26.81	23.19
Adultos	94.88	24.39	25.58

anual, mientras que los adultos liberaron en dos ocasiones. En contraste, Royer et al. (2008) al estudiar el desarrollo de la madurez gonadal en tres clases de tallas para *Crassostrea gigas*, reportaron que su ciclo reproductivo no presentó diferencia en función de la talla del ostión. En este mismo sentido, Quayle (1969) sugiere que el inicio en la actividad reproductiva en *Crassostrea gigas*, está más relacionado con factores ambientales (temperatura, salinidad, pluviometría, corrientes y alimento disponible) que con la misma talla del ostión.

En este estudio, tanto el ciclo reproductivo, como los índices reproductivos de ostiones subadultos y adultos no presentaron diferencias ($\alpha= 0.05$) en ninguna de sus fases gonadales. Con estos resultados, se muestra que los ostiones que hasta ahora son considerados subadultos, presentan la misma capacidad reproductiva que los ostiones adultos.

Debido a que no se tiene referencia de los ciclos en función de la talla, pueden considerarse dos hipótesis, la especie: a) tiene una reproducción óptima desde la talla de subadultos y/o b) ha desarrollado una estrategia reproductiva en el que el desarrollo gonadal se acelera para alcanzar la madurez a una menor longitud y de esa manera asegurar su permanencia como un síntoma de sobreexplotación.

AGRADECIMIENTOS

Este estudio se realizó con el apoyo del proyecto “Diagnóstico biológico-pesquero y sistema de información geográfica del recurso ostión de las lagunas de Veracruz para su uso, ordenamiento y manejo sustentable” (M0034-2008-02/109498) y la beca de Maestría del CONACyT N° 222628 otorgada a Luis Asencio Aguirre. Nuestro agradecimiento al laboratorio de Ictiología del Cinvestav-IPN, Unidad Mérida por el acceso a su equipo. A Ricardo Madrigal Chavero por su ayuda en la colecta de ostiones y a Teresa Colas Marrufo por su apoyo en el procesamiento histológico de las muestras.

RESUMEN

El ostión americano (*Crassostrea virginica*) es uno de los recursos de pesca mas importantes en el Golfo de México, donde es clasificado como “recurso aprovechado al máximo”. Desde 1994 las autoridades estatales fijaron una talla mínima de extracción de 70mm de longitud de concha (tamaño adulto); esto basado en estudios aislados de poblaciones. Comparamos el ciclo gonadal de subadultos y adultos. De enero a diciembre de 2011, se colectaron 90 ostiones mensualmente en la laguna de Tamiahua, Veracruz y se clasificaron como subadultos (40-69 mm) y adultos (>70mm). Los cortes histológicos de las gónadas se clasificaron en cuatrocategorías: reposo, gametogénesis, maduración y liberación de gametos. En subadultos, la categoría de reposo tuvo dos picos (enero 22% y junio 13%) y la gametogénesis entre enero y julio (22-74%). La maduración se observó en julio, agosto y setiembre (40, 64 y 41%) y la liberación en octubre (66%) y noviembre (74%). Correspondientemente, los adultos reposaban en enero y junio (17 y 13%), y la gametogénesis entre enero y julio (56-88%), maduraban en agosto y setiembre (64 y 42%) y liberaban gametos en setiembre y octubre (54 y 70%). El ciclo gametogénico fue similar entre ostiones subadultos y adultos: la especie se reproduce con tamaños igual o inferior a 50mm y esto lo deben considerar las autoridades.

Palabras Clave. *Crassostrea virginica*, ciclo gonádico, laguna de Tamiahua, histología, talla mínima reproductiva.

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Is the Queen conch *Strombus gigas* (Mesogastropoda: Strombidae) a species with Allee effect?

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Received 1-VIII-2013 Corrected 14-II-2014 Accepted 24-III-2014

Abstract: The marine park of Xel-Há has a population of *Strombus gigas* which breeds in the area. We determined the relationship between reproductive activity, conch density and environmental parameters. Samples were collected from February to December 2012, using the transect method, at four sites of Marine Park Xel-Ha, Quintana Roo, Mexico. Sediment samples were analyzed and classified using Folk & Ward's method. Temperature, salinity and dissolved oxygen were also recorded. Density had a small correlation with sediment (Pearson r=0.29 with very coarse and r=0.26 with coarse sand), while mating and spawning had a correlation of r=0.54 and 0.62 with medium sand, respectively. Density was high in the four sites and was not associated with mating and spawning (r=0.08 and 0.03, respectively). For reproduction, *S. gigas* requires specific substrate conditions (*sandy effect*) and not just a density of 56 Conch Ha^{-1} (A*llee effect*). Rev. Biol. Trop. 62 (Suppl. 3): 207-213. Epub 2014 September 01.

Key words: *Strombus gigas*, Allee effect, reproductive behavior, Sandy effect.

The queen conch *Strombus gigas* is distributed from Brazil and Venezuela in the south up to Florida and the Bahamas in the north, including all the lesser and greater Antilles. *S. gigas* is now a luxury food. It represents one of the most valuable resources in the region, and was considered as second most valuable fishery with incomes of 6 US$ millions/year, exceeded only by the spiny lobster *Panulirus argus* (Brownell & Stevely, 1981; Pérez-Pérez & Aldana-Aranda, 2000). Now *S. gigas* is an overfished species protected by CITES who is regulated by the international commerce of this resource (de Jesús Navarrete, 2001; Brito-Manzano, Aldana-Aranda, de la Cruz-Lázaro & Estrada-Botello, 2006). However, illegal catch is practiced in all countries of the Caribbean region.

This organism has internal fertilization, it produces an egg mass and its development is indirect (Randall, 1964). Given the regional importance of queen conch in the Caribbean, and the critical status of most populations, the reproductive biology of this species has been studied in several Caribbean countries (Aldana Aranda et al., 2003a to 2003e; Delgado et al., 2004; Aldana-Aranda, 2006; Castro, Frenkiel, Baqueiro & Aldana-Aranda*,* 2007; Bissada-Gooding & Oxeford, 2010). Stoner, Sandt& Boidron-Metairon (1992) related *S. gigas* reproduction with temperature, photoperiod and density of adult conchs.

Stoner & Ray-Culp (2000) observed that mating and spawning in the Bahamas never occurred at a density <48 Conch·Ha^{-1}. These authors mention that the "*Allee effect*" (or "depensation") (Gascoigne & Lipcius, 2004) has an influence in the reproductive activity of *S. gigas, c*oncluding that the overfishing of this resource affects in the recovering and reproduction rates. de Jesús-Navarrete and Valencia-Beltrán (2003) reported a migration for reproduction to sandy areas, associating the reproduction with density but not with sediment, based on these observations, the principal goal of this research was to evaluate the effect of the sediment, physicochemical and population parameters on the reproductive activity of *S. gigas* from February to December 2012.

MATERIALS AND METHODS

Study area: The study was carried in four sites of Xel-Há inlet (Bocana, Centro, Brazo Norte and Cueva) located in Quintana Roo, México, in the geographical coordinates 20°18’50”-20°19’17”N y 87°21’45.5”-87°21’02.5”W (Fig. 1). This site has a total water surface of 14Ha, where the average depth is 3.0m, showing a gradient in the physicochemical parameters (due to the underground river effluents).

Sample collection: In each site we placed three linear transects of 100 x 2m of length, giving an area of $200m^{-2}$ by transect. Weekly from February to December 2012, using scuba diving we registered the number of adult conch and the reproductive activity. Figures 2A-2C show mating, spawning and free egg masses of *S. gigas*. Monthly in each site siphonal length (mm) and thickness lip (mm) in adult conchs were measured. Temperature (°C), salinity (ppt), dissolved oxygen ($mg \cdot L^{-1}$) were measured and sediment samples were taken. The sediment samples were dried and classified with the Folk & Ward methodology (1957). The Infostat software was used to calculated means, standard deviation, one-way Anova and Pearson’s correlation among reproductive, physicochemical and granulometrics parameters.

RESULTS

Environmental parameters: Mean and standard deviation (S.D.) of temperature were 27.44±0.97°C**.** *Brazo Norte* showed the lowest records, while *Centro* recorded the highest (27.25±1.10 and 27.70±0.75°C, respectively). There was no significant variation between sites (p=0.2033). *Bocana* and *Cueva* showed mean salinities of 33.76±0.87 and 13.64±1.83ppt, respectively. Salinity showed significant

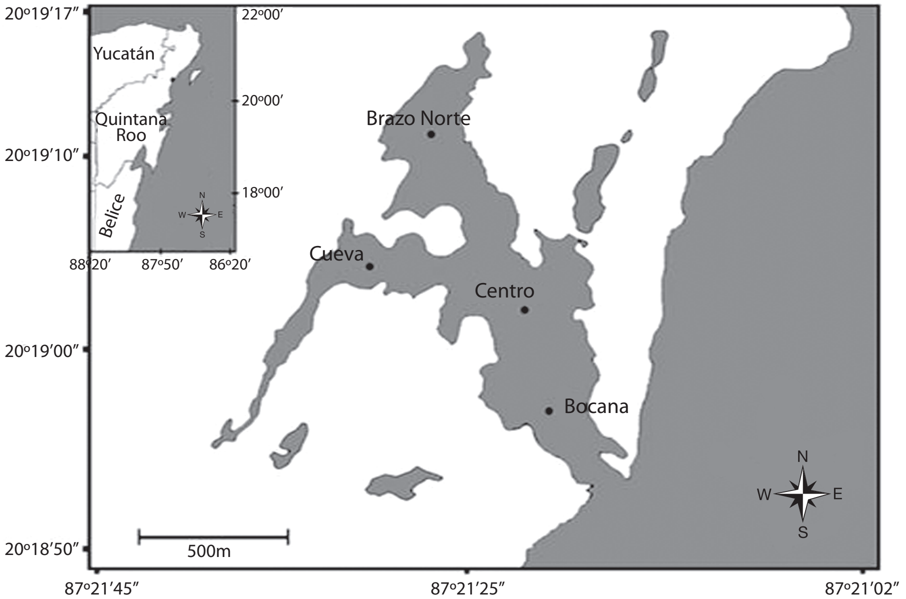

Fig. 1. Study area, Xel-Ha Park in the Mexican Caribbean, indicating four samples sites: Bocana, Centro, Brazo Norte and Cueva.

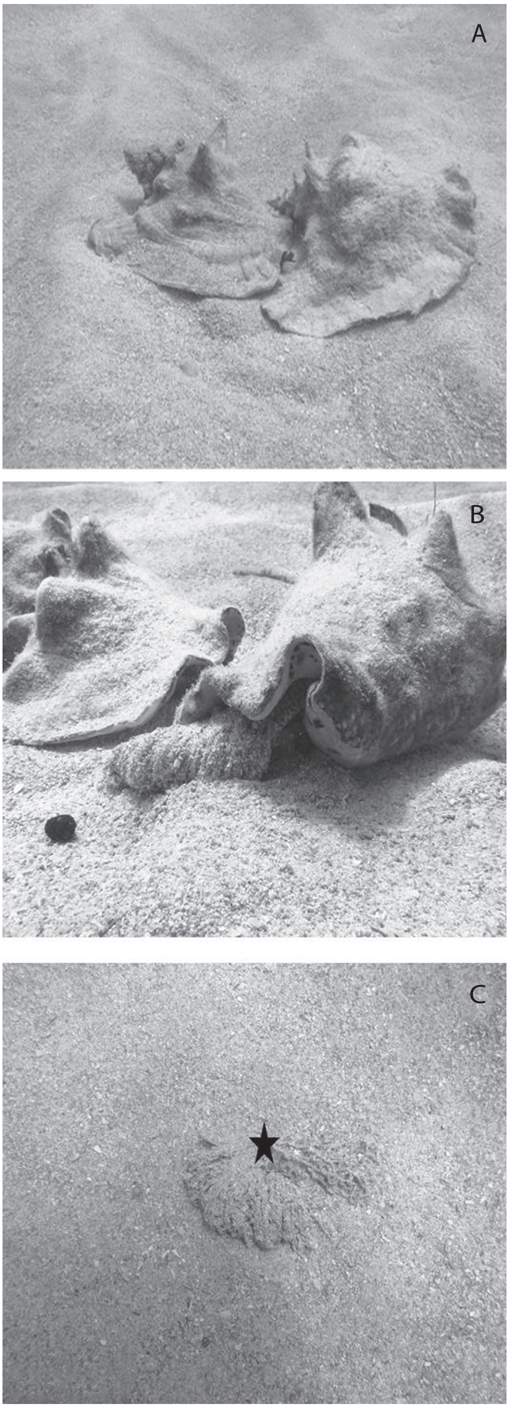

Fig. 2. Reproductive activity observed in Xel-Ha park during samplings: A) Mating conchs; B) Female spawning; C) Free egg mass (★). Photographies of Alejandro Aldana Moreno.

variation between sites ($p \leq 0.0001$). Mean of dissolved oxygen was $4.73 \pm 0.97 mg.l^{-1}$, with the highest concentration in *Bocana* and minor in *Cueva* (5.45 ± 1.28 and 4.01 ± 1.15 $mg.l^{-1}$, respectively), showing significant variation among sites ($p \leq 0.0001$). In relation to the sediments composition, *Bocana* showed 62% of coarse to medium to sands; *Centro* and *Cueva,* 60% to fine and very fine sands and *Brazo Norte*, 73.5% of fine to very fine sands (Fig. 3). The substrate composition among sites showed significant difference ($p \leq 0.0001$).

Sizes population: *Bocana* had a density of 665.58 ± 585.38 $Conch.Ha^{-1}$, followed by *Cueva*, *Brazo Norte* and *Centro* (647.17 ± 487.17, 596.92 ± 333.10 and 404.58 ± 454.21 $Conch.Ha^{-1}$) (Fig. 4A). Density was ≥ 10 times than density suggested by Stoner to have mating and spawning. There was significant variation among sites ($p \leq 0.0001$). The size structure in the four locations was very similar, with values of 203.68 ± 23.73mm of shell length in *Bocana*, to 187.61 ± 27.15mm in *Cueva* (Fig. 4B). Shell length did not change significantly among locations ($p=0.3080$). Using lip thickness (6mm) as an indicator of reproductive activity in conch (Aldana-Aranda & Frenkiel, 2007), we observed that conch of three sites have a lip thickness corresponding to adults: *Bocana, Centro* and *Cueva* with 15.25 ± 6.7, 11.66 ± 7.48 and 6.03 ± 5.47mm, respectively (Fig. 4C). However, lip thickness of conch showed significant variation among sites ($p=0.0198$).

Pearson correlation analysis showed a high association between mating and medium sands ($r=0.54$) and spawning with medium sand ($r=0.62$). Temperature was associated with spawning ($r=0.40$), while density conch exhibited a low association with mating and spawning ($r=0.08$ and $r=0.03$, respectively) (Table 1).

DISCUSSION

Stoner & Ray-Culp (2000) observed that mating never occurred when density was <56 $Conch.Ha^{-1}$, and spawning never occurred at

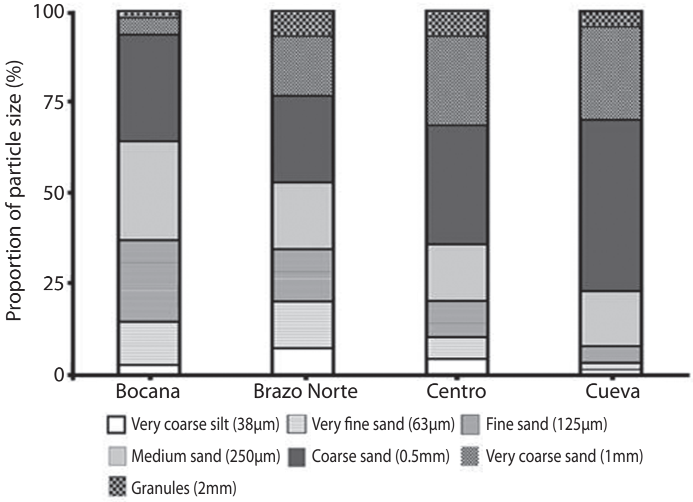

Fig. 3. Sediment category in percentage of four sampling areas in Xel-Há Park, Quintana Roo Mexico.

TABLE 1
Pearson correlation analysis between mating, spawning, density and environmental parameters (sediment category, temperature, dissolved oxygen and salinity)

Sediment category	Mating	Spawning
Granules (2mm)	-0.11	-0.16
Very coarse sand (1mm)	0.33	0.33
Coarse sand (0.5mm)	0.49	0.47
Medium sand (250µm)	0.54	0.62
Fine sand (125µm)	-0.20	-0.20
Very fine sand (63µm)	-0.62	-0.77
Very coarse silt (38µm)	-0.46	-0.57
Temperature (°C)	0.19	0.40
Dissolved Oxygen (mg·L^{-1})	0.34	0.23
Salinity (ppt)	-0.31	-0.10
Density (Conch.Ha^{-1})	0.08	0.03

<48 Conch.Ha^{-1}, demonstrating the operation of depensatory mechanisms. In this study mean density was >400 Conch.Ha^{-1} in four sites, however only the *Bocana* site showed mating and spawning behaviors. Peel and Aldana-Aranda (2012) reported a spatial segregation of juveniles and adults in Xel-Ha, pointing that the sites in the interior of the Inlet probably function as nurseries while *Bocana* could be associated with reproductive activity. It was observed in the present study that adults are placed in all the sites, which indicate that reproduction occurs in this inlet, but only at *Bocana* site. Stoner, Sandt and Boidron-Metairon (1992) and de Jesús Navarrete (1999) associated temperature with reproduction of *S. gigas*.

TABLE 2
Description of size classes of *Strombus gigas* of Xel-Ha park, Quintana Roo, Mexico, showing media and standard deviation (S.D.) of sifonal length and lip thickness, density and reproductive activity (mating, spawning and free egg masses). Sediment category is expressed in % (only coarse and medium sands are considered).

Indicator	Bocana	Brazo Norte	Centro	Cueva
Coarse + medium sands (%)	60.00	50.00	30.00	20.00
Density (Conch.Ha^{-1})	665.58±585.38	596.92±333.10	404.58±454.21	647.17±487.17
Shell lenght (mm)	203.68±23.73	212.92±54.57	197.03±19.58	187.61±27.15
Lip thickness (mm)	15.25±6.77	4.05±5.49	11.66±7.48	6.03±5.47
Mating.week-1	4.35±3.96	0.00	0.00	0.00
Spawning. week-1	14.71±7.61	0.00	0.00	0.00
Egg masses.week-1	26.18±14.15	0.00	0.00	0.00

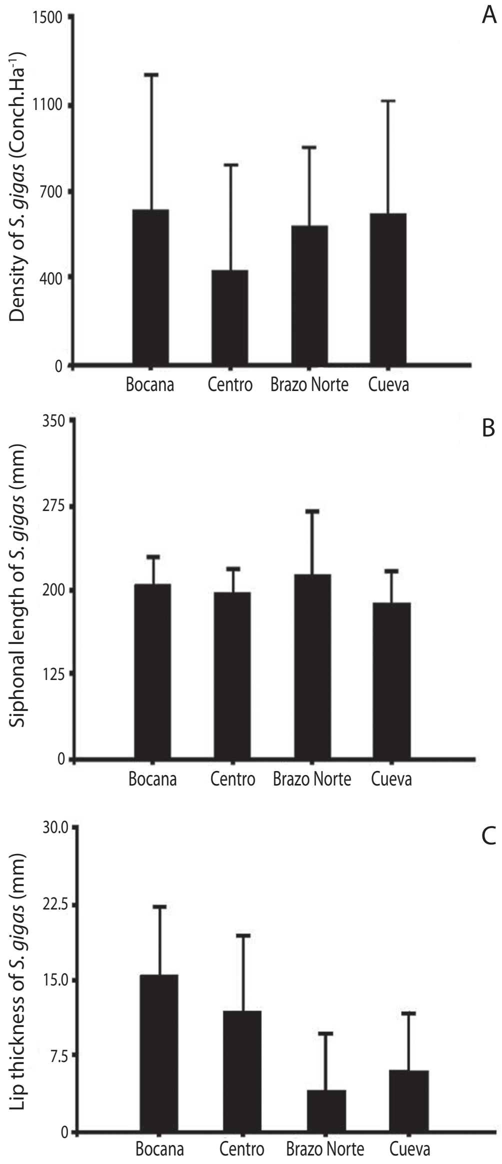

Fig. 4. Sizes population of *S. gigas* of four sites of Xel-Ha park, Quintana Roo, Mexico: A) Density (conch·m^{-2}), B) Siphonal length (mm), C) Lip thickness (mm).

In this study reproductive behavior was associated with temperature and dissolved oxygen, but conch presented mating and spawning only when sediments present ≥60 % of medium to coarse sands (Table 2).

Four sites exhibited a density suggested by Stoner & Ray-Culp (2000) to be related to reproduction, and had reproductive adults present at all times. Given that the physicochemical parameters were similar at all four sites, we suggest that *S. gigas* needs for mating and spawning a minimal density and a reproductive migration pattern related with sediment category (medium sand). Our theory is that *S. gigas* for reproduction is a species with a specific sandy habitat, having two effects: "*Allee*" and "*Sandy*" effects.

ACKNOWLEDGMENTS

This research was supported by project *Sistema de Información Geográfica para la Conservación del Patrimonio del Caribe y el Desarrollo Sustentable del Parque Xel-Há* (Innovatec-Conacyt: 183724). We would like to thank Alejandro Aldana Moreno for photography support, scholarships from Conacyt and staff of Laboratory of Biology and Aquaculture of Mollusks (Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional) for assistance in samplings.

RESUMEN

Es el caracol marino *Strombus gigas* (Mesogastropoda: Strombidae) una especie con efecto Allee? El parque marino de Xel -Há tiene una población de *Strombus gigas* que se cría en la zona. Determinamos la relación entre la actividad reproductiva, la densidad de la concha de *S. gigas* y los parámetros ambientales. Las muestras fueron recolectadas de febrero a diciembre de 2012, utilizando el método de transecto, en cuatro sitios del Parque Marino de Xel -Ha, Quintana Roo, México. Fueron analizados y clasificados utilizando la metodología de Folk & Ward. También se registraron temperaturas, salinidad y oxígeno disuelto. La densidad de concha mostró una baja correlación en la categoría de sedimentos ($r = 0.29$, con muy gruesos y $r = 0.26$ con arena gruesa), mientras que el apareamiento y desove con arena media mostraron una correlación de $r = 0.54$ y 0.62, respectivamente. Las densidades en cuatro sitios fueron altas y no se asociaron con el número de apareamientos y desove ($r = 0.08$ y 0.03, respectivamente). Para la reproducción, *S. gigas* requiere condiciones específicas de sustrato (efecto arenoso) y no sólo una densidad de 56 Conch Ha^{-1} (efecto Allee).

Palabras clave : *Strombus gigas*, efecto Allee, comportamiento reproductivo, efecto Sandy

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Eco-etología básica del caracol rosa *Strombus gigas* (Mesogastropoda: Strombidae), en Xel-Há, Yucatán, Caribe mexicano

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Received 15-VIII-2013 Corrected 12-III-2014 Accepted 01-IV-2014

Abstract: Basic eco-ethology of the queen conch, *Strombus gigas* **(Mesogastropoda: Strombidae) in Xel-Há, Yucatán, Mexican Caribbean.** The queen conch *Strombus gigas* is an important fishery in the Caribbean, whose populations are currently overexploited. Since the decade of 1980 there have been several studies on aquaculture, resource management and area rehabilitation. However, little is known about its behavior in a natural environment and the influence of environmental parameters. Monthly surveys, from January to November 2012 were conducted in in Xel Ha, to observe and quantify six behaviors of *S. gigas:* rest, feeding, movement, burying, copulation and spawning. The observations were made every hour from 8h to 17h by free diving through three transects with three replicates each. Each behavior was observed 90 times each month. Salinity, temperature and dissolved oxygen were registered at the bottom. We found the highest number of snails at rest in July and the lowest in March and September. Feeding and movements had a peak in August. Most buried in October and November. Copulation was first observed on March with a peak in June and July to October's spawning. In daytime observations restingt had a peak at 8h; feeding and moving at 12 to 17h. Copulation and spawning did not have a clear pattern. Variations between months and hours (resting, feeding, moving and buried) were significant ($p<0.05$). Resting correlated with temperature and being buried with oxygen level ($r=-0.5803$; $p=0.0536$). Feeding and moving correlated with temperature and salinity. These results should be useful for the conservation, restoration and aquaculture programs. Rev. Biol. Trop. 62 (Suppl. 3): 215-222. Epub 2014 September 01.

Key words: Behavior, conservation, feeding, move, spawning, queen conch.

El caracol rosa cuyo nombre científico actual es *Strombus gigas* (Linnaeus, 1758) es un gasterópodo herbívoro que llega a medir 30cm de longitud sifonal y a pesar 5kg a su madurez sexual entre los 5-6 años. Se le encuentra en aguas territoriales de 36 países y territorios del Mar Caribe (Davis, 2005), sur de Florida, Centroamérica, noreste de Brasil, Bahamas y Bermudas. Habita en lechos arenosos, en cama de pastos o en escombros de coral (Brownell & Stevely, 1981). *S. gigas* es vulnerable a la sobrepesca debido a su lento crecimiento, formación de grandes aglomeraciones en aguas profundas, tardía maduración y tendencia a desovar en aguas someras. Además, tiene importancia comercial y artesanal en el Caribe siendo la segunda pesquería más importante después de la langosta espinosa (Davis, 2005). En los 1970's, la densidad de adultos de *S. gigas* iba de cientos a miles de individuos por hectárea, actualmente la densidad se encuentra por debajo de los 100 individuos por hectárea en la mayoría de las regiones del Caribe. La disminución de las poblaciones del caracol rosa hizo que a partir de 1992 fuera enlistada en el apéndice II de CITES, donde se encuentran especies amenazadas o que necesitan estricta regulación (CITES, 2003). Se han realizado estudios sobre su cultivo, ecología y manejo pesquero, dentro de éste último punto, se han establecido vedas temporales y permanentes (Davis, 2005), así como áreas marinas protegidas y cuotas de captura (Aldana & Brulé, 1994). La efectividad de las áreas protegidas depende de la identificación de zonas de desove así como áreas de crianza, sin embargo, en muchos países los esfuerzos de conservación son pobres, y la sobrepesca, así como la pesca ilegal sigue ocurriendo (CITES, 2003; FAO, 2007). Para complementar los estudios que se han hecho para la conservación de esta especie es necesario conocer algunos de sus comportamientos como: reposo, movimiento, alimentación, enterrados, cópula y desove, que son los más reportados en la literatura, sin embargo, éstos estudios previos no presentan un patrón de comportamiento a través del tiempo, ni los relacionan con los parámetros ambientales, por lo que el principal objetivo de éste estudio fue conocer el patrón de comportamiento de *S. gigas* en diferentes escalas de observación temporal (diaria y anual) y su relación con los parámetros ambientales. Los resultados obtenidos en éste estudio serán de importancia para el cultivo de la especie, ya que, al conocer los periodos diarios y/o anuales de su comportamiento se puede contar con las instalaciones adecuadas y optimizar la administración del alimento.

MATERIALES Y MÉTODOS

Área de estudio y muestreo: Xel-Há se ubica en la costa de la Península de Yucatán en el Caribe mexicano, entre los 20°20' latitud N y los 87°21' longitud W. La caleta tiene una superficie de 0.3 km^2 y presenta tres apéndices (Aldana et al., 2005). La principal característica es la mezcla de agua dulce y salobre, tiene una profundidad de 2 a 4m y fondos principalmente arenosos con parches de pastos marinos. Se eligió Xel-Há por ser una área marina protegida, donde la remoción de flora y fauna está prohibida; además es considerada un santuario para la conservación del caracol rosa en la Rivera Maya Mexicana (Peel et al., 2010), ya que sostiene una densidad de juveniles y adultos por arriba de lo que recomienda Stoner (2002).

El sitio que se eligió para monitorear el comportamiento de los caracoles adultos dentro de la Caleta de Xel Há fue "Bocana", que es la zona que comunica al mar y presenta un sustrato arenoso-medio con parches de pastos marinos. Los comportamientos cuantificados en este estudio fueron: reposo (organismos donde se observa la concha sobre el sedimento sin ningún desplazamiento y la probóscide se encuentra retraída), alimentación (organismos con la probóscide fuera de la concha realizando escaneo sobre el fondo o los pastos marinos), movimiento (organismos que por medio de pequeños saltos continuos se desplazan de un punto a otro), enterrado (organismos que únicamente muestran las espinas, el canal y la muesca sifonal de la concha y el resto está cubierto por sedimento), cópula (dos caracoles alineados donde la parte delantera de la concha del macho está cubriendo la parte posterior de la hembra) y desove (organismos donde se observa una madeja parecida al estambre, de color blanquecino saliendo de la concha del caracol). Mensualmente de enero a noviembre de 2012 se recorrieron por triplicado tres transectos de 100m de longitud por 2m de ancho, anotando en cada recorrido el número de caracoles en cada uno de los comportamientos señalados. Las observaciones fueron realizadas cada hora por medio de buceo libre de 8 a las 17h, con un número alto de observaciones (n= 10800). Simultáneamente, se registraron temperatura, salinidad y oxígeno disuelto de fondo con un YSI 85.

Análisis estadísticos. Se realizaron gráficas de barras con desviación estándar por comportamiento a través de las horas y los meses del año (INFOSTAT versión 1.1, 2002). Así mismo, se elaboraron histogramas con la finalidad de conocer si los datos eran normales, en el caso de no ser normales se realizó una transformación utilizando la fórmula Ln (x+1). Se realizaron ANOVAS de una vía entre las categorías de comportamiento cuantificadas y el tiempo (horas y meses), con la finalidad de conocer si existen diferencias del comportamiento a través del tiempo, y en caso de existir diferencias significativas se aplicó un análisis *post hoc* (Tukey HSD).

Para analizar el posible efecto de los parámetros ambientales se elaboraron gráficas de dispersión con línea de tendencia, y se calculó el valor de la correlación de Pearson así como su significancia; se utilizaron los promedios de temperatura, salinidad y oxígeno disuelto de todos los meses así como los promedios de los comportamientos dominantes (mayor número de organismos y observados durante todo el año) utilizando el programa STATISTICA 8, 2006.

RESULTADOS

Todos los comportamientos del caracol rosa presentaron diferencias significativas a través de los meses, sin embargo, en un ciclo diurno el comportamiento reproductivo no presenta variación. En relación a los parámetros ambientales, la temperatura es la que influye más en el comportamiento del caracol que las otras variables.

Comportamiento mensual del caracol rosa de *S. gigas:* El reposo presentó diferencias significativas a través de los meses (ANOVA $p<0.05$), con el mayor número de organismos en julio y el menor número en marzo y septiembre (Fig. 1a). La alimentación mostró diferencias significativas entre meses (ANOVA $p<0.05$), con un pico entre febrero-octubre del 35% en promedio y valores bajos en enero y noviembre (Fig. 1b). El movimiento presentó diferencias significativas entre meses (ANOVA $p<0.05$), agosto y septiembre con el mayor número de organismos (16%) y julio y noviembre con el menor número de organismos (4%) (Fig.1c). En octubre y noviembre se observó el mayor número de organismos enterrados y en mayo el menor número de caracoles con este comportamiento, habiendo diferencias significativas entre meses (ANOVA $p<0.05$) (Fig. 1d). La cópula se empezó a observar en marzo, con un pico en junio y julio presentando diferencias significativas (ANOVA $p<0.05$) de estos meses con el resto del año (Fig. 1e). El desove se observó de julio a octubre. En julio se tuvo el pico de desove presentando diferencias significativas (ANOVA $p<0.05$) (Fig. 1f).

Comportamiento diurno del caracol *S. gigas:* Los caracoles presentaron en sus actividades un ciclo diurno. Por lo que se refiere al reposo, este fue alto a las 8h, donde 70% de la población de caracoles se encontró en éste comportamiento. El mínimo se observó a las 14h (33%), habiendo diferencias significativas entre horas (Fig. 2a). La alimentación aumentó de manera gradual de las 8h a las 14h, manteniéndose con valores altos hasta las 17h (promedio 39-41% de la población en alimentación). La prueba de ANOVA ($p<0.05$) mostró diferencias significativas en la alimentación entre horas (Fig. 2b). Los caracoles presentaron un patrón de movimiento diurno, no teniendo variación de las 10-17h (10%), sin embargo, en las primeras horas de la mañana la motilidad fue muy reducida (<5%). La prueba de ANOVA ($p<0.05$) mostró diferencias significativas del movimiento entre horas (Fig.2c). Los caracoles se enterraron más por la mañana (8-9h) que en la tarde, habiendo diferencia significativa entre horas (Fig. 2d). La cópula así como el desove no presentaron diferencias significativas a través de las horas (ANOVA $p>0.05$).

Interacción entre comportamiento y variables ambientales: Se realizaron correlaciones de Pearson entre los comportamientos que se cuantificaron de *S. gigas* (reposo, movimiento, alimentación y enterrados) a lo largo de un año de muestreo con observaciones diurnas y mensuales y los parámetros temperatura, salinidad y oxígeno disuelto. El reposo y la alimentación presentaron una correlación significativa y alta con la temperatura (r 0.70558 [p= 0.0171] y r 0.66304 [p=0.0503] respectivamente), además la alimentación presentó una correlación significativa con la salinidad (r=0.6305 [p=0.0216]) (Figs. 3a y 3b). El movimiento también presentó una correlación

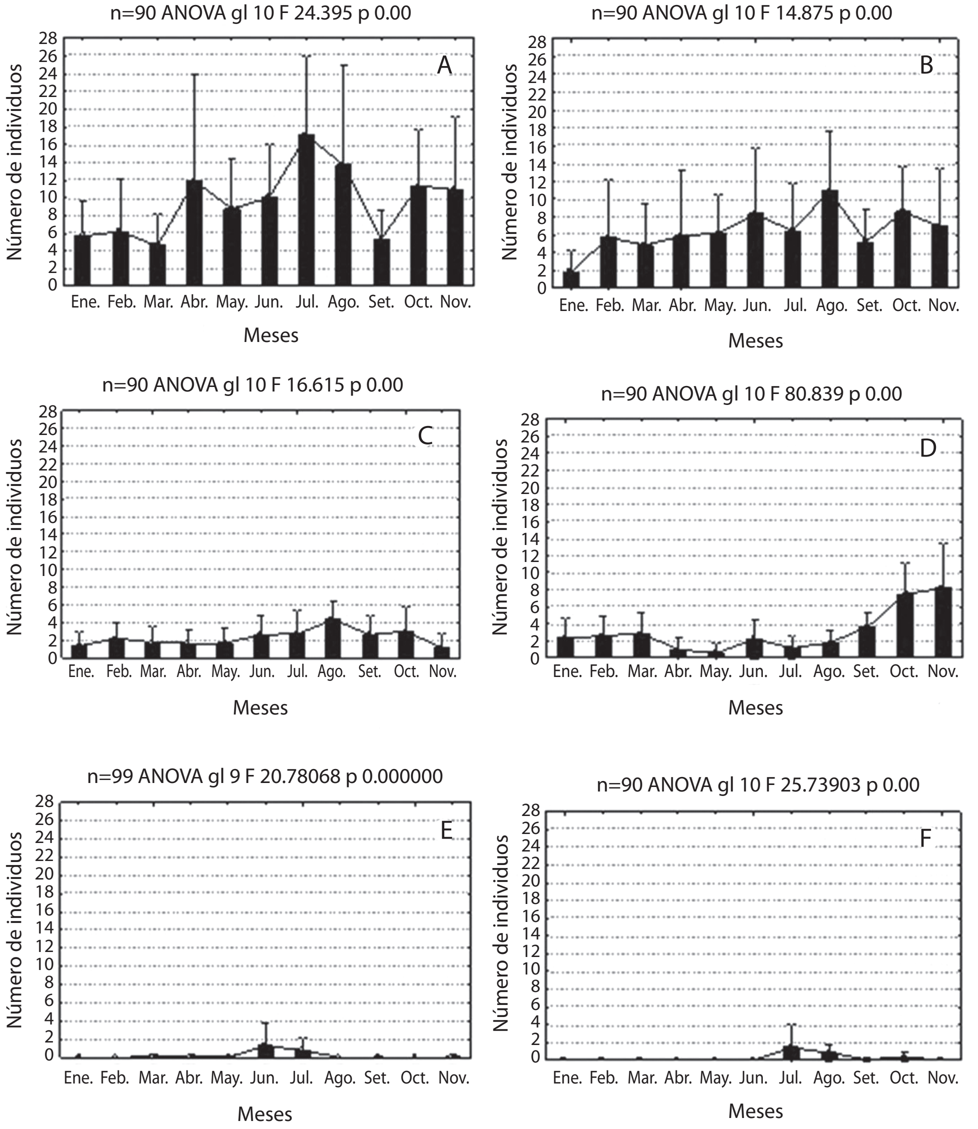

Fig. 1. Variaciones mensuales del comportamiento de *S. gigas*: a) reposo, b) alimentación, c) movimiento, d) enterrados, e) cópula y f) Desove. *diferencia significativa, n=90.

Fig. 1. Monthly behavior of queen conch *S. gigas*: a) resting, b) feeding, c) moving, d) buried, e) copulating, f) spawning. *Significant difference, n=90.

significativa, alta y directa con la temperatura (r 0.73647 [p=0.0022]) (Fig. 3c). El porcentaje de caracoles enterrados presentó una correlación negativa y significativa con el oxígeno disuelto (r-0.5803 [p=0.0536]) (Fig. 3d).

DISCUSIÓN

A lo largo del año los organismos de *S. gigas* presentaron variaciones significativas en sus comportamientos. Se observó actividad

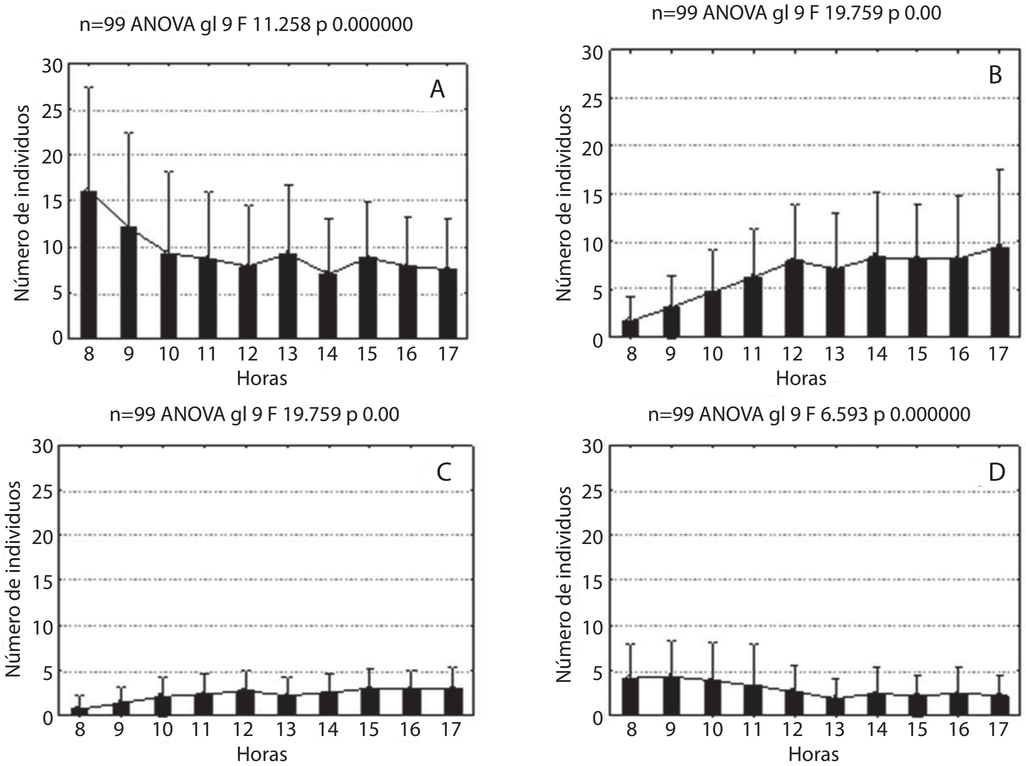

Fig. 2. Variaciones diurnas del comportamiento de *S. gigas*: a) reposo, b) *alimentación, c) movimiento, d) enterrados.* *diferencia significativa, n=99.

Fig. 2. Diurnal behavior of queen conch *S. gigas*: a) resting, b) feeding, c) moving, d) buried. * Significant difference, n=99.

reproductiva (cópula y desove) de marzo a octubre, resultados que coinciden con lo reportado por Aldana Aranda et al. (2005; 2006). La cópula empezó a observarse en marzo con un pico en junio, coincidiendo a lo reportado para el Arrecife Alacranes (Pérez & Aldana, 2003) y lo observado en Turk y Caicos, por Davis, Hesse y Hodgkins (1987), con esto queda demostrado que el caracol rosa presenta un periodo de reproducción, lo cual debe tomarse en cuanta a la hora de establecer los periodos de veda. Randall (1964) observó que los caracoles se entierran hasta la base de la espina principalmente en invierno o por efecto de fuerte marea y Hesse (1979) observó que cuando el mar está tempestuoso por efecto de vientos del este y del norte los caracoles se entierran (noviembre a febrero). Jesús Navarrete (comm pers) señala que el caracol puede enterrarse por periodos prolongados en sus primeras etapas de desarrollo o cuando las condiciones ambientales son adversas. En éste estudio el mayor número de caracoles enterrados se encontró de octubre-febrero, que corresponde a la época de nortes, coincidiendo con lo reportado por los autores antes señalados. El movimiento tuvo un pico en agosto, coincidiendo con lo que mencionan Stoner y Sandt (1992), quienes señalan que la temporada de migración de esta especie está generalmente asociada al desove, donde los caracoles migran de aguas profundas a someras para la reproducción (Randall, 1964). Sin embargo, Aldana (2006) señala que *S. gigas* tiene una migración reproductiva y que ésta se encuentra influenciada por la granulometría del sedimento, (*S. gigas* prefiere un diámetro de partículas de arenas medias para el desove) y no solo por la batimetría o el efecto Alee

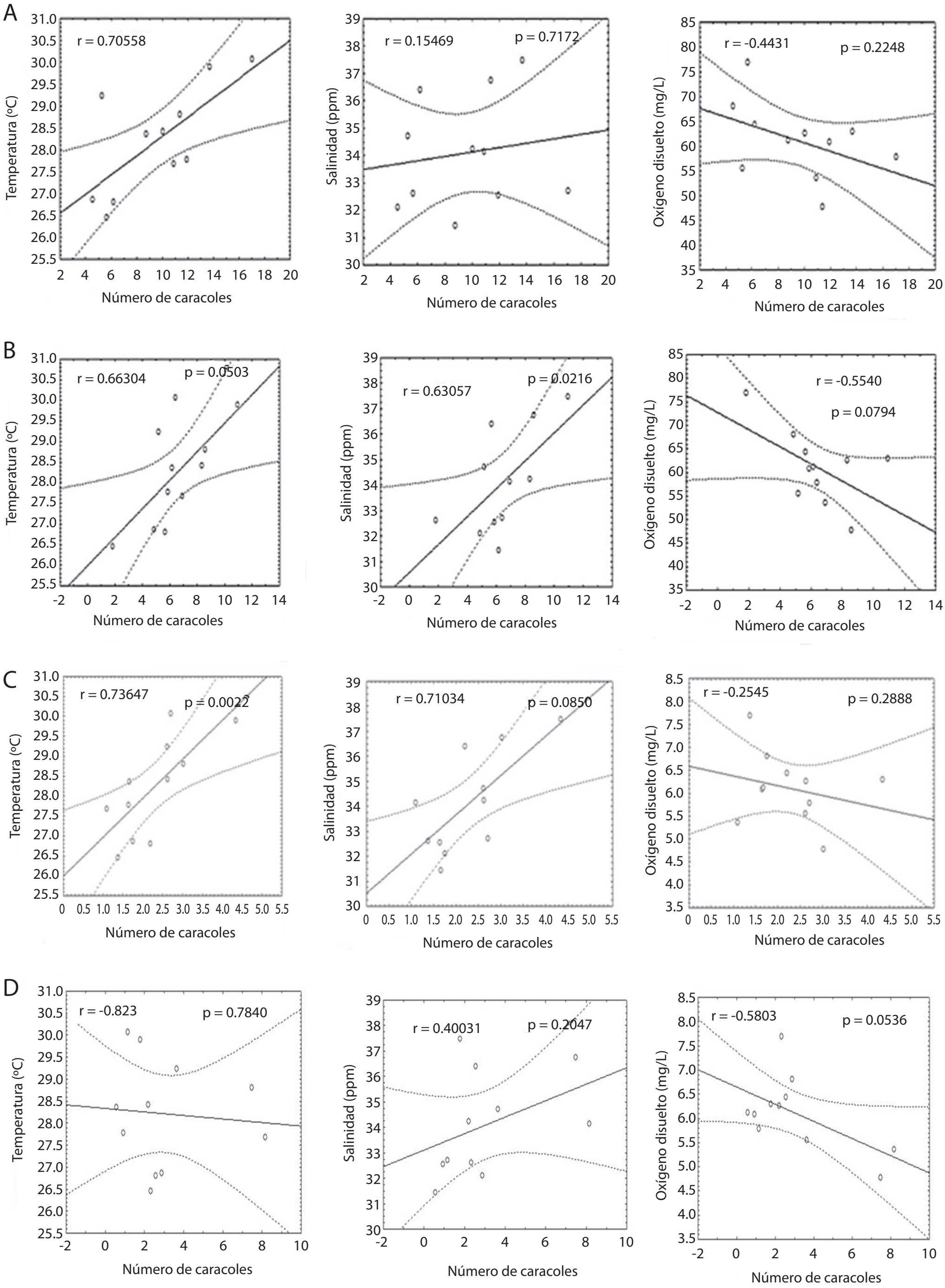

Fig. 3. Correlación de los comportamientos en *S. gigas* de reposo (a), alimentación (b), movimiento (c), enterrados (d) con la temperatura**,** salinidad y con oxígeno disuelto.

Fig. 3. Correlation of behavior of *S. gigas* (a), resting, b) feeding, c) moving, d) buried with temperature, salinity and dissolved oxygen.

descrito por Stoner y Ray-Culp (2000). Entre la alimentación y el movimiento existe una relación directa, por lo que se afirma que el caracol requiere desplazarse para alimentarse, presentando un ciclo diurno en su alimentación con dos picos de ingesta: 12-17h y otro nocturno (22h) ésta observación concuerda con lo reportado por De Santis (1982) que observa un aumento de la actividad alimentaría en paralelo con un incremento de la motilidad. Randall (1964) reportó que *S. gigas* se alimenta todo el día sin precisar la metodología empleada. De Santis (1982) en el archipiélago de los Roques Venezuela, observa cuatro picos en la alimentación: 8am, 12pm, 2pm y 4-5pm. En éste estudio se encontró que la alimentación y el movimiento presentan un pico entre 12–5pm, señalando que las curvas de inactividad (reposo/enterrados) son imagen especular de las curvas de actividad (movimiento/alimentación).

Orr y Berg (1987) reportan que el movimiento de *S. gigas* depende de la temperatura y que éste es mayor durante los meses cálidos; lo cual coincide con lo observado en éste trabajo, con correlación positiva alta entre temperatura con alimentación y movimiento. El conocimiento del patrón del comportamiento de *S. gigas* obtenido en este trabajo es el primero en que se realiza para una serie de tiempo con observaciones temporales en un ciclo diurno y mensual durante todo un año. Es un aporte además original, dónde esta investigación aporta información valiosa al conocimiento de la ecología y la etología de *S. gigas*, siendo esta útil para los programas de conservación y restauración de poblaciones en áreas marinas protegidas y para su cultivo, en las fases de engorde de juveniles y maduración reproductiva de adultos en sistemas de encierros.

AGRADECIMIENTOS

Al proyecto INNOVATEC-CONACYT No. 183724 "Sistemas de información geográfica para la conservación del patrimonio del Caribe y el desarrollo sustentable del Parque Xel-Há". A CONACYT por la Beca de maestría 2011-2013, No.: 271214. A la infraestructura del laboratorio de Biología y cultivo de moluscos CINVESTAV IPN Unidad Mérida y a su equipo por el apoyo en los muestreos (Manuel Sánchez Crespo, Luis Alfonso Ascencio Aguirre, José Francisco Chávez Villegas, Nuria Estrada Saldívar, Irma Pérez García, Wendy González López, Alejandro Aldana Moreno y Francisco Gameros Escoto). Al Parque Xel-Há por su apoyo logístico y operacional y facilidades brindadas durante los muestreos.

RESUMEN

El caracol rosa *Strombus gigas* tiene importancia pesquera en el Caribe, cuyas poblaciones se encuentran sobreexplotadas. Desde la década de 1980 se han desarrollado estudios de acuacultura, manejo del recurso y rehabilitación de áreas con la finalidad de proteger e incrementar sus poblaciones. Sin embargo, poco se sabe sobre el comportamiento del caracol rosa en su medio natural y la influencia de los parámetros ambientales. Mensualmente de enero a noviembre de 2012 en la caleta de Xel Há se observaron y cuantificaron seis comportamientos de *S. gigas*: reposo, alimentación, movimiento, cópula, enterrados y desove. Las observaciones se realizaron cada hora de 8h a 17h por medio de buceo libre en tres transectos con tres repeticiones cada uno. Cada comportamiento fue observado 90 veces cada mes. Se registraron datos de salinidad, temperatura y oxígeno disuelto en el fondo. El comportamiento anual de *S. gigas* presentó el mayor número de caracoles en reposo en julio. La alimentación y el movimiento tuvieron un máximo en agosto. La mayoría de caracoles enterrados se encontró en octubre y noviembre. La cópula comenzó a observarse en marzo con un máximo en junio y el desove de julio a octubre. En las observaciones diurnas e independientemente de los meses, el reposo tuvo un pico a las 8h, alimentación a las 12 y movimiento a las 17h. La cópula y el desove no presentaron un patrón en su comportamiento. Existieron variaciones significativas entre meses y horas (reposo, alimentación, movimiento y enterrado) ($p<0.05$). El reposo se correlacionó con la temperatura y los enterrados con el oxígeno ($r=-0.5803$; $p=0.0536$). La alimentación con temperatura, salinidad y oxígeno. El movimiento con temperatura y salinidad. Estos resultados son útiles para programas de conservación, restauración y cultivo de la especie.

Palabras clave: caracol rosa, comportamiento, conservación, alimentación, desove, movimiento.

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Abundancia y diversidad larval de gasterópodos en el Caribe Mexicano en relación con la temperatura, la salinidad y el oxígeno disuelto

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Recibido 24-VIII-2013 Corregido 12-III-2014 Aceptado 02-IV-2014

Abstract: Abundance and larval diversity of gastropods in the Mexican Caribbean in relation with temperature, salinity and dissolve oxygen. Quintana Roo has over 500 species of gastropods but little is known of the larval stages. We sampled four sites monthly from January to December 2008 with plankton tows in triplicate and a conical net of 300μm mesh. Puerto Morelos had the highest records (41.26±63.23 larvae·10m^{-3}), followed by Mahahual (14.78±28.21 larvae·10m^{-3}); Sian Ka'an and Xel-Ha had the lowest densities (9.16±16.73 and 3.35±4.33 larvae·10m^{-3}, respectively). May and August had the highest records (33.66±67.39 and 31.78±25.92 larvae·10m^{-3}, respectively), March and December the lowest (1.70±1.88 and 3.18±5.27 larvae·10m^{-3}, respectively). There were differences in the spatial mean density ($p < 0.0001$) and time ($p = 0.0275$). We identified 33 species, genera *Strombus, Natica, Cerithium, Nassarius, Neritidae, Cerithiopsis, Nannodiela, Rissoina, Bulla, Bittium, Modulus* and *Prunum*, of which 28 species were recorded in Puerto Morelos. *Natica, Epithonium* and *Cerithium* had the highest incidence in the four locations. Rev. Biol. Trop. 62 (Suppl. 3): 223-230. Epub 2014 September 01.

Key words: larvae, gastropods, composition, Mexican Caribbean.

Las larvas de organismos marinos como indicadores biológicos permiten conocer el estado de salud y potencial reproductivo de las poblaciones adultas (Scheltema, 1971; Sale et al., 2010). Quintana Roo tiene más de 500 especies de gasterópodos descritas (Vokes & Vokes, 1983), sin embargo se sabe muy poco de las etapas larvales (de Jesús Navarrete & Aldana Aranda, 2000).

Scheltema (1971) brinda las primeras observaciones de los factores de dispersión larval, corrientes y la identificación de diez especies de gasterópodos de aguas tropicales y templadas del Atlántico Norte. Para el Caribe Mexicano, Oliva Rivera y de Jesús Navarrete (2000) identificaron 27 especies de gasterópodos para la zona sur de Quintana Roo, México (Banco Chinchorro y Punta Gavilán) y norte de Belice (Reserva de la Biosfera de Hol-Chan). Valtierra Vega, de Jesús Navarrete y Oliva Rivera (2000), quienes identificaron 36 especies para la costa centro del estado de Quintana Roo y por último Oliva Rivera y de Jesús Navarrete (2007) reportan 31 especies para la zona sur de Q. Roo.

Actualmente no existen estudios que incluyan al norte del Caribe Mexicano (CM) en la descripción de la composición del conjunto ("ensamble") larval de gasterópodos, por dicha razón, el objetivo principal de este estudio fue conocer la distribución, abundancia y diversidad larval de gasterópodos en el CM.

MATERIALES Y MÉTODOS

Área de estudio: Cuatro sitios ubicados a lo largo de la costa del Caribe Mexicano fueron seleccionados a fin de conocer la diversidad larval de gasterópodos y su variación estacional en esta región. El primero de los sitios es Puerto Morelos, cuya ubicación geográfica es 20°49’21”-20°51’21”N y 86°51’50”-86°52’45”W; el segundo es Xel-Há, localizado en las coordenadas 20°18’51”-20°19’00”N y 87°21’20”-87°21’25”W; el tercer sitio es Sian Ka’an, localizado geográficamente entre los 19°44’28”-20°00’58”N y 87°27’10”-87°28’10”W; el cuarto es Mahahual ubicado entre los 18°42’15”-18°42’57”N y 87°42’10”-87°42’30”W (Fig. 1).

Muestras: Se realizaron tres arrastres superficiales en cada sitio de muestreo, empleando una embarcación con motor fuera de borda a una velocidad constante de 5m·min. La duración del arrastre fue de 5 minutos a una profundidad de 1m, empleando una red cónica de 30cm de diámetro de boca, 1.5m de largo y una abertura de malla de 300µm. Los muestreos se realizaron entre la línea costera y la barrera arrecifal de cada sitio con excepción de Xel-Há. A la par de los monitoreos, mensualmente se realizaron registros de temperatura (°C), salinidad (ppm) y de oxígeno disuelto (mg·L^{-1}), empleando un medidor de parámetros YSI-55.

El análisis de muestras se realizó en el Laboratorio de Biología y Cultivo de Moluscos del CINVESTAV-IPN, Unidad Mérida. Las muestras fueron filtradas a 80µm a fin de eliminar el exceso de formol. Posteriormente se realizó la separación y conteo de larvas empleando un microscopio estereoscópico Leica Zoom 2000, las larvas fueron preservadas en alcohol al 70%. Las larvas de gasterópodos fueron identificadas utilizando las guías de identificación de Thiriot Quievreux (1983), Davis et al. (1993) y Oliva Rivera y de Jesús Navarrete (2000 y 2007). Fueron tomadas imágenes de las larvas mediante Microscopía Electrónica de Barrido en el Laboratorio de Microscopía Electrónica del Cinvestav-IPN, Mérida.

Análisis de datos: Para estimar la densidad larval en los sitios muestreados se estandarizaron los resultados obteniendo un volumen de larvas·10m^{-3}, dicho resultado se obtuvo empleando la siguiente fórmula:

$$\text{Biomasa (larvas}\cdot 10\text{m}^{-3}\text{)}: [\text{N° Organismos / Volumen (m}^{-3}\text{)}]*10$$

Se empleó el programa InfoStat Profesional/Versión 1.1 para calcular media y

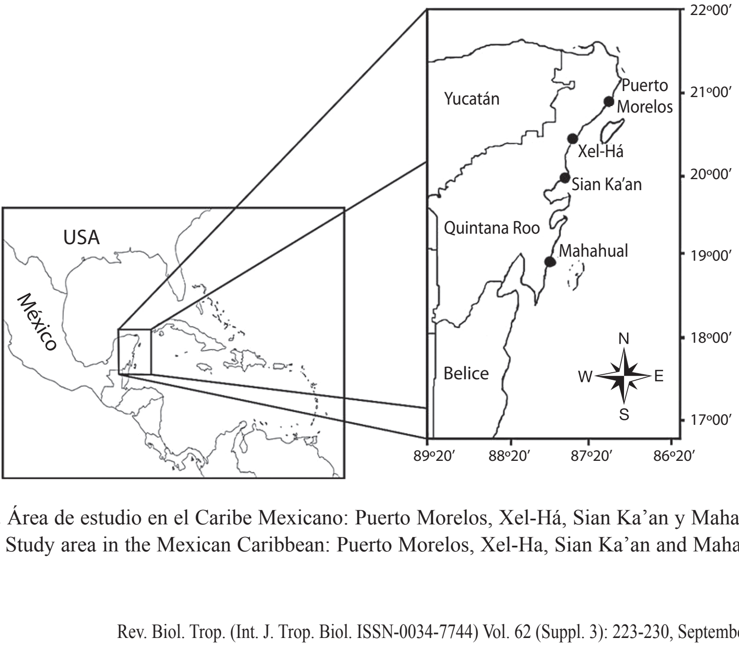

Fig. 1. Área de estudio en el Caribe Mexicano: Puerto Morelos, Xel-Há, Sian Ka’an y Mahahual.
Fig. 1. Study area in the Mexican Caribbean: Puerto Morelos, Xel-Ha, Sian Ka’an and Mahahual.

desviación estándar, análisis de varianza de una vía y prueba de comparación de medias de *Tukey* para la densidad larval y parámetros fisicoquímicos entre localidades y tiempo, asimismo, se realizó una correlación de *Pearson* entre parámetros fisicoquímicos y densidad larval.

RESULTADOS

Parámetros fisicoquímicos: El valor medio de *Salinidad* (ppm) fue 32.80±4.99ppm; en junio y septiembre se presentaron las máximas salinidades (34.52±1.19 y 34.50±0.87ppm, respectivamente) y en diciembre la menor (31.24±8.41ppm).

La salinidad mensual por localidad fue constante en el tiempo para Mahahual, Sian Ka'an y Puerto Morelos (35.00ppm), mientras que Xel-Há presentó variación anual (32.40ppm en junio y 16.20ppm en diciembre). Salinidad fue significativamente diferente solo entre localidades ($p_{(\alpha 0.05;\ g.l.\ 4:44)}$: <0.0001), siendo diferente Xel-Há (*Tukey*: ≤0.05).

La temperatura media fue de 27.02±1.43°C. El análisis de varianza de una vía no mostró diferencias significativas en la temperatura media entre localidades ($p_{(\alpha 0.05;\ g.l.\ 4:44)}$: 0.2720), pero si en el tiempo ($p_{(\alpha 0.05;\ g.l.\ 11:44)}$: 0.0002) siendo diferente los valores registrados durante julio (*Tukey*: ≤0.05).

La concentración media de oxígeno disuelto ($mg\cdot L^{-1}$) fue de 5.64±1.98$mg\cdot L^{-1}$, con mayores registros de marzo a abril (7.82±0.33 y 7.68±0.38$mg\cdot L^{-1}$, respectivamente) y menores en octubre (3.68±0.52$mg\cdot L^{-1}$). El Oxígeno disuelto no mostró diferencias significativas entre localidades ($p_{(\alpha 0.05;\ g.l.\ 4:44)}$: 0.8835), pero si en el tiempo y tiempo ($p_{(\alpha 0.05;\ g.l.\ 11:44)}$: <0.0001) diferencias marcadas por el período marzo-mayo (*Tukey* : ≤0.05).

Abundancia espacial y temporal de gasterópodos: La densidad media de larvas ($larvas\cdot 10m^{-3}$) de gasterópodos para las cuatro localidades del CM varía por localidad (Fig. 2). Puerto Morelos tuvo los mayores registros (41.26±63.23 $larvas\cdot 10m^{-3}$), seguido por Mahahual (14.78±28.21 $larvas\cdot 10m^{-3}$), mientras que Sian Ka'an y Xel-Há presentaron las menores densidades (9.16±16.73 y 3.35±4.33 $larvas\cdot 10m^{-3}$, respectivamente). El análisis de varianza registró diferencias significativas en la densidad media entre localidades ($p_{(\alpha 0.05;\ g.l.\ 4;167):}$ <0.0001) Siendo estadísticamente diferente la localidad de Xel-Há (*Tukey* : ≤0.05).

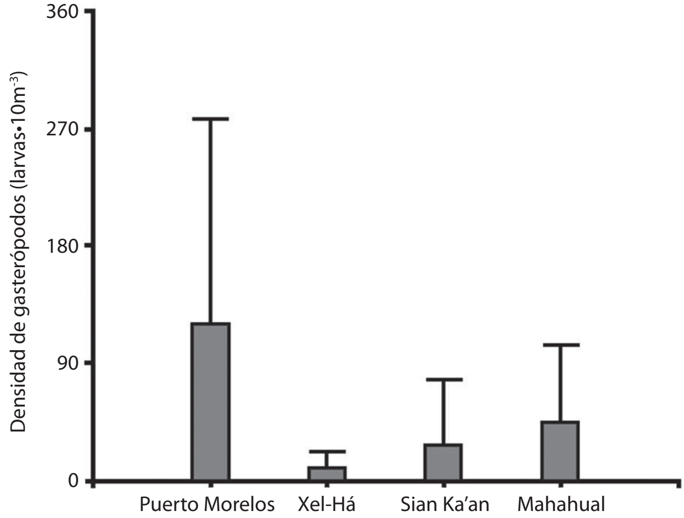

Fig. 2. Densidad media larval de gasterópodos en el Caribe Mexicano.
Fig. 2. Average larval density of gastropods in the Mexican Caribbean.

La densidad media (larvas·10 m^{-3}) de gasterópodos varia en espacio y tiempo (Fig. 3). Las mayores densidades se presentaron de junio a septiembre. En Puerto Morelos los mayores registros se observaron en abril y mayo (129.35±41.83 y 150.90±76.31 larvas·10m^{-3}), n Xel-Há durante julio y septiembre (8.87±5.96 y 12.98±2.45 larvas·10m^{-3}), para Sian Ka'an las densidades fueron de 59.60±4.62 y 13.59±11.77 larvas·10m^{-3} en agosto y septiembre, respectivamente, mientras que en Mahahual las mayores densidades se observaron en junio y agosto (61.78±83.48 y 47.65±5.17 larvas·10m^{-3}).

El análisis de varianza mostró diferencias significativas para tres localidades ($p \leq 0.0001$) con excepción de Mahahual donde se obtuvo un valor de $p_{(\alpha 0.05;\ g.l.\ 11;24)} = 0.0850$). Temperatura y salinidad fueron las variables que muestran una correlación significativa, sin embargo la salinidad (r= 0.6307; p< 0.0001) muestra una correlación más robusta con la disponibilidad de larvas que la temperatura (r= 0.3840; p= 0.2720) (Cuadro 1).

Diversidad estacional y espacial: El cuadro 2 y figura 4 (a, b y c) muestran la diversidad larval de gasterópodos en el CM. Se registró un total de 34 especies correspondientes a 22 géneros. La mayor diversidad de larvas se registró durante la temporada de lluvias con 25 especies, seguida de nortes (12 especies). La localidad con mayores registros de larvas fue Puerto Morelos con 28 especies, mientras que Xel-Há presentó la menor diversidad (14 especies).

Los géneros con mayor número de especies en el CM fueron *Natica* (con cinco especies) y *Epithonium* con tres especies. 23.52%

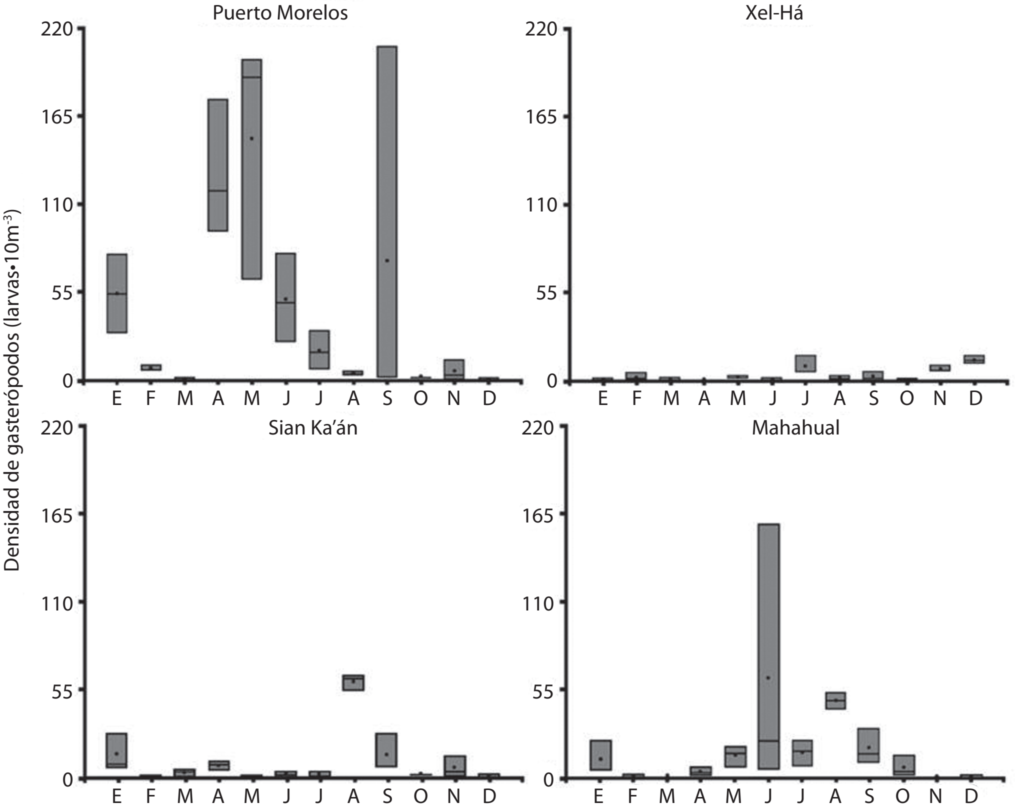

Fig. 3. Densidad media mensual de larvas de gasterópodos en el Caribe Mexicano.
Fig. 3. Monthly average density of gastropods larvae in the Mexican Caribbean.

CUADRO 1

Medias y Análisis de correlación de Pearson (r) entre parámetros fisicoquímicos (Salinidad: ppm; temperatura: °C; Oxígeno disuelto: $mg{\cdot}L^{-1}$) y densidad larval de gasterópodos ($larvas{\bullet}10\ m^{-3}$) en el Caribe Mexicano

TABLE 1

Media and Pearson correlation analysis (r) among physicochemical parameters (Salinity: ppm; temperature: °C; dissolved oxygen: $mg{\bullet}L^{-1}$) and gastropod larval density ($larvae{\bullet}10\ m^{-3}$) in the Mexican Caribbean

Parámetro	Localidades				Media(n= 48)	r	p
	Puerto Morelos	*Xel-Há*	*Sian Ka'an*	*Mahahual*			
ppm	35.01	23.76	35	34.96	32.7	0.6307	0.000016
	±0.05	±5.27	±0.00	±0.13	±5.00		
°C	26.43	27.48	26.51	27.18	26.85	0.3840	0.2720
	±1.59	±1.31	±1.53	±1.94	±1.60		
$mg{\cdot}L^{-1}$	5.47	5.71	5.34	5.84	5.6	0.2197	0.0900
	±1.48	±1.06	±1.43	±1.40	±1.34		
$Larvas{\cdot}10\ m^{-3}$	41.26	3.35	9.16	14.78	50.56	1.000	1.000
	±63.23	±4.33	±16.73	±28.21	±90.05		

de las especies registradas se distribuyen de Norte a Sur en las cuatro localidades de estudio, mientras que sólo 12.50% se encuentra solo en la zona Norte.

DISCUSIÓN

Stoner, Sandt y Boidron Metairon (1992) y de Jesús Navarrete (1999) señalan que la temperatura se asocia a la abundancia larval de gasterópodos, sin embargo de Jesús Navarrete (1999) no encontró una relación ente la abundancia larval y parámetros fisicoquímicos. Pacheco Archundia (2007) y Chávez Villegas (2011) señalan que la salinidad (ppm) influye en la distribución y densidad larval de gasterópodos, concretamente de *S. gigas*, lo cual concuerda con lo registrado en el presente estudio donde la salinidad se asoció en un 63% con la presencia de larvas en el CM.

La comparación de la diversidad planctónica de gasterópodos en la zona resulta difícil, debido a la escasez de trabajos realizados. En el sur del CM Oliva Rivera y de Jesús Navarrete (2000) registraron 27 especies, Valtierra Vega et al. (2000) reportan 36 especies y Oliva Rivera y de Jesús Navarrete (2007) registraron 31 especies en la zona sur de Quintana Roo y norte de Belice. Chávez Villegas (2011) señala la presencia de 32 especies de larvas de gasterópodos en el Sistema Arrecifal Mesoamericano, sin embargo no se realiza una identificación a nivel especie de estos organismos.

Actualmente no existen estudios de la diversidad larval de gasterópodos para Puerto Morelos, Sian Ka'an y Xel-Há. Oliva Rivera y de Jesús Navarrete (2000) reportan 11 especies para la costa sur de Quintana Roo (región cercana a Mahahual), de las cuales cinco especies corresponden a las 19 registradas en esta zona (*Rissoina* sp., *Natica* sp., *Mitrella* sp., *Epitonium* sp. *y Cerithium* sp.), asimismo, estos autores reportan una mayor abundancia y diversidad de larvas en la temporada de secas (mayo-junio), lo cual difiere a lo observado en este estudio, donde se registró una mayor diversidad en la temporada de lluvias (julio-octubre).

La mayor presencia y diversidad de larvas en el norte del CM (Puerto Morelos) podría atribuirse al efecto ascendente de las corrientes por el canal de Yucatán, sin embargo Mariño Tapia et al. (2011) señalan un fuerte flujo de corrientes internas en la laguna de Puerto Morelos, lo cual se traduce en una circulación interna de nutrientes y larvas, asimismo Coronado et al. (2007) mencionan que la tasa de intercambio entre la laguna y el océano es baja,

CUADRO 2

Diversidad larval de gasterópodos por Temporada (Secas, lluvias y nortes) y localidades en el caribe Mexicano

TABLE 2

Diversity larval gastropods by season (Dry, rain and north wind) and localities in the Mexican Caribbean

Especie	Temporada			Localidades			
	Secas (Mar-Jun)	Lluvias (Jul-Oct)	Nortes (Nov-Feb)	Puerto Morelos	Xel-Há	Sian Ka'an	Mahahual
Alaba incerta		X		X	X		X
Bittium sp. 1		X		X			
Bittium sp. 2		X			X	X	X
Bulla striata		X		X			
Bulla sp.		X			X	X	X
Cerithiopsis hero			X	X	X	X	X
Cerithium atratum		X		X			
Cerithium sp.		X		X	X	X	X
Choristes tenera	X			X		X	
Cyclostremiscus schrammii		X	X	X			
Epithonium albidum		X		X	X	X	X
Epithonium krebssi	X	X	X	X		X	
Epithonium lamellosum		X			X		
Euchelus guttarosea			X	X			
Mitrella lunata		X		X		X	
Modulus modulus	X	X		X		X	
Nassarius albus		X	X	X		X	X
Nassarius sp.		X		X	X	X	X
Natica canrena			X	X			X
Natica cayenensis	X			X	X		
Natica lívida		X		X			
Natica pusilla	X	X	X	X			X
Natica sp.	X			X	X	X	X
Nitidella nítida		X		X			
Odostomia solidula		X				X	X
Parviturboides interruptus		X				X	
Pseudostomatella coccinea			X	X		X	X
Rissoina multicostata		X		X			
Rissoina sp.		X	X	X	X	X	X
Sinum maculatum		X	X	X	X	X	X
Sinum perspectivum		X	X	X		X	X
Teignostoma megastoma		X			X	X	X
Triphora nigrocincta			X	X	X	X	X
Strombus gigas	X	X		X		X	X
n	7	25	12	28	14	21	19

lo cual sugiere que los organismos encontrados en la región provienen de la población de adultos de la localidad.

Con este trabajo se asume que los sitios estudiados en el CM, especialmente los situados en la zona norte, actúan como fuente de larvas de gasterópodos, siendo sitios importantes para preservar la diversidad larval en la región.

Con base en los resultados obtenidos podemos determinar que existe un significativo

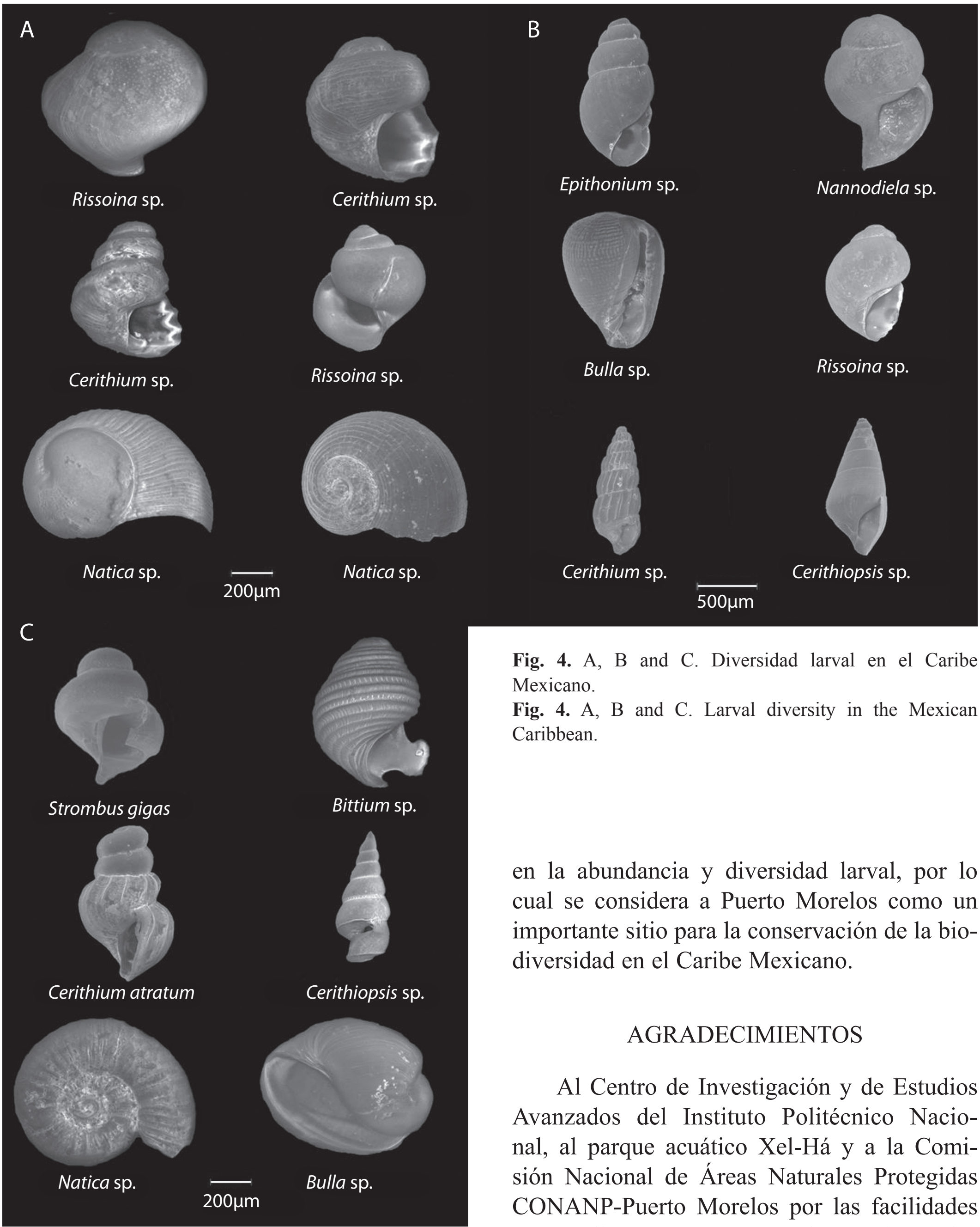

Fig. 4. A, B and C. Diversidad larval en el Caribe Mexicano.
Fig. 4. A, B and C. Larval diversity in the Mexican Caribbean.

efecto de la salinidad sobre la diversidad larval de gasterópodos en el Caribe Mexicano determinado por la presencia de lluvias, época en la que se presenta la mayor diversidad y abundancia larval. Se observó un gradiente (Norte-Sur) en la abundancia y diversidad larval, por lo cual se considera a Puerto Morelos como un importante sitio para la conservación de la biodiversidad en el Caribe Mexicano.

AGRADECIMIENTOS

Al Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, al parque acuático Xel-Há y a la Comisión Nacional de Áreas Naturales Protegidas CONANP-Puerto Morelos por las facilidades para realizar este proyecto. Al Consejo Nacional de Ciencia y Tecnología (Conacyt) por financiar este proyecto y por la beca N° 240157 otorgada a JF Chávez Villegas y al proyecto “Variación espacio temporal del patrón reproductivo del caracol rosado *Strombus gigas* en diferentes hábitats y su modelo biofísico de conectividad para el Caribe" (Clave: 50094) por financiar esta investigación. A Dora Huerta y Ana Cristóbal del Laboratorio de Microscopia Electrónica del Cinvestav-IPN por su apoyo en la toma de imágenes.

RESUMEN

Quintana Roo tiene mas de 500 especies de gasterópodos pero muy poco se conoce de los estadios larvales. Muestreamos cuatro sitios mensualmente de enero a diciembre de 2008 con arrastres de plancton por triplicado y con una red cónica con malla de 300μm. Puerto Morelos tuvo los mayores registros (41.26±63.23 larvas·$10m^{-3}$), seguido por Mahahual (14.78±28.21 larvas·$10m^{-3}$), Sian Ka'an y Xel-Há presentaron las densidades menores (9.16±16.73 y 3.35±4.33 larvas·$10m^{-3}$, respectivamente). Mayo y agosto presentaron los mayores registros (33.66±67.39 y 31.78±25.92 larvas·$10m^{-3}$, respectivamente), marzo y diciembre los menores (1.70±1.88 y 3.18±5.27 larvas·10 m^{-3} respectivamente). Se registraron diferencias significativas en la densidad media espacial (p:<0.0001) y temporal (p: 0.0275). Identificamos un total de 33 especies de gasterópodos de los géneros *Strombus, Natica, Cerithium, Nassarius, Neritidae, Cerithiopsis, Nannodiela, Rissoina, Bulla, Bittium, Modulus* y *Prunum,* de las cuales 28 especies se registraron en Puerto Morelos. *Natica, Epithonium* y *Cerithium* fueron los géneros con mayor incidencia en las cuatro localidades.

Palabras clave: Larvas, gasterópodos, composición, Caribe Mexicano.

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Rapid reassessment of the eutrophication status of Kingston Harbour, Jamaica using the zooplankton community

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Received 01-IX-2013 Corrected 31-III-2014 Accepted 01-IV-2014

Abstract: Previous extensive studies of zooplankton distribution in the eutrophic Kingston Harbour established that it was being continuously contaminated. We assessed the community in 2011, 17 years after a previous study and five years after the introduction of a tertiary waste water system. Sampling was conducted for four weeks at eight stations identical to those sampled in a previous study. We used horizontal surface tows with a 200µm net. A total of 73 zooplankton taxa were identified and copepods dominated with 20 species. Mean total abundances were high, ranging from a minimum of 2 383 animals m^{-3} in the southern region of Hunts Bay to 194 166 animals m^{-3}at the Inner Harbour. Five zooplankton taxa (*Acartia tonsa, Paracalanus spp., Temora turbinata, Penilia avirostris* and *Lucifer faxoni*) that were previously identified as indicators, were again important in the Harbour. The overall zooplankton abundances were similar and in some cases higher than the previous study. There was no significant improvement in the water quality since the introduction of the treatment system at Soapberry. This may be a result of unknown nutrient inputs or of nutrient remaining in the sediments. Rev. Biol. Trop. 62 (Suppl. 3): 231-239. Epub 2014 September 01.

Key words: Kingston Harbour, zooplankton, rapid assessment, waste-water, eutrophic.

Previous extensive studies of zooplankton distribution in the eutrophic Kingston Harbour established that the harbor was being continuously contaminated (Grahame, 1974; Dunbar, 1997). Based on the different zooplankton communities, the harbor was zoned with the Upper Basin and Hunts Bay being the most eutrophic, the Inner Harbour, showing less contamination and the Outer Harbour least eutrophic (Dunbar, 1997; Dunbar & Webber, 2003). Dunbar recommended on-going monitoring of Kingston Harbour water quality using the zooplankton indices: total abundances, total number of species and the number of the "indicator" species especially at stations representing the previously defined zones. Since these recommendations, one key change has occurred through the implementation of centralized tertiary sewage treatment system for the city of Kingston; located at Soapberry in St. Catherine. The aim was to "significantly reduce pollution in Kingston Harbour and thus redress the existing environmental concerns" (Urban Development Corporation, 2006). The construction of a cross-island highway system- "Highway 2000" which involved extensive mangrove removal as well as reclamation and dredging of parts of Hunts Bay to expand the container shipment terminal by the Port Authority of Jamaica are the other two major changes which have occurred since the previous extensive study in the 1990's.

Approximately 17 years have passed since the 1990's study and with the changes as described above; a rapid assessment was needed to determine whether Kingston Harbour water quality had begun to improve and required a new baseline. It was hypothesized that areas closest to the Soapberry outfall (Hunts Bay) as well as areas closest to the previous sewage plants (Inner Harbour) would first experience change in eutrophication status and thus in the zooplankton community.

The objectives of the study were therefore to determine zooplankton abundance and species composition in representative areas of Kingston Harbour and to compare these to abundance and species found 17 years ago at the same stations.

MATERIALS AND METHODS

Station selection: Eight stations were selected throughout the Kingston Harbour between 17°57’ 14.0” N and 76° 48’13.33”W. The stations were identical (Fig. 1, Table 1) to those sampled by Dunbar (1997) and Ranston (1998) and represented each of the zones identified by Dunbar & Webber (2003). Sampling was conducted for four weeks between May 21, 2011 and June 9, 2011.

Zooplankton collections: *Outer, Upper and Inner Harbour*- Zooplankton collections were made with a SCOR, WP2 pattern 20µm plankton net with a hoop diameter of 0.5m (United Nations Educational, Scientific and Cultural Organization [UNESCO], 1968). Horizontal surface tows were conducted in a circular path at approximately 1knot (0.5ms^{-1}). Each tow lasted for two minutes with the net kept just below the surface of the water. Flow meter readings were taken before and after each tow using a calibrated (one revolution= 0.048m) General Oceanics flow meter which hung in the mouth of the net. This replicated the sampling method employed by the previous baseline study (Dunbar & Webber, 2003).

Hunts Bay-Replicate zooplankton samples were collected at each station using a 100µm mesh aperture net with a 12.5cm hoop diameter. Replicate oblique or vertical hauls were done at each station through the water column. The net with attached weight and rope (marked at 1m intervals) was hand-thrown as far as possible from the boat. It was allowed to sink far

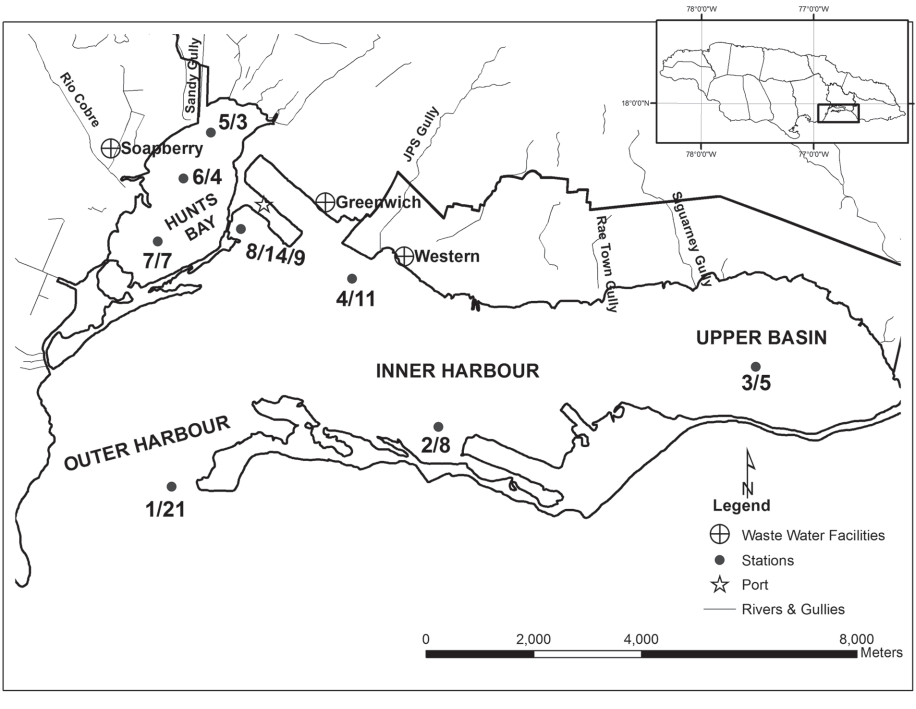

Fig. 1. Study area showing the location of sampling stations.

TABLE 1
Location of stations sampled in present and past studies (Fig. 1)

Kingston Harbour Representative Zone	Current Study	Dunbar 1997	Ranston 1998	GPS coordinates
Outer Harbour-Harbour Shoal Beacon (HSB)	Station 1	Station 21		N 17°56'101" • W76°50'927"
Inner Harbour Port Royal Mangrove (IHM)	Station 2	Station 8		N17°56'657" • W76°48'639"
Upper Basin (UB)	Station 3	Station 5		N 17°57'337" • W 76°45'638"
Inner Harbour Shipping Channel (SC)	Station 4	Station 11		N17°58'129" • W76°49'218"
North Bay (NB)	Station 5		Station 3	N17°59'279" • W76°50'464"
Middle Bay (MB)	Station 6		Station 4	N17°58'471" • W76°50'499"
South Bay (SB)	Station 7		Station 7	N17°58'332" • W76°51'920"
Hunts Bay Bridge (HBB)	Station 8	Station 14	Station 9	N17°58'597" • W76°50'418"

enough below the surface then an oblique/vertical haul was done at a steady pace at approximately $2ms^{-1}$ at the total distance hauled with this net was at least 8m. With this deployment the net sampled both the upper fresh water and lower more saline layers of the water column without disturbing the soft sediment at the bottom of the bay. This replicated the sampling method employed during the previous sampling of Hunts Bay by Ranston (1998).

Samples at each station were immediately fixed in the field using 10ml of full strength formalin (37% formaldehyde) and later preserved in 10% formalin. The volume of sea water filtered was calculated using the formula $\pi r^2 h$, where 'r' is the radius of the hoop of the plankton net and 'h' is distance towed; determined by the number of revolutions of the calibrated flow meter. The filtering efficiency (FE) of each net was applied to the volume calculations based on FE values generated from studies done by Dunbar (1997).

Identification and counting of the zooplankton were conducted on preserved sub-samples obtained using the beaker split method (Van Guelphen, Markle, & Duggan, 1982; Webber, Roff, Chisholm, & Clarke, 1996; Dunbar, 1997). Each sub-sample was transferred to a Bogorov tray and counted using a Wild M5/M7 Binocular Microscope. The taxonomic guides employed to identify the animals included: Davis (1955), Gonzales and Bowman (1965), Wickstead (1965), Owre and Foyo (1967), Newell and Newell (1977), Ramirez and Zamponi (1981), Michel (1984), Campos–Hernández and Suárez-Morales (1994), Todd, Laverack and Boxshall (1996) and Webber (2004). The numbers of each species were converted to numbers per m^3 using the formula and the relevant dilution factors. All samples were pseudo-replicated.

Physico-chemical data were collected at each station on each sampling occasion using a Hydrolab® Surveyor DS5. These included depth (±0.08m); Temperature (±0.15°C); Salinity (±0.1ppt); pH (±0.2 units); dissolved oxygen (±$0.2mgl^{-1}$).

Statistical analysis: Two tailed t-tests were applied to normally distributed physio-chemical and biological data to determine if there were significant differences between the present and previous studies.

RESULTS

Variation in physico-chemical parameters: Temperature, Salinity and Dissolved Oxygen were the primary physico-chemical parameters which varied significantly across the Harbour. The variations in temperature were minimal with values ranging from 28°C at Outer Harbour to 31ºC at Hunts Bay. The greatest temperature was recorded at the Hunts Bay stations 5 to 7. Temperatures recorded in 2011were not significantly different from those recorded in 1994.

In both studies, Hunts Bay stations 5 to 8 had the lowest salinity values (Fig. 2B), while

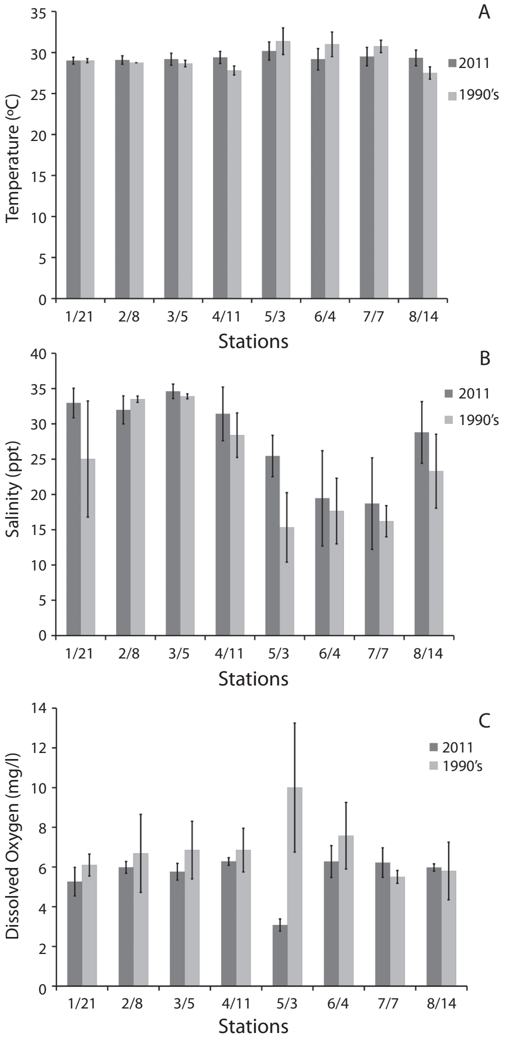

Fig. 2. Mean (±1SE) physicochemical parameters sampled in the 1990's and 2011 studies. (A) Temperature, (B) Salinity and (C) Dissolved Oxygen. Vertical bar denotes standard errors.

Outer Harbour, Inner Harbour and Upper Basin stations (1 to 4) had greatest salinity values. Low salinity is indicative of fresh water inputs from the Rio Cobre, Duhaney River and Sandy Gully. The salinity values in 2011 were shown to be significantly higher than those of the previous study.

Higher Dissolved Oxygen (D.O.) readings were recorded in the 1994 study at all except stations 7 and 8 (Hunts Bay) where the 2011 study had slightly higher dissolved oxygen readings. The lowest DO reading for 2011 was recorded at station 5/3 in Hunts Bay. This is the opposite to the findings of the previous study where that station recorded the highest DO value. The two t-test revealed no significant difference in dissolved oxygen between the studies.

Variation in zooplankton parameters: A total of 73 zooplankton taxa were identified from the eight stations sampled during the present study which is the same amount (73 species) found in the 1994 study of the harbor. Again the copepods were the most dominant group, however only 20 species were recorded, 18 species less than previously (Dunbar, 1997; Dunbar & Webber, 2003). In the present study, eight copepod species were from the order Calanoida, one more than Cyclopoida (seven species) while the Harpacticioda had five species. The second most dominant group after copepods was the group comprised of larvae with 19 species. The average number of species varied significantly (p=0.01, Table 2) between the two studies (Fig. 3). Station 1/21 had the highest average number of species 28 and 35 for the 2011 and 1994 studies respectively. The lowest number of species were found at the Hunts Bay stations with station 6 having the lowest (7 species) for the 2011 study and station 3 (10 species) for the 1994 study.

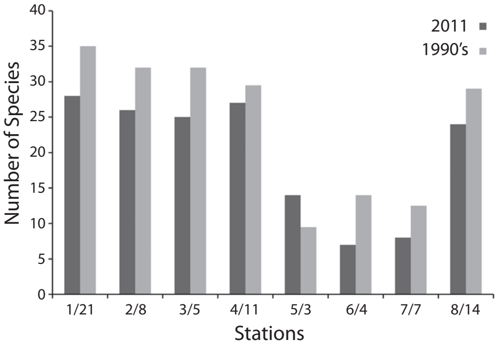

Fig. 3. Number of zooplankton species recorded for the 1990's and 2011 studies.

TABLE 2
Results of the tailed test on physicochemical and biological parameters

Variable	Deg. of Freedom	T-value	P-value
Temperature	7	0.007	0.50
Salinity	7	2.757	**0.01****
Dissolved Oxygen	7	1.577	0.08
No. of species	7	3.134	**0.01****
Total Zooplankton	7	2.252	**0.03***
Acartia sp.	7	1.573	0.08
Penilia avirostris	7	2.649	**0.02***
Temora turbinate	7	0.057	**0.04***
Lucifer faxoni	7	1.000	0.17
Paracalanus spp.	7	1.841	**0.05***

**significance.

Mean zooplankton abundances ranged from 2 383 animals m^{-3} at Station 7 Hunts Bay- South to 194 166 animals m^{-3} at station 4 in the Inner Harbour near the Shipping Channel (SC) for the 2011 study (Fig. 4). In 1994, a minimum value of 381 animals m^{-3} were found at station 4 (middle of Hunts Bay) and maximum of 81 742 at station 8 (near the Port Royal Mangroves). The two-tailed test revealed significantly higher abundances for the 2011 study over the 1994 study (p=0.03), with higher abundances at the Inner Harbour stations (2 and 4) and lower abundances at the Hunts Bay stations (5 to 7). During the present study five indicator species were identified, *Acartia spp.*, *Paracalanus spp.*, *Penilia avirostris, Temora turbinata* and *Lucifer faxoni*. These species had a similar distribution to the mean total zooplankton numbers, with maximum numbers at the airport-mangrove station and minimum numbers at the Hunts Bay stations (Fig. 5). *T. turbinata* was the only species with maximum numbers at the shipping channel station. The 1994 study had *T. turbinata, Paracalanus spp*. and *P. avirostris* showing dominance at the airport-mangrove station while *Acartia spp.* and *Lucifer faxoni* were dominant at the shipping channel station. *T.* turbinata*, Paracalanus spp*. and *P. avirostris* were found to be significantly different between the two studies with *T. turbinata* and *Paracalanus* spp. having higher abundances during 2011 and *P. avirostris* being more abundant in 1994.

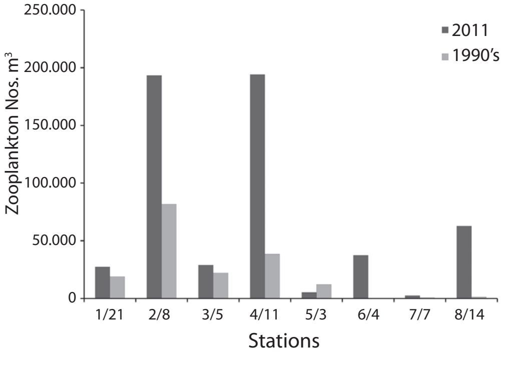

Fig. 4. Mean total number of zooplankton numbers found in the 1990's and 2011 study for at the same stations and for the same months.

DISCUSSION

Although the results showed significant difference in the abundance between the two studies, there was no difference in relative eutrophication levels between zones, based on the zooplankton. Hunts Bay remained the most eutrophic area and the Outer Harbour, the least eutrophic. Although zooplankton abundances at the pairs of Hunts Bay stations were higher in the present study than in previous study in 1994, the abundances were low in comparison to the other areas of the Harbour. Webber and

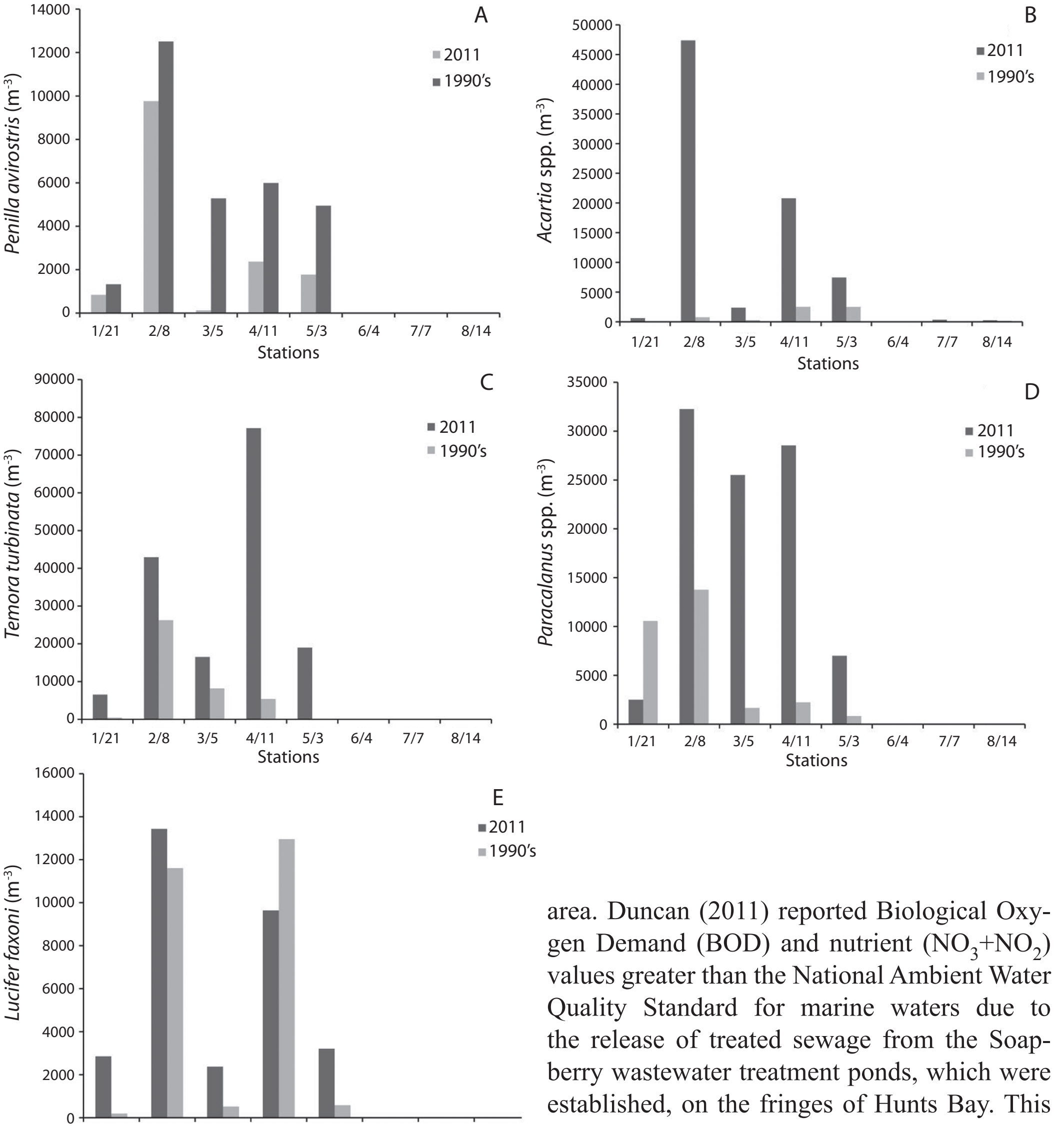

Fig. 5. Mean total numbers of indicator species. (A) *Penilia avirostris*, (B) *Acartia spp*., (C) *Paracalanus spp*., (D) *Temora turbinata* and (E) *Lucifer faxoni.*

Wilson-Kelly (2003) suggested that the very poor water quality of Hunts Bay can cause a decline in the zooplankton abundances and species richness. They further concluded that high nutrient and fresh water inputs and proliferation of algal blooms were the main reasons for the decline in the water quality of the Hunts Bay area. Duncan (2011) reported Biological Oxygen Demand (BOD) and nutrient (NO_3+NO_2) values greater than the National Ambient Water Quality Standard for marine waters due to the release of treated sewage from the Soapberry wastewater treatment ponds, which were established, on the fringes of Hunts Bay. This explains the continued low species number at the Hunts Bay stations in comparison to the other stations.

This and other studies (Webber et al. 1996; Dunbar & Webber, 2003) have shown Outer Harbour to be the least eutrophic due to its influence by mesotrophic waters and the introduction of species from the shelf area. The diversity (number of species) found in the Outer Harbour in this present study, though higher than the other sections of the harbor, was lower than that obtained by Dunbar (1997). This was accompanied by increased zooplankton abundances, which are indices of increased eutrophication (McArthur, 1955; Clutter, 1972).

In the 1974 study of the Harbour, Grahame found the plankton community of the Upper basin to be the "most diverse and biologically accommodating, offering the largest number of niches available to the zooplankton in the Harbour". It was therefore expected that the zooplankton community observed in this area would be different from the other areas of the Harbour. The mean abundance for the Upper Basin was higher than what was observed by Dunbar (1997), but lower than adjacent areas of the harbor during the present study. High numbers were also reported by Grahame (1974) in the Upper Basin. This suggests relative stability in the water quality within the Upper Basin, which could be explained by a lack of any major inputs to that area. The upper basin has no major rivers or gullies but is influenced by a series of small gullies (22), which, as shown by Webber and Wilson-Kelly (2003), are only of significance during periods of heavy rainfall.

Like the previous studies (Grahame, 1974; Dunbar, 1997), the Inner Harbour had the greatest zooplankton abundances. High zooplankton abundances were recorded at the airport-mangrove station (2) and the shipping channel station (4). The greatest abundance was recorded at station 4, which is probably due to the proximity to direct sewage inputs caused by the dysfunctional Greenwich sewage treatment plant outflow (Francis, 2011). In a contemporaneous study of the harbor by Duncan (2011), high nutrient levels at this station were reported suggesting that sewage is still flowing through the Greenwich treatment plant, instead of going to Soapberry. An alternative explanation is that the sediments in that area are a continuous source of eutrophication due to several years of continued large scale inputs. This sediment-source will continue to supply nutrients to the water column for several years after the inputs have stopped (Clau, 2004).

The maximum abundance (193 287 animals m^{-3}) found at station 2 (Airport runway/mangroves) is similar to the maximum of 194 248 animals/m^3 reported by Dunbar (1997) for the 1994 study. These values were significantly higher than the mean number recorded by Grahame (1976) of 25 248 animals m^{-3}. The mangrove area is said to be "one of the most productive areas in the Harbour" (Dunbar, 1997). The high abundance of this station could therefore be attributed to the station's proximity to the mangroves.

Conditions within the harbour have not changed significantly since the last baseline conducted 17 years ago by Dunbar (1997) and the implementation of the Soapberry treatment facility five years ago. The most eutrophic area remains within the Hunts Bay as indicated by minimal species diversity and zooplankton abundances. The abundance and diversity within the Upper Basin were lower than the Inner Harbour, suggesting deterioration of the water quality in the Upper Basin. However, overall the Upper Basin area was relatively unchanged. The Outer harbour, while remaining the least eutrophic area of the Kingston Harbour, had higher abundances than in previous studies.

It therefore can be concluded that while changes (slight improvements) have taken place in areas like Hunts Bay, where the new Soapberry sewage treatment system outfall is located; there was no significant improvement in the water quality in the Kingston Harbour since the last baseline study or the introduction of the tertiary sewage treatment system at Soapberry. There either continues to be unregulated nutrient inputs into the harbour or the nutrient loading of the sediments over the last 25-30 years makes them a continued source of nutrients to the water column.

ACKNOWLEDGMENTS

We thank our research partners Sheree Broomfield, Anya Duncan, Helen Liu, Leon Grant and the staff of the Port Royal Marine Laboratory, University of the West Indies (UWI) for their assistance with fieldwork collection. Department of Life Sciences, UWI provided funding for this research.

RESUMEN

Reevaluación rápida del estado de eutrofización del puerto de Kingston, Jamaica utilizando la comunidad de zooplancton. Extensos estudios previos de la distribución de zooplancton en el Puerto de Kingston estableció que ha sido contaminado continuamente. Evaluamos la comunidad en el 2011, 17 años después de un estudio previo y cuatro años después de la introducción de un sistema de lagunas de aguas residuales terciarias. Utilizamos arrastres superficiales horizontalescon una red de 200 µm. Se identificó un total de 73 taxones de zooplancton y copépodos de los cuales los predominaron 20 especies. La media de las abundancias totales fueron altas y los valores oscilaron entre un mínimo de 2 383 animales m^{-3} en la zona sur de Bahía Hunts a 194 166 animales m^{-3} en lo interior del puerto. Cinco taxones de zooplancton (*Acartia tonsa, Paracalanus spp., T. turbinata, Penilia avirostris* y *Lucifer faxoni*) identificados previamente como indicadores, fueron importantes de nuevo en la Bahía. La abundancia total de zooplancton fue similar y en algunos casos superior a la del estudio anterior. No hubo mejoría significativa en la calidad del agua desde la introducción del sistema de tratamiento terciario en Soapberry. Esto puede ser resultado de la entrada continua de nutrientes desconocidos y no regulados en los sedimentos.

Palabras clave: Puerto Kingston, zooplancton, evaluación rápida, aguas residuales , eutrófico.

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Assessing the phytoplankton and water quality of Kingston Harbour and Hellshire coast, Jamaica, after the implementation of a waste water treatment facility

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Received 29-IX-2013 Corrected 12-III-2014 Accepted 24-III-2014

Abstract: Deteriorating water quality of Kingston Harbour, due primarily to sewage discharge and its effect on nearby Hellshire Coast, has been an issue since the 1970s. The implementation of a new sewage treatment facility in 2007 to receive the harbour's waste at Soapberry was expected to make a positive difference. Physico-chemical and biological parameters were used to assess water quality to determine the effect of the facility. Eleven stations used in earlier studies (1990 to 1998) were re-sampled to represent Kingston, Hunts Bay and North East Hellshire coastline over a four week sampling regime between May and June 2011. While temperature, salinity, turbidity, dissolved oxygen and pH remained unchanged between the 1990's and 2011, BOD_5, faecal coliform and nitrate concentrations indicated that the water quality had improved minimally in Kinsgton and Hellshire,and deteriorated significantly in Hunts. Phytoplankton biomass decreased in Kingston (from 3.84 mg m^{-3} in 1998 to 2.81 mg m^{-3} in 2011) and increased significantly in Hunts (from 14.69 mg m^{-3} in 1998 to 24.17 mg m^{-3} in 2011). Biomass along Hellshire was similar (2.15 mg m^{-3} in 1998; 2.45 mg m^{-3} in 2011). In 1998 the nanoplankton biomass (2.7 to 20µm) dominated throughout the Harbour. In 2011 Hunts Bay was dominated by net-plankton (>20µm), indicative of eutrophic waters. Rev. Biol. Trop. 62 (Suppl. 3): 241-248. Epub 2014 September 01.

Key words: Soapberry, waste water, Kingston Harbour, Hunts Bay, Hellshire, eutrophication.

Kingston Harbour on the south east coast of the capital of Jamaica (17º58'N and 76º48'W), is a multipurpose resource with more than a half a million people and a variety of industries at its shores (Wade, 1972). These residencies and industries are the source of large volumes of waste introduced into the Harbour daily (Webber et al., 2003). Historically, the most significant point source contributors of organic pollution to the Harbour were the Greenwich and Western sewage treatment plants discharging 20mgd (Webber & Wilson-Kelly, 2003). Outflow from the eutrophic Kingston Harbour has been documented to flow south-easterly to impact the nearby recreational areas of Hellshire Coast (Webber, Webber & Roff, 1992; Webber & Roff, 1996). A new sewage treatment facility, Soapberry, was constructed and implemented in 2007 to accept and properly treat the waste from the city of Kingston. It is not however clear whether the implementation of the Soapberry system has significantly affected the water quality of Kingston Harbour and resulted in an improvement of water quality along the Hellshire Coast. A rapid ecological assessment was therefore conducted. It was designed to:

- Spatially assess and compare the existing water quality of Kingston Harbour, Hunts Bay and North East Hellshire Coastline (using physiochemical and biological indices).

- Determine if there was significant improvement or deterioration in water quality when compared to the earlier baseline studies (i.e. prior to the Soapberry waste treatment implementation).

MATERIALS AND METHODS

Sample programme: A total of four sampling sessions were conducted during the period of May 21st to June 19th,2011, between the hours of 0700hours and 1200hours. Eleven stations (Fig. 1) were strategically selected along the North East Hellshire coastline (Stations 1-3), throughout Kingston Harbour (Stations 4–7) and in Hunts Bay (Stations 8–11), and based on previous studies by Webber and Roff (1996), Dunbar (1997), Ranston (1998) and Webber & Webber (1998). At each station physicochemical parameters were recorded using a Hydrolab Surveyor with a Datasonde 5 multi-parameter probe and whole water samples were collected at (i) the surface and (ii) 2m above the substrate (±0.10°C temperature; ±0.2ppt Salinity; ±0.01mg l^{-1} LDO; ±1.0NTU Turbidity; and ±0.2units pH).

Whole water samples: Samples were collected from the surface (fresh water) layer as well as the underlying deeper (more saline layer) using a 6L Niskin bottle. At Hunts Bay, surface samples were collected (i) just below the surface of the water and (ii) deeper samples at 2m above the substrate using a horizontal position Niskin bottle (Ranston, 1998). An aliquot of each water sample was then transferred to 3L plastic bottles and kept in the dark until filtration was possible, generally within four hours of collection. The samples for Biochemical Oxygen Demand (BOD) analysis were collected in 300mL BOD bottles then stored on ice for three (3) hours, prior to analysis. A YSI Model 57 Oxygen meter (±0.1mg l^{-1} on 0-10 scale) was used to determine the initial dissolved oxygen of each sample. Samples were then incubated for five (5) days at 20°C in total darkness with subsequent re-testing for dissolved oxygen (Eaton, Clesceri & Greenberg, 1995; Webber & Wilson-Kelly, 2003). The BOD_5 for each sample was derived using the formula: BOD_5 = [(Initial DO-Final DO) × (1 000mL)]/300mL).

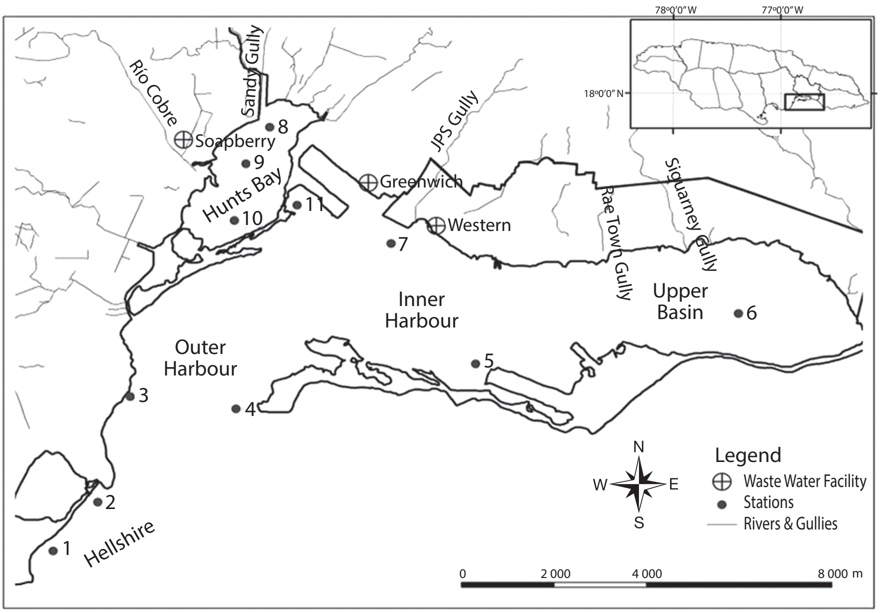

Fig. 1. Study area showing location of stations and waste water facility.

The 3L samples were filtered through a size fractioning tower with three filters of known pore sizes (Nitex screening: 20µm, Whatman glassfibre filters (GFD): 2.7µm and Whatman glassfibre filters (GFF): 0.7µm). Samples were gently homogenised prior to filtration. Two pseudo-replicates for each station at each depth were then poured through the fractionating tower. Size fractioning filtration was done within four hours of collection time (Parsons, Maita & Lalli, 1984). Each filter was rolled and then placed in labelled vials and stored in a freezer for later Chlorophyll *α* analysis. Chlorophyll α was extracted using 90% acetone (Parsons et al.,1984) under dark conditions for 24 hours in a refrigerator (Ranston, 1998). Each extracted sample was read on a Turner Flourometer TD-700. Values were recorded within 12 seconds of cuvettes being placed into the flourometer. Samples that contained high Chlorophyll that could not be read by the flourometer were diluted as outlined in Parsons et al. (1984). Chlorophyll *α* was calculated using the formula:

$$\text{mg Chlorophyll } \alpha \text{ m}^{-3} = R \times (v/V) \times \text{Dilution Factor}$$

(Parsons et al., 1984)
Where: R = Flourometer reading; ν = acetone extraction volume (mL); V = volume of seawater filtered (l)

Nutrient Analysis: Approximately 250mL of the filtrate from the size fractioning tower for each station was frozen for nutrient analysis. Nutrient samples were analysed on a Lachat QuickChem 8 000 Flow Injection Analyser (±0.001mg l^{-1}), using sulfanilamide colour reagent, ammonium chloride buffer, and a cadmium reduction column. Samples were run with the cadmium column online for total nitrate+nitrite analysis, and offline for phosphate and nitrate analysis.

Bacteriological analysis: Coliform bacterial density was determined as Most Probable Number (MPN) counts using the multiple tubes fermentation technique. A series of dilutions of the samples were prepared; these dilutions were 1.0mL, 0.1mL and 0.01mL. Five aliquots of each were inoculated into the growth medium and were incubated. A positive score was recorded whenever bubbles were formed as a result of fermentation. Lauryl Tryptose broth formed the presumptive phase and *Escherichia coli* broth medium with Durham inverted tube formed the confirmatory phase (Eaton et al., 1995).

RESULTS

The one month survey of the water quality of the Kingston Harbour provided important insight into the changes in that body of water. These changes were as a result of the introduction of a diverted sewage discharge over a short time period. The evidence of the spatial changes in key water quality parameters are divided here into physicochemical and biological indices.

Physiochemical indices: Temperature, salinity, dissolved oxygen; turbidity and pH were all within the expected ranges for coastal nearshore systems and demonstrated the spatial pattern consistent with the findings of Webber & Webber (1998). Lowest salinity and temperature accompanied by highest dissolved oxygen and pH were evident in Hunts Bay, while highest salinity and temperature and lowest pH were observed along the Hellshire Coast. There were also no significant differences in physicochemical indices in the 2011 study when compared to data collected in the surveys from the 1990's.

Nitrate-N concentrations were spatially variable with the expected increase from the previously classified mesotrophic Hellshire Coast, into the eutrophic Hunts Bay. The concentrations of nitrates were lowest along the Hellshire coast (0.63 to 0.78mg l^{-1} at stations 2 and 3), marginally higher in the Kingston Harbour (0.63 to 0.94mg l^{-1} at stations 6 and 7) and highest in Hunts Bay (1.45mg l^{-1} at station 9). While nitrate concentrations were much lower in 2011 than in the 1990's (Fig. 2) values in both studies were higher than the NEPA (2009)

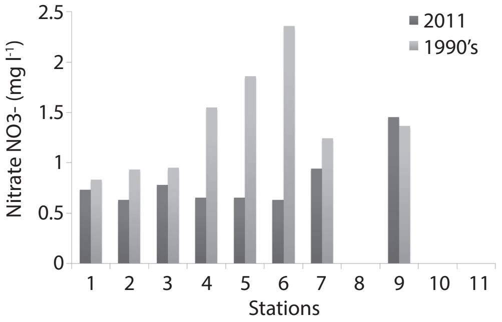

Fig. 2. Graph comparing Nitrate NO_3 (mg l^{-1}) concentrations at stations in the 1990's and 2011 studies.

ambient marine water quality nitrate standard of 0.007-0.014 mg l^{-1}.

Biological indices: Mean phytoplankton biomass (as Chlorophyll *α*) in the 2011 study increased from the Hellshire Coast (1.8 to 2.19mg m^{-3} at Stations 2 and 3) into the Kingston Harbour (1.7 to 3.8mg m^{-3} at stations 6 and 7) and reached a maximum in Hunts Bay (12.6 to 33.1mg m^{-3} at stations 8–11). While this spatial pattern was similar to the 1998 studies, t-tests revealed significant difference (p= 0.02) between the two studies. The highest biomass in 1990's of 13.5 mg m^{-3} was observed in Hunts Bay with lowest values at Hellshire Bay 1.38mg m^{-3}. Phytoplankton biomass in the Kingston Harbour was however unchanged between 1990's and 1998. The single exception was at station 6 where biomass values decreased from 4.17 to 1.70 mg m^{-3} between 1998 and 2011. Both surface and deep water phytoplankton biomass in 2011 were greater than in the 1990's except at stations 9 and 11 (Hunts Bay) where sub-surface biomass in 1990's were greater than 2011 (Fig. 3a, b, c & d).

The nanoplankton biomass size fraction dominated surface waters at all stations in both the 2011 and 1990's studies, although the net plankton biomass size fraction accounted for a larger proportion of total phytoplankton biomass in the 2011 samples. This was especially so in Hunts Bay (stations 8-11) which clearly reflected that deep waters were

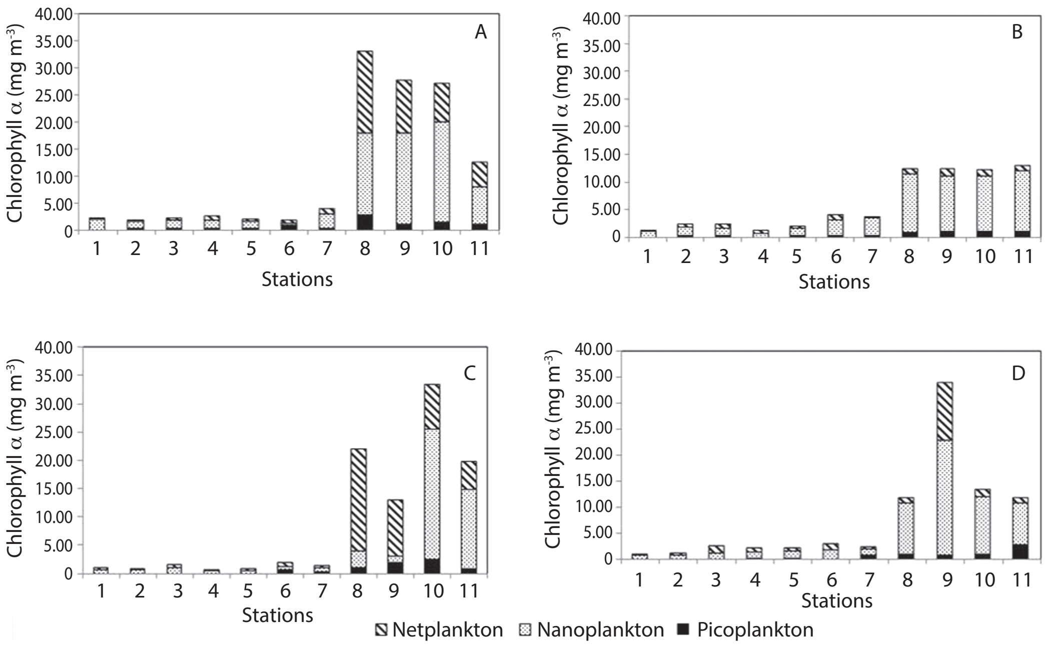

Fig. 3. Mean size fractionated biomass (mg m^{-3}) values at stations for 1990's and 2011 studies. 2011 surface, B) 1990's surface, C) 2011 deep, D) 1990's deep.

dominated by the net plankton biomass size fraction (Fig. 3c & 3d).

Faecal coliform counts increased from station 1 along Hellshire coast to station 9 in Hunts Bay (Fig. 4). Coliform concentration ranged from <20 to 1 200MPN/100mL with highest concentration at station 9, while the lowest concentrations were found at stations 1 to 3 (Hellshire Coast). Apart from station 9 in Hunts Bay all other values were below the World Health Organization (WHO) 1988 standard of 1 000MPN/100 mL (Owili, 2003) but higher than the National Environment and Planning Agency [NEPA], 2009) standard of <2-13MPN/100mL for ambient marine waters. Faecal coliform counts along the North East Hellshire coast and in the Kingston Harbour were generally lower in the 2011 (20 to 300MPN/100 mL) than the 1990's (>500MPN/100 mL) while counts in Hunts Bay were higher in 2011 (>2 400MPN/100 mL) than in the 1990's (1 200MPN/100 mL).

The BOD_5 values recorded in both studies ranged from 1 to 52mg l^{-1}. The lowest BOD_5 value was recorded along the Hellshire Coast at station 3 (2.8mg l^{-1}) in 2011 and station 1 (1mg l^{-1}) in 1990's. While samples from the Kingston Harbour were observed to have much reduced BOD_5 in 2011(4.6 to 4.9mg l^{-1}) over the 1998 data (10-35mg l^{-1}), water samples from Hunts Bay were observed to consistently have the highest BOD_5 in both studies 50 to 52mg l^{-1} (Fig. 5).

DISCUSSION

Physico-chemical parameters and the phytoplankton community were used to assess the current water quality in The Kingston Harbour, Hunts Bay and the North East Hellshire Coastline. The objectives of the study were to spatially compare the existing water quality of and to determine if there was significant change in water quality when compared to the earlier baseline studies (i.e. before the Soapberry Treatment Facility implementation).

A specified concentration of nutrients in an environment has the ability to serve as an indicator of pollution to that environment (James & Adejare, 2010). Nitrate concentrations at all sample stations were several times greater than the upper limit established by NEPA. This is due to the nutrient rich waters which enter the Harbour from sewage treatment as well as river and storm water inflow (Webber & Wilson-Kelly, 2003) as well as the nitrate recycling that is thought to take place from the benthos. Though greater than the NEPA standard, according to Seroka (2004) and James & Adejare (2010), nitrate values less than 5mg l^{-1} can still be indicative of unpolluted waters. Therefore Kingston Harbour nitrate values are not a good index of water quality. However, lower nitrate values in the Kingston Harbour and Hellshire coast suggest a reduction in

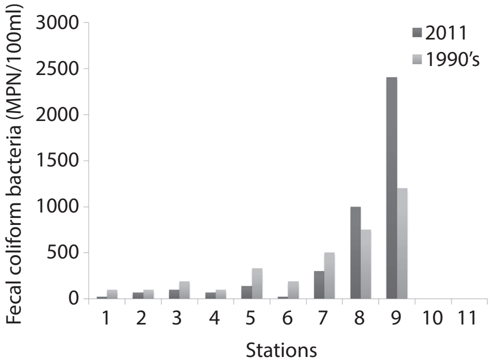

Fig. 4. Mean Faecal coliform concentrations at the stations in 1990's and 2011 studies.

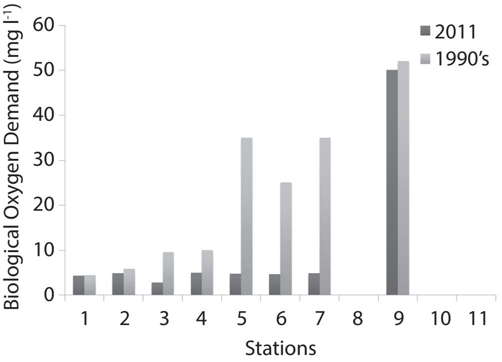

Fig 5. Mean Biological Oxygen Demand (B.O.D) concentrations at stations in 1990's and 2011 studies.

nutrient input or uptake by the biota resulting in improved water quality.

Using the Faecal coliform bacteria counts as the index, Hunts Bay, the Kingston Harbour and the Northern Hellshire Coast are all still heavily polluted based on NEPA standards for coastal waters. By WHO standards, the sample area is moderately polluted with Hunts Bay continuing to be extreme. However at the same time, Kingston Harbour and the Hellshire Coast coliform counts have reduced from the initial 1990's values indicating some improvement. These data imply that improperly treated sewage is still entering the Harbour area and that its waters are not safe for human contact with human skin. Based on the relative locations of the previous point sources (now diverted to the Soapberry Treatment Facility) and the discharge from that facility into Hunts Bay, it appears that the improvement in water quality in Kingston Harbour and Hellshire Coast and reduction in Hunts Bay are associated with the Soapberry Treatment Facility implementation.

Biochemical Oxygen Demand values obtained for each station surpassed the range (1.16mg l^{-1}) set out by NEPA for ambient marine water. This suggests a general poor water quality throughout the area. Although all values were in excess of the national threshold (i.e. NEPA), the spatial differences observed were not unexpected. That is, with Hunts Bay having the highest BOD_5 and thus the poorest water quality and the Harbour and Hellshire Coast both having similar but lower BOD_5 values (2.8 to 4.8mg l^{-1}). This was also expected since Hunts Bay is almost totally enclosed and receives inflows from (i) Sandy Gully which is the largest storm water drainage gully in the City of Kingston, (ii) the Rio Cobre which drains extensive farming areas of Jamaica as well as (iii) the newly commissioned Soapberry Treatment Facility. The significantly lower BOD_5 values observed in 2011 compared with the 1990's values indicate that despite the improvement in water quality in the Harbour and along Hellshire Coast since the 1990's, the levels are still elevated indicating the presence of organic and inorganic pollution, especially in Hunts Bay.

Nutrients, water clarity, biochemical oxygen demand, chemical contaminants and bacteria are the indices frequently employed in determining water quality. Although the planktonic community is tedious to analyse, it is perhaps the most reliable tool in the assessment of water quality and possible changes due to eutrophication (Webber & Webber, 1998). This can be due to nutrients being taken up rapidly by the phytoplankton (Satsmadjis, 1985), short generation times, motile existence and reaction with pollutants such as oils and toxins (Webber & Webber, 1998).

Total phytoplankton biomass values as Chlorophyll *α*, were generally higher for all stations located in Hunts Bay than for those recorded in Kingston Harbour and Hellshire. This pattern is similar to that observed in the extensive studies of the 1990's (Ranston, 1998). However, while the pattern remains the same, the doubling of phytoplankton biomass values observed in Hunts Bay indicates a significant increase in nutrient, or introduction of biomass. Thompson & Ho (1981) examined the effects of sewage discharge on phytoplankton population in Hong Kong. Their results showed estuarine waters influenced by riverine discharge had Chlorophyll *α* values between 2 and 6mg m^{-3} while values ranged between 12 and 20mg m^{-3} in waters that were influenced by untreated sewage effluent. Hunts Bay values are extremely elevated (33.1mg m^{-3}) compared with Thompson & Ho (1981) values. This suggests that Hunts Bay is even more eutrophic than in the 1990's when average values were approximately 13.5mg m^{-3}. The pattern was repeated for subsurface total biomass with Hunts Bay demonstrating reduced water quality. However Kingston Harbour and Hellshire Coast had lower total biomass values indicating improved water quality.

Simmonds (1997) and Ranston (1998) found that the waters throughout Kingston Harbour and Hunts Bay were dominated by the nanoplankton Chlorophyll *a* size fraction which accounted for more than 50% of the standing crop. Ranston and Webber (2003) determined that there was a sporadic enrichment of relatively higher concentrations of nutrients, which could occasionally support greater proportions of net plankton biomass throughout Hunts Bay. The 2011 dominance of the net plankton size fraction biomass in both the surface and the deep values in Hunts Bay suggest that nutrient inputs increased significantly since the 1990's and resulted in the proliferation of larger size fraction. In 1998, Ranston suggested that while Hunts Bay nutrient values were high for both surface and deep waters, low variability among values suggested that there are consistently high nutrient inputs but not high enough to support large proportions of net plankton. Smaller cells can grow faster at lower nutrient concentrations, whereas larger cells require higher concentrations to achieve equivalent growth rates (Hopcroft & Roff, 1990). The dominance of net plankton, which are better able to absorb nutrients when present in large quantities, is an indication of nutrient enriched waters in Hunts Bay (Webber & Webber, 1998). Nanoplankton have greater surface to area volume and can absorb nutrients more efficiently at lower concentrations than net plankton (Ranston, 1998). Picoplankton are indicators of oligotrophic waters as their small size allows them to absorb nutrients when nutrient levels are low (Ranston et al., 2003).

Another possible explanation for the size class shift in the phytoplankton is the possible release of larger species or chains of phytoplankton cells from the Soapberry Treatment Facility, especially since the species used in the pond treatments are large and chain forming (e.g. *Scenedesmus* sp. and *Spirulina* sp.). Such species would both increase the biomass and change the size fraction dominance. However, Polat and Aka (2007) stated that the physical and chemical properties of a given environment are very important in controlling phytoplankton size distribution and further state that both the large and small size fractions can contribute similarly to the overall total phytoplankton biomass. Hunts Bay may be a one of those areas with special chemical and physical properties (Ranston & Webber, 2003).

The comparison between this study and the one conducted by Webber and Webber (1998) provides evidence that the water quality in the Kingston Harbour has indeed improved over the 15 year period due to the 73% reduction seen in nitrates, 82% reduction in Biochemical Oxygen Demand and 50% reduction in phytoplankton biomass (all of which were significant). However despite these general reductions, areas of the Harbour are still very polluted with Hunts Bay having reduced water quality since the 1998 study. This is evident by the higher nitrates (increased by 6%) and Biochemical Oxygen Demand concentrations (increased by 4%) than previously observed in 1998. Moreover, Chlorophyll α values at stations in Hunts Bay were increased by almost 90% over previously recorded 1998 values. There was also a shift in phytoplankton size class domination towards a more eutrophic profile in Hunts Bay. Therefore, after the implementation of a new waste water treatment facility for the city of Kingston, the water quality of the Kingston Harbour and the northern Hellshire Coast has improved, while important parameters indicate a deterioration of water quality in Hunts Bay.

ACKNOWLEDGMENTS

We thank the staff of the University of the West Indies, Port Royal Marine Laboratory for their assistance with fieldwork collection. Funding was provided by the Department of Life Sciences, UWI.

RESUMEN

Evaluación de la calidad de las aguas de la Bahía de Kingston y la costa Hellshire, Jamaica, después de la implementación de una planta de tratamiento de aguas residuales. El deterioro de la calidad del agua del puerto de Kingston es debido principalmente a la descarga de aguas residuales y su efecto en los alrededores de la Costa de Hellshire, esto ha sido un problema desde la década de 1970. La implementación de una nueva planta de tratamiento de aguas residuales en 2007 para recibir residuos del Puerto de Kingston en Soapberry se esperaba hiciera una diferencia positiva. Parámetros físico-químicos y biológicos fueron utilizados para evaluar la calidad del agua y determinar el efecto de la planta de tratamiento. Once estaciones que fueron utilizadas en estudios anteriores (1990-1998) se muestrearon nuevamente para representar el puerto de Kingston, Bahía Hunts y la costa North East Hellshire sobre un régimen de muestreo de cuatro semanas entre mayo y junio de 2011. Mientras la temperatura, salinidad, turbidez, oxígeno disuelto y pH se mantuvieron sin cambios entre los años noventa y 2011, BOD_5, coliformes fecales y concentraciones de nitratos indicaron que había mejorado la calidad del agua del puerto y la costa mínimamente mientras que la calidad del agua en la bahía Hunts se había deteriorado significativamente. La biomasa del fitoplancton disminuyó en el puerto de Kingston (de 3.84mg m^{-3} en 1998 a 2.81mg m^{-3} en el 2011), y aumentó significativamente en bahía Hunts (de 14.69mg m^{-3} en 1998 a 24.17mg m^{-3} en el 2011). La biomasa en la costa permaneció similar (de 2.15mg m^{-3} en 1998 a 2.45mg m^{-3} en 2011). En 1998 la biomasa de nanoplancton (2.7 a 20µm) dominó a lo largo del puerto. En el 2011 la bahía Hunts era dominada por neto-plancton (>20µm), indicativo de aguas eutróficas.

Palabras clave: Soapberry, aguas residuales, Puerto de Kingston, eutrofización, Bahía Hunts, Hellshire

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Development of a protocol for sampling and analysis of ballast water in Jamaica

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Received 10-VIII-2013 Corrected 19-II-2014 Accepted 24-III-2014

Abstract: The transfer of ballast by the international shipping industry has negatively impacted the environment. To design such a protocol for the area, the ballast water tanks of seven bulk cargo vessels entering a Jamaican port were sampled between January 28, 2010 and August 17, 2010. Vessels originated from five ports and used three main routes, some of which conducted ballast water exchange. Twenty-six preserved and 22 live replicate zooplankton samples were obtained. Abundance and richness were higher than at temperate ports. Exchange did not alter the biotic composition but reduced the abundance. Two of the live sample replicates, containing 31.67 and 16.75 viable individuals m^{-3}, were non-compliant with the International Convention for the Control and Management of Ships' Ballast Water and Sediments. Approximately 12% of the species identified in the ballast water were present in the waters nearest the port in 1995 and 11% were present in the entire bay in 2005. The protocol designed from this study can be used to aid the establishment of a ballast water management system in the Caribbean or used as a foundation for the development of further protocols. Rev. Biol. Trop. 62 (Suppl. 3): 249-257. Epub 2014 September 01.

Key words: ballast water, zooplankton, protocol, Jamaica.

The transfer of ballast water allows a vessel to regulate its weight depending on how much cargo is being transported, in order to set the trim, list and overall stability of the vessel. However, such transfer by the international shipping industry has negatively impacted the health of humans, the environment as well as the economy of numerous countries worldwide as global markets encourage the global transfer of aquatic organism across natural barriers (Ruiz, Carlton, Grosholz & Hines, 1997). Monitoring of ballast water to be discharged in any particular country and the subsequent establishment of protocols will therefore be crucial to the future implementation of Ballast Water Management Systems (BWMS) on a large scale. Currently, no protocol has been described for the sampling of ballast water in any Caribbean territory when most have rich biodiversity of flora and fauna, densely populated coastal towns and cities and economies that depend significantly on the ocean. A suitable protocol could be used to enforce compliance to standards from the International Maritime Organization (IMO) as well as to enable the Caribbean territories to focus their resources on fewer vessels that are more likely to introduce alien, invasive species or 'Harmful Aquatic Organisms and Pathogens' (HAOP). Such a protocol has to be simple and economical so as to be implemented in as many territories as possible.

Successful introduction and establishment of organisms by ballast water discharge in a new habitat is most likely to occur when such organisms are released alive and in high abundances (Hayes, 1998; Olenin, Gollasch, Jonušas & Rimkutė, 2000) in a singular event. This situation is present amongst bulk cargo vessels which receive raw materials (dry bulk) at a particular port, and have a transfer time less than a month. The transfer time would be the time the vessel would take to leave their off-loading port (uptake ballast water) and reach the up-loading port (discharge ballast water). During this leg of the journey, vessels travel with ballast tanks filled to capacity and with empty cargo holds. Although the conditions within the tanks are harsh, hardy organism can survive if the transfer time is short (David et al., 2007; Wetseyn & Vink, 2001), allowing the release of live stowaways. Due to the discharge of all the ballast tanks that arrived full, large numbers of live organisms tend to be released. The analysis of ballast water of tanks from these vessels will therefore characterize the greatest threat posed by ballast water transfer so as to prevent another invasion such has the *Perna viridis* in the Kingston Harbour, which was suspected to be introduced from discharged ballast water (Buddo et al*.,* 2003).

The protocol to be outlined can be used to sample ballast water from cargo vessels throughout the Caribbean region. The types of access points, location and management, represent the range to be found on cargo ships that visit the region. Multiple teams can use this protocol to sample other tanks simultaneously.

MATERIALS AND METHODS

The Protocol: The protocol described below was conducted within a study that aimed to characterize the biotic components of ballast tanks that were to be discharged into a Jamaican port (Mitchell, 2012). It serves as a basic methodology that can be used when surveying other bulk cargo vessels at other Jamaican ports and similar ports within the Caribbean.

Gaining access: Being able to gain access to the sample is paramount to any study and is one of the steps used to carry out this protocol. Several considerations were included in gaining access to a ballast water sample, which started with obtaining security clearance to the port of interest. Once obtained, the team requested and acquired permission to enter the port and board the vessel for each sampling occasion. The partnership of a liaison is crucial to the continuation of the study as the project can be explained and permission to sample requested from the Ship Master - Captain, Chief Officer, etc. (Ruiz & Smith, 2005) by someone that is trusted and respected by both sides. Once permission to sample was granted, the Ship Master had to give permission to access either the manhole or the sounding pipe. The Ship Master was also critical in providing information for the ballast water protocol form (Appendix) which was developed specifically for this research.

As advised by AQIS (1998), the designation of a at least one suitable tank (Ruiz & Smith, 2005) as well as the access point was carried out by the Ship Master. Although several starboard tanks were designated, port tanks were requested when the option was available as they were considered to be safer options for sampling as loading and off-loading occurs on the starboard side (Dodgshun & Handley, 1997). The sampling equipment and basic methodology for sampling ballast water from manholes, called Set up 1 (Fig. 1A) were developed from recommendations from MEPC (2005a). Set up 1 was comprised of a 6 m long reinforced hose with an inner diameter of five centimetres and a smooth inner surface. A foot check-valve was clamped to one end of the hose and a diaphragm pump clamped to the other end via a reducer. A second reinforced hose, 32cm long and 3 cm in outer diameter, with a smooth inner surface with 2.5cm in inner diameter, connected the pump to an inline flow meter. The outlet of the flow meter was directed to the opening of the cod-end (cylindrical bottle that receives water from the outlet of the pump and flow meter), which was fitted with a mesh with aperture of 50µm.

Sampling the ballast water: Set-up 2 (Fig. 1B) was used to collect samples via sounding pipes. It was designed from the

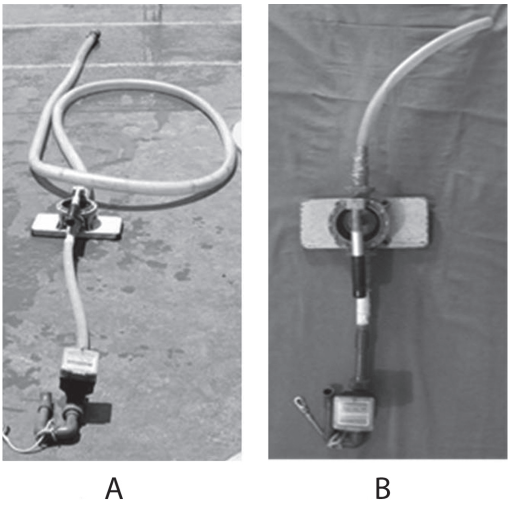

Fig. 1. (A) Set-up 1 and (B) Set-up 2. (A) Sampling equipment used to sample the manhole, consisting of a 20 ft reinforced hose, a diaphragm pump, a smaller reinforced hose and a flow meter. (B) Sampling equipment used to sample the sounding pipe; modified from Set-up 1, consisting of a small reinforced hose, duct tape, diaphragm pump and a flow meter.

Fig. 1. (A) Instalación 1 y (B) Instalación 2. (A) El equipo de muestreo utilizado para probar la boca de inspección, que consiste en una manguera de 20 pies, una bomba de diafragma, una manguera reforzada más pequeña y un medidor de flujo reforzados (B) Equipo de muestreo utilizado para el muestreo del tubo de sonda; modificado de instalación 1, que consta de una pequeña manguera reforzada, cinta aislante, bomba de diafragma y un caudalímetro.

equipment used to produce the original set-up (Set-up 1) but was comprised of the smaller hose described above being connected directly to the inline flow meter. The pump and flow meter were kept in the same orientation and as close together as possible. 75% of the 12 samples collected via sounding pipes (vessels 1, 4, 6 and 7) were sampled with Set-up 2. The other 25% were collected using an air-driven pump owned and operated by vessel 4. Vessels with sounding-pipe access should be encouraged to obtain such a pump to facilitate sampling as part of their compliance.

While the set-up of the equipment varied according to the type of access point available, (either a manhole or a sounding pipe), both arrangements had the diaphragm pump ultimately leading to the flow meter. The equipment that was used to sample from a manhole access point varied according to the position and number of hoses used, with the reinforced hose #1 forming the inlet, fitted with a foot check valve at the end. The reinforced hose #2 was positioned between the pump and the flow meter. Reinforced hose #1 was graduated at 0.25m intervals so that the depth to which the hose was deployed could be known.

The manhole was the preferred access point, but it was not always available for sampling as the opening of manholes of Ballast tanks which are filled to capacity and are therefore pressurized, would not be safe (Sutton, Murphy, Martin & Hewitt, 1998). The sounding pipes were only sampled if the manhole was not available and the pressure within the tank allowed water to either overflow or remain at the top near the lid. There were four tanks which were accessed from pressurized manholes. Sampling of such tanks was done after the pressure was released, either by discharging a small volume of water from the tank outlet or by slowly releasing the cover of the manhole until the pressure was low enough to safely remove the manhole lid , the second of which was more time consuming. In one instance, the location of the released water was deemed to create an unsafe environment during the loading process, as explained by AQIS (1998). Therefore, the 5th top-side tank from the bow on the port-side (TST P 5) was used for sampling on subsequent voyages of that particular vessel. When sampling using the manhole, the depth at which the sample was retrieved was kept constant at relatively half of the maximum depth of the ballast tank (Ruiz & Smith, 2005). The entire equipment was flushed with ballast water from each tank for 2 - 5 mins (approximately 40 l) at the beginning of the retrieval of each sample (Dodgshun & Handley, 1997; Murphy, Ruiz & Sytsma, 2005) so as to remove any material from previous samples.

A 20L bucket was placed beneath the cod-end to collect the filtered water. Sampling was done in replicates of two. The filtered water for each replicate was then transferred to a squeeze bottle (Dodgshun & Handley, 1997), which was used to wash the residue from the mesh into a 250mL plankton sample bottle, which did not contain any preservative. Dodgshun and Handley (1997)., The salinity of the ballast water of each sample was tested using a refractometer by collecting a 2L bottle of filtrate and carrying it back to lab along with the plankton samples. This water could also be used for other chemical tests. The sample-set was therefore comprised of two replicates of live zooplankton and two replicates of preserved zooplankton. Each replicate was obtained by filtering a known volume of $15m^3$ or $16m^3$ of ballast water. Miller et al. (2011) supports the statistical accuracy of using several trials of $7m^3$ each, when testing the level of compliance of ballast water to IMO viability standards once subjected to ballast water treatment systems. Separate cod-ends and meshes were used to collect the live and to-be-preserved replicates. The bottles were colour-coded with a blue tape for the live sample and with brown tape for the preserved sample. Labels were not completed on site so as to minimise use of ships time for sampling. Each sample set was collected in approximately forty minutes. Dodgshun and Handley (1997) expressed the importance of keeping the sample collection time to a minimum so as not to delay normal shipping operations. The impervious cone that was included in the Ballast Water Sampling Kit (MEPC, 2005a; Mitchell, 2012) was not used as the flow rates used in this study (9-20L min^{-1}) did not require the precaution of reducing the velocity at which the sample left the flow meter. Additionally, the height of the cone prevented it from being fully extended at the sampling site.

Sample analysis: The samples were carried to the lab where processingwas initiated within 1 hour after collection. The labelling of each bottle was then completed with sample number, type (live/preserved), replicate number, date of collection and the volume filtered. The live samples (Part I) were placed in the refrigerator at a temperature of 5°C which had the effect of slowing down the metabolism of the specimens. This allows the live animals to survive until they can be processed as slowing them down also retarded predation. Part II of the samples was preserved in 8% formalin also within an hour of arriving at the lab. The ballast water collected after removal of organisms, was filtered further through a 0.7µm Glass Fibre filter paper and used for salinity determination and The analysis of the live samples was completed within 6 hours of its collection. Viable counts were conducted where viability was determined by motility. MEPC (2005b) indicated that viability could be determined by morphological change, mobility, staining using vital dyes or molecular techniques.

Counts were done in two stages starting with the larger and faster plankton, which were counted at x 60 magnification. At a higher magnification, such plankton would swim out of the field of view and may easily be recounted. The second stage was done at x 500 magnification, were much smaller plankton were counted easily within the field of view. Regulation D-2 of the compliance standards (IMO, 2011) only requires a viability count that indicates whether there are more or less than 10 viable organisms of 10µm and 50µm minimum dimensions per cubic meter. The collection and study of organisms with a minimum dimension of 10µm was outside the scope of this study. This count provides an estimate of the conditions within the tank, whether or not they are suitable to sustain a standard abundance of life. A total abundance count was not done for the live samples.

The preserved samples were analysed after the live sample analysis was completed. Total counts were done for each taxonomic group of zooplankton observed. Counts were not taken for empty exoskeletons and damaged organisms, thus excluding plankton that were unlikely to be alive within the ballast tank prior to sampling or preservation. Whole sample counts were done for 93% of the samples. The remaining 7% were two replicates from separate samples that were too dense and so sub samples were enumerated (1/8 and ¼ of the samples, respectively). It was deemed important to do as many complete counts as possible as the relative abundance of organisms in most of the samples was low. Each new organism was recorded by the use of codes, which were based on the first sample in which it was found, whether the sample was live-(L) or preserved-(P), the particular replicate and its order of appearance. The organisms observed were identified to the species level, where possible. This was difficult as many of the organisms were larvae of marine organisms which are difficult to identify to species (Sutton et al., 1998).

A reference collection of isolated specimens was created with each new specimen in small glass jars with glycerol and 10% formalin. The bottles were labelled with the specimen-code created, a short description, date, source details and collector's initials. Each specimen was either documented by notes, drawing, and photographs or by a combination. The following printed and web-source identification keys were used: Rammner (1939), Klie (1944a), Klie (1944b), Farran (1951), Davis (1955), Lovegrove (1956), Forneris (1957), Naylor (1957a), Naylor (1957b), Berzins (1960a), Berzins (1960b), Berzins (1960c), Berzins (1960d), Hadfield (1964), Ryland (1965), Be (1967), Bottazzi and Nencini (1969), Marshall (1969a), Marshall (1969b), Harding and Smith (1974), Newell and Newell (1977), Gerber (2000), Smith (2001), Wallace and Snell (2001), Razouls et al. (2005-2011).

Salinity readings were taken to determine if ballast water exchange (BWE) was conducted, as outlined in Regulation D-1 of the compliance standard of the convention (IMO, 2011). The salinity was determined by the use of an optical refractometer (±)0.01 ppt). All data were added to spread-sheets for graphing and analysis. All information obtained on the particulars and procedures of the vessel was also added to the database.

RESULTS

The protocol is represented as a cyclic flow chart (Fig. 2) which facilitates easy communication. The first step consists of making initial contact with the vessel as it prepares to dock to the recording of the data obtained, which is the final stage to be considered for that particular vessel.

Abundance and richness of the samples were higher than observed in ballast water from previous studies conducted at temperate

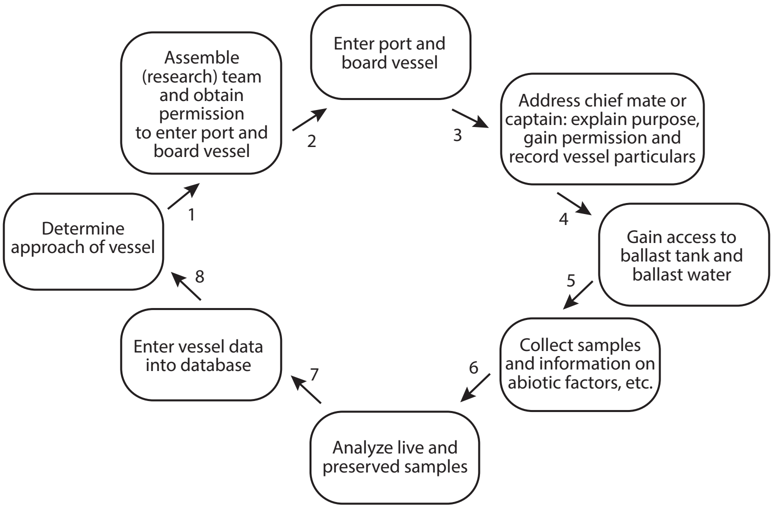

Fig. 2. Steps for the Ballast Water Sampling and Analysis Protocol.
Fig. 2. Pasos para el Muestreo de Agua de Lastre y el Protocolo de Análisis.

TABLE 1
Summary of results gleaned by using the Ballast Water Sampling and Analysis Protocol

CUADRO 1
Resumen de los resultados del Muestreo de Agua de Lastre y el Protocolo de Análisis

	Protocol Data	Literature	
Abundance	13 445 individuals (ind.)	1 349 individuals (ind.)	Drake and Lodge 2007
	448.167 ind. m^{-3}	154.467 ind. m^{-3}	David *et al.* 2007
	Copepoda, Mollusca, Cnidaria	Annelida, Mollusca, Crustacea (Copepoda, etc.)	
Richness	16 phyla	12 phyla, 11 invertebrate phyla	Chu *et al.* 1998 Locke *et al.* 1993
Impact of Source	Port-composition remained Abundance was reduced	Port-composition remained Abundance was reduced	Taylor and Bruce 1999 Levings *et al.* 2004

ports. The total organisms counted in this study was 13 445 individuals and the density obtained was 448.167individuals m^{-3}. Therefore, the observed abundance is greater than the expected abundance. Ballast water exchange did not alter the biotic composition of the tank but it did reduce the abundance of organisms in the tank (Table 1). Fifteen phyla were identified consisting of nineteen taxonomic groups. The three most species-rich adult groups were Copepoda, then Rotifera, then Cladocera. Tintinnida was the only group that was more abundant than the group Copepoda when both adults and juveniles counts were combined. Two of the live sample replicates, containing 31.67 viable individuals m^{-3} and 16.75 viable individuals m^{-3}, were non-compliant with the Standard Regulation D-2 of the International Convention for the Control and Management of Ships' Ballast Water and Sediments. Approximately 12% of the species identified in the ballast water were present at the station nearest the port in 1995 and 11% were present in the entire bay in 2005.

Salinity readings fell within the expected range of the general salinity regime of the source point of the water. For instance, ballast water from tanks that were filled from within a river (not near the mouth) had a salinity that was also between 0-5 ppt. However, two samples did not have salinity readings that coincided with their source point. One sample had a reading of 9ppt with a source point salinity regime of 36-40 ppt and a source port salinity regime of 18-35ppt. The other sample had a reading of 36ppt with a source point and port salinity regime of 0-5ppt.

DISCUSSION

The discharge of ballast water containing viable organisms is considered the ultimate step in the transfer of species from ballast water operations. All mitigation strategies are therefore aimed at managing such an outcome, from reducing the likelihood of taking up threat species, the removal of such species either by exchange or by applying treatments aimed at reducing viability within the tank as well as reducing the likelihood of viable species. Therefore, any ballast water study should not be conducted without accessing the viability levels of the tanks sampled.

Obtaining permission from the shipping agencies involved was the most critical step as providing access to ballast water was voluntary due to the current absence of legislation about ballast water management and regulation in Jamaica. However, with or without legislation, once access to the port is obtained permission must still be sought from the Ship Master to sample any ballast tank and its contents (Dodgshun & Handley, 1997). Barring this, sampling of any ballast tank could not be done despite any arrangement carried out before.

The urgent need for protocols is indicated by the findings of this study, in that total number of organisms counted from Ballast tanks was 10 times higher than that of Drake & Lodge (2007b) who counted a total of 1 349 individuals. Densities were twice those previously reported by David et al. (2007) who found 154.467 individuals m^{-3}. This may be due to the higher abundance and diversity of organisms within the tropics. Salinity variations in the ballast tanks also pointed to varied practices carried out by the vessel. Salinity is critical as it can confirm the carrying out of exchanges, especially where source ports are of very different salinities. All these findings point to the critical need for ballast water assessments to be conducted in the Caribbean and other tropical areas.

ACKNOWLEDGMENTS

The research was funded by a grant from the Environmental Foundation of Jamaica to the University of the West Indies. We are grateful to the entire staff of the Discovery Bay Marine Lab and Field Station who played an important role in ensuring that the research program was a success.

RESUMEN

Desarrollo de un protocolo de muestreo y análisis de agua de lastre en Jamaica. La transferencia de lastre por el transporte marítimo internacional ha impactado negativamente el ambiente. Con el fin de diseñar un protocolo, los tanques de agua de lastre de siete barcos carga en el puerto jamaiquino fueron muestreados entre el 28 de enero del 2010 y el 17 de agosto del 2010. Contenedores provenían de cinco puertos, utilizan tres rutas principales, algunos de los cuales conllevan un intercambio de agua de lastre. Se obtuvieron 26 muestras de zooplankton preservado y 22 vivo durante este periodo. La abundancia y riqueza de las muestras fue superior que en clima templado. El intercambio de agua de lastre no alteró la composición biótica pero disminuyó la abundancia. Dos de las muestras vivan, contenían 31.67 y 16.75 individuos viables m^{-3}, no compatibles con el Reglamento D-2 estándar de la Convención Internacional para el control y manejo del agua de lastre y sedimentos de barcos. Aproximadamente el 12% de las especies identificadas en el agua de lastre estaban presentes en las aguas del puerto más cercano en 1995 y 11% estaban presentes en toda la bahía en el año 2005. El protocolo diseñado a partir de este estudio puede ser utilizado para ayudar al establecimiento de un sistema de gestión del agua de lastre en el Caribe o usado como una base para el desarrollo de futuros protocolos.

Palabras clave: agua de lastre, zooplancton, protocolo, Jamaica.

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TABLE 2
Form used to record information from the vessel being sampled

CUADRO 2
Formulario utilizado para registrar la información de la embarcación muestreada

BALLAST DATA FORM

Name of Vessel: ______________________________
IMO number: ______________________________
IMO certificate (if applicable): ______________________________
Tank Type: ______________________________
Tank Capacity: ______________________________
Tank Volume: ______________________________
Tank Depth: ______________________________
Salinty: ______________________________

Ballast water management plan: ______________________________
____
____
____

Ballast Water Exchange Protocol: ______________________________
____
____
____

Source- [Discrete: Mixed: Unknown]: ______________________________

Time and date of uptake [Bay/Ocean]: ______________________________
____

Previous ports:
1. ______________________________
2. ______________________________
3. ______________________________
4. ______________________________

Sampling method: ______________________________

Volume of water sampled: ______________________________

Stage of Discharged: ______________________________

Voyage duration: ______________________________ [DAYS]

The planktonic communities of the Jamaican south-east coast; a comparison of harbor, shelf and oceanic areas

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Received 19-IX-2013 Corrected 31-III-2014 Accepted 01-IV-2014

Abstract: Few studies have compared water quality and plankton along the eutrophication gradient from Kingston Harbour to oceanic waters around Jamaica. To compare the planktonic community along the expected nutrient gradient, we sampled every two weeks at four stations, from eutrophic Kingston Harbour to oceanic California Bank. Phytoplankton was assessed from whole water Niskin bottle casts and zooplankton by vertical hauls with plankton nets of three different mesh sizes: 64µm, 200µm, and 600µm. Total phytoplankton biomass declined sharply away from the harbour (1.0 µg L^{-1} at the Harbour Shoal Beacon to 0.2 µg L^{-1} at California Bank). Characteristic estuarine phytoplankton genera -such as *Ceratium, Gonyaulax, Gyrodinium and Rhizosolenia*- dominated harbour samples while genera characteristic of offshore locations -such as *Asterionelliopsis, Navicula, Nitzschia, Rhizosolenia and Thalassionema*- dominated California Bank. Highest phytoplankton densities (mean values of 34 174 cells L^{-1}) were found at the harbor mouth. Mean zooplankton abundances ranged from maximum (5 858.5m^{-3}) at Beacon to minimum (2 124.2 m^{-3}) at California; 171 species of zooplankton were identified and copepods dominated with 76 species. Overall, 75 species of zooplankton were identified from Beacon, 107 from Port Royal Cays- South East Cay, 110 from the exposed shelf edge- Windward Edge, and 95 from the oceanic California Bank. Larval forms dominated; copepod nauplii, fish eggs and echinoderm larvae occurred at all sites. *Lucifer faxoni* and *Penilia avirostris* were indicative of harbor waters and *Microsetella* sp. and *Farranula carinata* of offshore waters. Some zooplankton taxa, like *L. faxoni, Paracalanus parvus* and copepod nauplii, despite showing gradual decline with distance from Beacon to the Edge, increased in abundance at the furthest station, California. California Bank clearly experiences enrichment which at times can be as high as near-shore areas, but the planktonic community is unique and similar only to those at other offshore station. To be reliable, characterization of water masses must involve a range of physicochemical and biological parameters. Rev. Biol. Trop. 62 (Suppl. 3): 259-272. Epub 2014 September 01.

Key words: Plankton, Water quality, Kingston Harbour, South-east coast, Jamaica.

There is now a great deal of information concerning the planktonic communities of the Kingston Harbour and the nearby coastal shelf areas (Moore & Sander, 1979; Webber & Roff, 1996; Webber & Webber, 1998; Dunbar & Webber, 2003; Campbell, Manning, Webber & Webber, 2008). Some of these studies have been quite extensive covering distances from Kingston Harbour to as far as 5km to the shelf edge (Moore & Sander, 1979) or parallel to the coast for 15km (Lindo, 1991). Other studies have covered extensive areas of the Port Royal cays (Webber et al., 1996; Webber & Roff, 1996, Persad, Hopcroft, Webber & Roff, 2003) in an effort to indicate the extent of Kingston Harbour influence and to identify indicator species of the water masses in the area. In most cases, the Kingston Harbour has been cited as a source of eutrophication with polluted waters leaving the mouth and being diluted by oceanic waters as the distance increased. However, it is believed that the outflow from Kingston Harbour, mainly affects the Hellshire coastline and proximal areas of the Port Royal cays and so progressively improved water quality and pristine conditions should be experienced with increasing distance form Kingston Harbour and the south coast shelf.

Few studies have adequately compared water quality and plankton along this eutrophication gradient from Kingston Harbour to oceanic waters around Jamaica. Indeed, the only previous study was conducted in 1964 and compared the zooplankton community and water quality between Kingston Harbour, the Port Royal Cays and an offshore station located 5 km away from the coastline of Jamaica (Moore & Sander, 1979). Moore and Sander (1979) indicated a gradient of conditions including, increased zooplankton abundances, phytoplankton biomass and nutrients across the stations towards the harbor. The increase in zooplankton abundances and phytoplankton biomass observed was found to be due to various factors: upwelling, run-off of nutrient rich waters, freshwater and local current dynamics. These factors had the effect of enhancing the nutrient levels thereby increasing productivity.

The area beyond the southern Jamaican shelf although influenced by predominantly oceanic sources, Grant and Wyatt (1980), is very productive in some locations. These locations include the offshore banks, e.g. California Bank and the edges of the Jamaican shelf and are considered as a moderate fisheries resource (Munro, 1983).

The paucity of studies comparing oceanic, shelf and harbor waters on the south coast is due primarily to the extent of the south coast shelf (28km at its widest point) and the local unavailability of vessels capable of safely embarking on voyages to areas far offshore. Compounding this problem is the difficulty in the actual data collection and processing while offshore. In general, work on water quality and plankton in Jamaica's offshore locations has been limited to occasional cruises on large scientific vessels or to the opportunistic trips on Jamaican Coast Guard vessels. Thus these voyages provide inadequate descriptions of the offshore planktonic communities and little opportunity for contemporaneous collections in near-shore waters that would allow for adequate examination of an inshore to offshore gradient.

The primary aim of this investigation was therefore to compare water quality and plankton along a gradient from expectedly pristine areas well beyond the shelf with areas close to shore and ultimately high nutrient areas like Kingston Harbour. The study was intended to:

1. Identify and confirm a eutrophication gradient between Kingston Harbour, the Port Royal Cays and offshore areas,
2. Compare the planktonic communities along the gradient and
3. Identify planktonic indicator species or communities characteristic of the areas along the gradient.

MATERIALS AND METHODS

Study sites: Four sites were selected (Fig. 1) to represent four contrasting marine environments with increasing linear distance from Kingston Harbour (Table 1). The linear distance represented a nutrient gradient from the eutrophic Kingston Harbour to oligotrophic California Bank (furthest away). The first site (Harbour Shoal Beacon - HSB) was located at

TABLE 1
Location of sampling sites in WGS 84 (Decimal Degrees)

Station	Latitude (Easting)	Longitude (Northing)	Distance from starting point at Port Royal Marine Laboratory (PRML)
Harbour Shoal Beacon (HSB)	17.93	-76.85	2 km
South East Cay (SEC)	17.90	-76.80	7 km
Windward Edge (WE)	17.84	-76.79	10 km
California Bank (CB)	17.75	-76.77	22 km

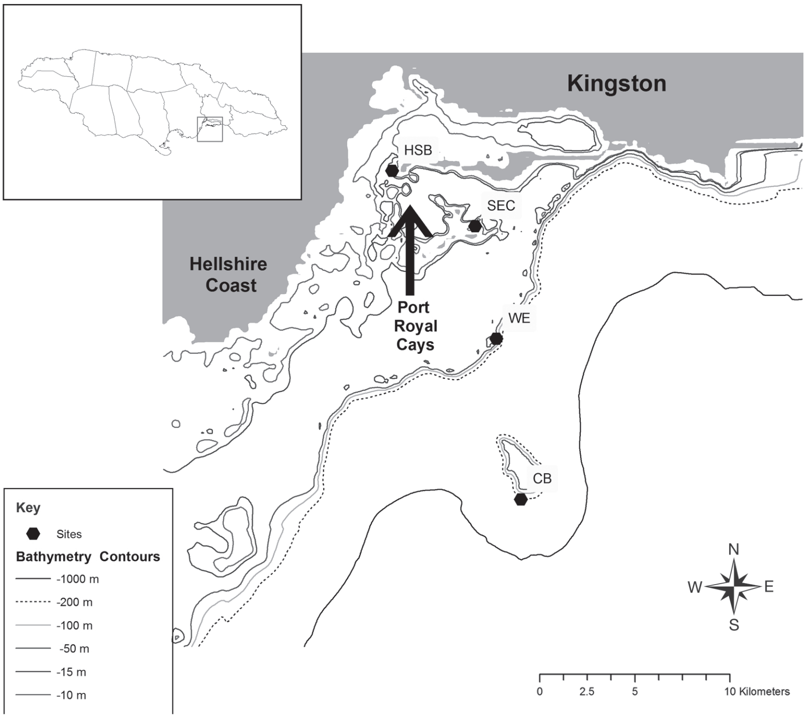

Fig. 1. Location of the study area showing stations sampled. HSB- Harbour Shoal Beacon, SEC- South East Cay, WE- Windward Edge, CB- California Bank.

the mouth of Kingston Harbour which has been characterized as eutrophic since the 1970's (Goodbody, 2003; Wade, Antonio & Mahon, 1972). Kingston Harbour receives agricultural runoff and partially treated sewage effluent which serve as a source of nutrient enrichment. The second site (South East Cay - SEC) was located 5 km from HSB. This location represents a coral cay and is one of a number of cays on the south coast shelf of Jamaica referred to as the Port Royal Cays. The Port Royal Cays are important for near-shore fishery and recreational sites for locals and visitors (Steele, 1998). The third location (Windward Edge - WE) was located 7km from the SEC, on the south-coast shelf edge and as such is exposed to oceanic influences. The coral reefs of this location are deep, patchy and often senescent (Munro, 1983). The fourth sampling location (California Bank - CB) was the furthest being ten 10km from the third site (WE) or 22km from Kingston Harbour. California Bank represents a small offshore bank, 8.6km^2 in area with immediate surrounding waters of approximately 700km depth. The water depth on the bank ranges between 35-45m. Munro (1983) also describes the reefs of this location to be sparse in coral cover and with sills that are not well developed.

Sampling programme: Sampling was carried out every two weeks from April to December 2004. Table 1 has the G.P.S coordinates of the stations that were occupied for sampling. On each occasion, sampling commenced from the station furthest offshore (California Bank) and progressed towards the more eutrophic station (Harbour Shoal Beacon). All four stations were sampled between 0830 and 1300 hours on the same day.

Water quality and phytoplankton assessment: Physical and chemical parameters including: temperature, salinity, oxidative redox potential, turbidity and light were collected *in situ* on each sampling occasion using a hydro-lab multi-parameter probe. Light values at specific depths (starting from 1.0m) were used to calculate the extinction coefficient (Poole & Atkins, 1929). Sampling from California Bank, Windward Edge and South East Cay was done at 5m intervals starting at the surface (0.1m) to a maximum depth of 20m. However, collections from Harbour Shoal Beacon were done at 1 m intervals starting at the surface to a maximum of 5m due to the shallow nature of that site.

Whole water samples, collected using a 6L Niskin water bottle, were used to determine total and size fractionated phytoplankton biomass, phytoplankton species composition and abundance as well as nitrate and phosphate concentrations. Whole water samples from California Bank, Windward Edge and South East Cay were collected with the Niskin bottle at depths of 20m, 10m and at the surface 0.5m; while at Harbour Shoal Beacon samples were collected from 5m and 0.5m depths. Phytoplankton samples were kept in the dark to protect them from light shock and processed within a maximum holding time of 5h (Parsons, Maita & Lalli, 1984).

A 250mL portion of each sample was immediately preserved (poured directly from the Niskin bottle into 250mL plastic bottle) containing 2.5mL of acidized Lugol's solution for counting and identification while the remainder of the sample was filtered through Nalgene size fractionating tower into three size classes. Separation was done using the appropriate size filters as follows: Nitex screening - 20µm; Whatman glassfibre filters, GDF - 2.7µm and Whatman glassfibre filters, GDF - 0.7µm.

Chlorophyll *a* content was determined using 6mL of 90% acetone to extract the chlorophyll (Arar & Collins, 1997). The quantity of Chlorophyll *a* in the extract was determined using a Turner Design Fluorometer TD700. Lugol's preserved phytoplankton samples were gently homogenized and 100mL portions used to fill settling chambers which were allowed to stand for 24 hours before examination using a Carl Zeiss inverted microscope with phase contrast (Model # 401672). Where cell numbers were low, the entire sample was enumerated (e.g. from California Bank, Windward Edge and South East Cay). However, cells from 30 random fields of view (Paerl, 1978) were counted from the Harbour Shoal Beacon. The number of phytoplankton genera and the total number of cells per liter were determined from the analysis.

Nitrates and phosphate were determined from the filtrate produced after the phytoplankton filtering. The filtrate was frozen as soon as possible after collection. Nitrate values were determined using a modified cadmium reduction column method. Phosphate analysis was done using the Molybdate Colorimetric method (Parsons et al., 1984). Ammonium was not determined as the detection limit of the methods (APHA-AWWA-WPCF, 1980) was exceeded by background values, thus making sample values negligible and very unreliable.

Zooplankton assessment: SCOR, WP2 pattern plankton nets (UNESCO, 1968) of three different mesh sizes: 600µm, 200µm and 64µm were used to collect zooplankton samples in replicate (n=2) vertical hauls. The hoop diameter of the 600µm net was 1 m while the diameter of the 200µm and 64µm net was 0.5. Samples were collected from a depth of 20m from California Bank, Windward Edge and South East Cay but from a 5m depth at Harbour Shoal Beacon. The net was hauled at a speed of approximately 0.5ms^{-1} using a manual winch. Plankton nets were washed between stations to prevent artificial transfer of species.

Zooplankton samples were fixed upon collection by pouring the contents of the cod end into 1 l containers containing 10mL of full strength formalin. All samples were later preserved in 10% formalin. Zooplankton species identification and enumeration were conducted on a sub-sample obtained using a modification of the beaker split method (Van Guelphen, Markle & Duggan, 1982). The sub-sample was transferred into a Bogorov tray and analyzed using a Wild (M7) binocular microscope.

Zooplankton organisms were enumerated and identified to genus and species where possible using guides including: Owre and Foyo (1967), Newell and Newell (1977), Michel (1984) and Todd, Laverack & Boxshall (1996).

RESULTS

A total of 10 physicochemical, five phytoplankton and 13 zooplankton parameters were collected and analyzed each as 105-108 discrete samples during this investigation. All data were assessed for normal distribution using STATISTICA 7 and Log $_{(x+1)}$ transformations applied where necessary. Temporal differences were not significant (MANOVA, $p>0.05$) but spatial variability was significant for eight of the physicochemical, all of the phytoplankton (size fractionated biomass (pico, nano and netplankton), abundance and richness, and eight of the zooplankton parameters (total abundance, species richness, abundance of copepods, calanoids, larvae, decapods, cladocerans and cnidarians). All significant variables were used in stepwise variable selection multiple regression models.

Physicochemical parameters: Mean **temperature** values showed a slight decrease with increasing distance from Harbour Shoal beacon (HSB). Values ranged from 29.53°C at HSB to 28.50°C at California Bank (Fig. 2). Nevertheless, temperatures were significantly different between the stations (MANOVA, $P=0.003$). Mean **salinity** values (MANOVA, $P < 0.001$) increased sharply from Harbour Shoal Beacon (35.76$^{o}/_{oo}$) to South East Cay (36.19$^{o}/_{oo}$) and remained almost constant as distance increased from South East Cay (SEC) to offshore stations (Fig. 2). Significant differences in **turbidity** values were not observed (MANOVA, $P=0.165$) and there was no trend in the distribution of turbidity as distance increased. However, extinction coefficient (MANOVA, $P< 0.001$) initially declined from 0.53 at Harbour Shoal Beacon to 0.068 at South East Cay, before gradually decreasing as distance offshore increased, reaching 0.044 at California Bank (Fig. 3).

Oxidative redox potential (ORP) values (MANOVA, $p = 0.011$) increased as distance offshore increased (Fig. 3) but Phosphate (MANOVA, $P = 0.027$) showed similar values at the Harbour Shoal Beacon as at California Bank. **Phosphate values** ranged from a low of 0.055 µg at L^{-1} at Windward Edge to a high of 0.099µg at L^{-1} at Harbour Shoal Beacon with California Bank being a close second with high values of 0.098µg at L^{-1} (Fig. 4). However, **nitrate values** showed no significant differences between stations (MANOVA, $P = 0.079$).

Phytoplankton: A severe decline in mean chlorophyll *a* total biomass (MANOVA p =

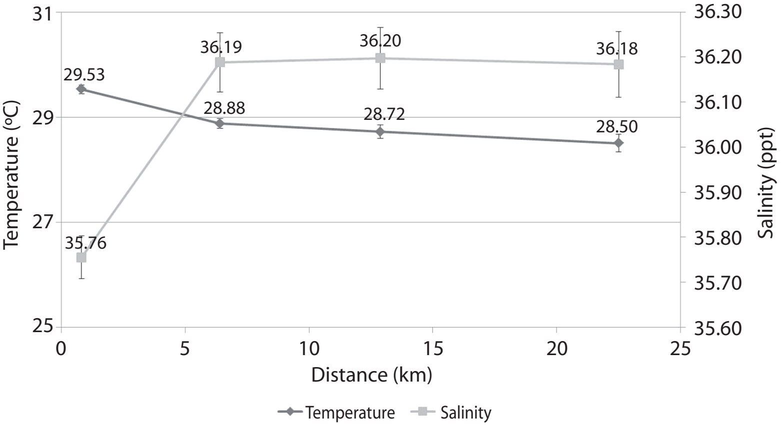

Fig. 2. Mean temperature and salinity values at the stations samples (with standard error).

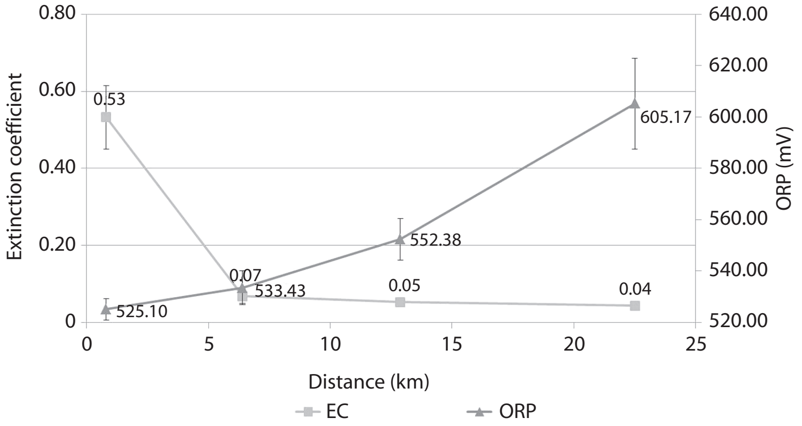

Fig. 3. Mean turbidity, extinction coefficient and oxidative redox potential values at the stations samples (with standard error).

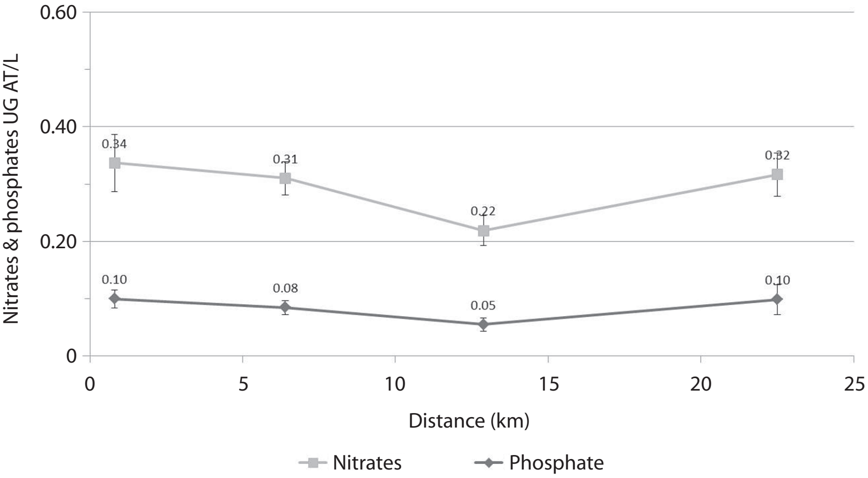

Fig. 4. Mean nitrate and phosphate values at the stations samples (with standard error).

< 0.001) was seen from Harbour Shoal Beacon (1.25µg L^{-1}) to South East Cay (0.25µg L^{-1}). A more gradual decline was observed towards Windward Edge (0.2µg L^{-1}) then to California Bank (0.125µg L^{-1}). Also as depth increased, chlorophyll *a* values showed small increases at all stations and were found to not be significant (Fig. 5).

Examination of the proportion contributed by each phytoplankton size fraction (Fig. 6) showed that the picoplankton (0.7µm) contributed the dominant portion of the biomass at California Bank, Windward Edge and South East Cay while the netplankton (20µm) dominated only at Harbour Shoal Beacon. Generally the picoplankton fraction increased and netplankton decreased with distance from Kingston Harbour. The nanoplankton fraction (2.7µm) showed the least pattern across all stations (Fig. 6). Chlorophyll *a* values for all size classes of phytoplankton showed significant spatial variation (MANOVA P <0.001) after log transformation.

Stepwise, variable selection multiple regression tests showed that 56% of the variation in netplankton was related to variation in

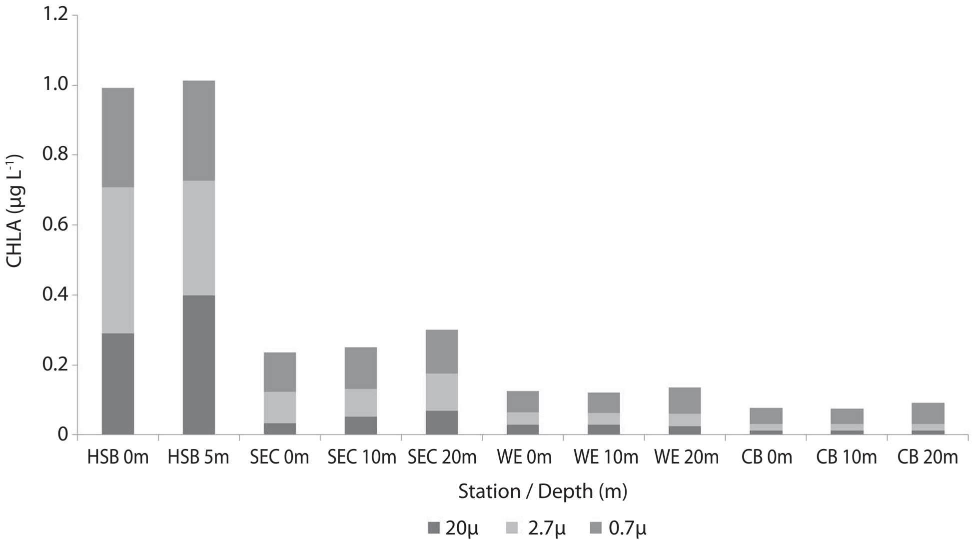

Fig. 5. Mean total and size fractionated chlorophyll a biomass values at the stations samples at the different depths sampled.

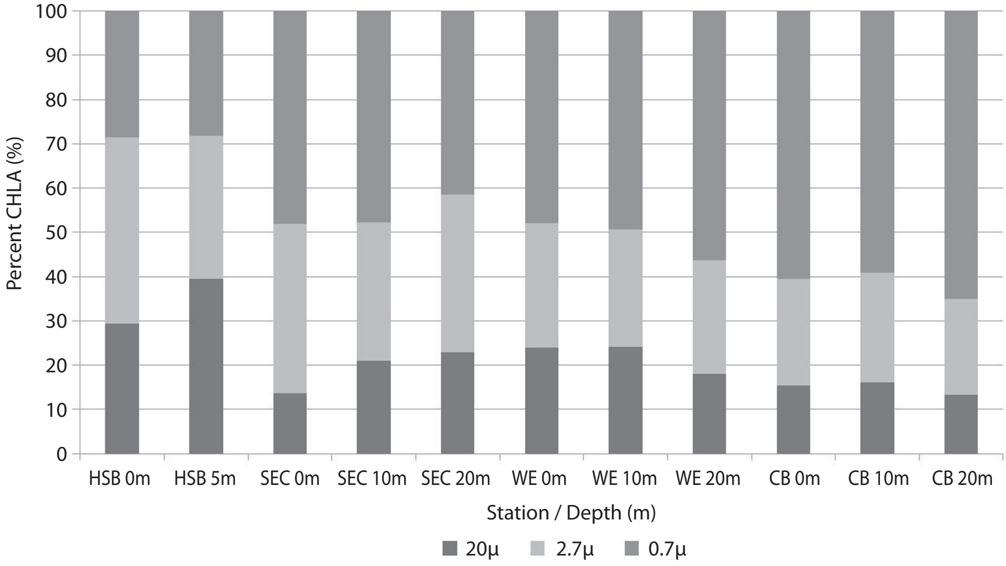

Fig. 6. Mean total and size fractionated chlorophyll a biomass values expressed as a percentage at the stations samples at the different depths sampled.

distance, temperature, pH and dissolved oxygen (R^2=55.75%, $P<0.005$), while 72% of the variation in nanoplankton was related to variation in distance, temperature, specific conductivity and phosphates (R^2=71.38%, $P<0.005$). Variation in distance, dissolved oxygen and salinity were attributable for 54% of the variation in picoplankton (R^2=53.29, $P<0.005$).

The **number of phytoplankton taxa** (richness) increased from Harbour Shoal Beacon (mean of 12) to South East cay with a mean of 19 (MANOVA, $P < 0.001$). However, as distance increased further offshore a general decline was then observed with Windward Edge having a richness of 15 genera, the same as California Bank (Fig. 7). Stepwise variable selection multiple regression showed that variations of 13% in the number of phytoplankton genera could be directly attributable to variation in nitrates and dissolved oxygen (R^2=12.58%, P<0.05), with both having a negative relationship to richness.

Phytoplankton abundance (# of cells l^{-1}) followed a similar spatial distribution pattern (MANOVA, P<0.001) where a severe decrease was seen from Harbour Shoal Beacon (34 173.51 cells l^{-1}) to South East Cay (507.67 cells l^{-1}). A gradual decrease was then obtained from South East Cay as distance offshore increased. Windward Edge had mean abundance values of 320.30 cells l^{-1} while California Bank had 137.71 cells l^{-1} (Fig. 6). Stepwise variable selection multiple regression showed that 61% of the variation in number of cells was attributable to distance and total dissolved solids (R^2=60.79%, P<0.05), both having negative relationships to the number of cells l^{-1}.

Jaccard community coefficient (JCC) analysis indicated that the communities at Harbour Shoal Beacon and South East cay were 45% similar, Harbour Shoal Beacon and Windward Edge were 46% similar while Harbour Shoal Beacon and California Bank were 38% similar. South East Cay and Windward Edge were 63% similar and South East Cay and California Bank 49% similar. Finally, phytoplankton communities at Windward Edge and California Bank were 53% similar (Table 2).

Zooplankton species richness and total abundances: The overall number of zooplankton species encountered during the sampling period (total richness) ranged from 81 species at Harbour Shoal Beacon (HSB) to 115 species at Windward Edge (MANOVA, P<0.001). HSB also consistently had the lowest mean richness (Fig. 8). Contrastingly, HSB had the greatest mean zooplankton abundance (Nos. m^{-3}) when compared to the other three stations (MANOVA, P<0.001). Mean zooplankton abundance at HSB was 5 963 individuals m^{-3} while South East Cay (SEC), Windward Edge (WE) and

TABLE 2

Mean Jaccard Community Coefficient values comparing the phytoplankton species at the locations investigated

	HSB	SEC	WE	CB
HSB	1			
SEC	0.45	1		
WE	0.46	0.63	1	
CB	0.38	0.49	0.53	1

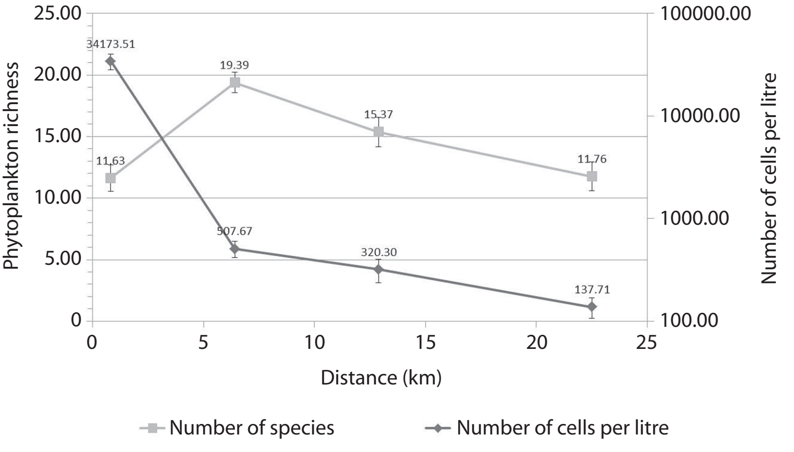

Fig. 7. Mean number of phytoplankton species and number of phytoplankton cells per litre values at the stations samples (with standard error).

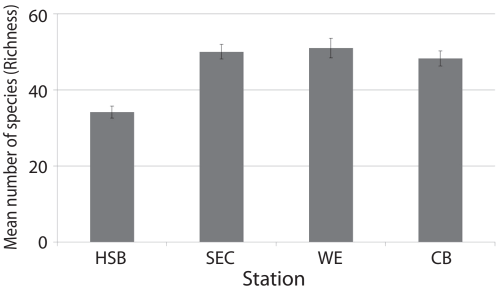

Fig. 8. Mean number of zooplankton species (richness) at the stations sampled (with standard error).

California Bank (CB) had abundance values of approximately 2 000 individuals m^3 (Fig. 9).

When all net collections were combined, larvae (invertebrate and vertebrate) were the most abundant group being the greatest proportion of the collections from all four stations. Larvae accounted for more than half of the total abundance at CB (Fig. 9). Of the larval group, copepod nauplii were numerically the most dominant taxon. These occurred universally across all stations and sampling occasions with highest numbers observed at HSB followed by CB. The other two stations (SEC and WE) showed similar low numbers. Adult copepods were the second most abundant taxonomic group (after larvae). Cnidarians made the smallest contribution at each station, but were still most abundant at Harbour Shoal Beacon.

Potential **zooplankton indicator species** were examined in terms of their relative abundance across the four stations. Species like ***Penilia avirostris*** and ***Lucifer faxoni*** had been identified as Kingston harbor indicators (Lindo, 1991; Webber, Roff, Chisholm & Clarke, 1996). *P. avirostris* showed greatest abundance at Harbour Shoal Beacon (Table 4) and then declined exponentially to the stations further offshore (MANOVA P > 0.001). *L. faxoni* was similar with maximum abundances at HSB, followed by a severe decline at SEC and WE. However, abundances showed a slight increase at CB, above values recorded at SEC and WE.

Microsetella sp. occurred at all four stations investigated and abundances gradually increased with distance (MANOVA, P<0.001) from the Harbour Shoal Beacon, where mean abundances were less than 5 individuals m^{-3}.

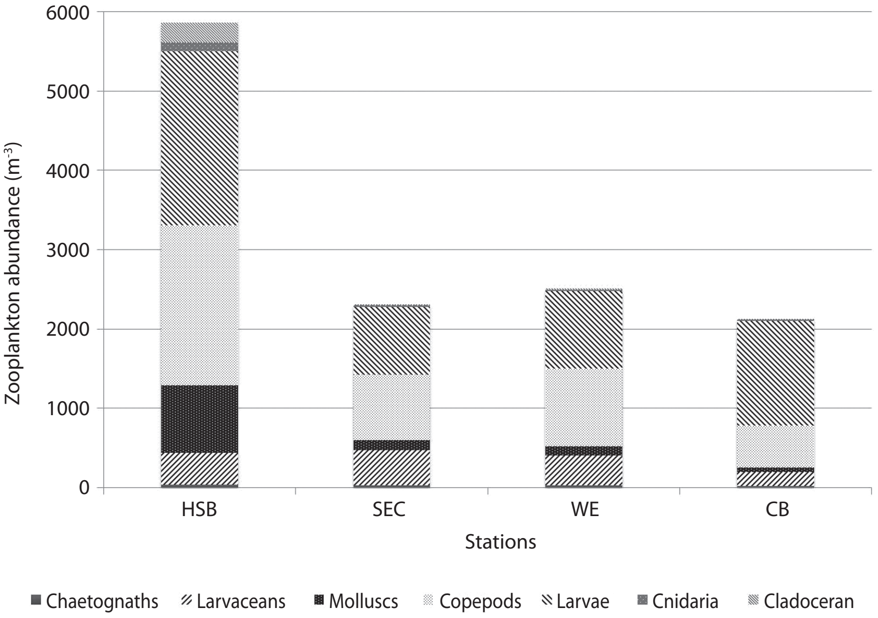

Fig. 9. Mean zooplankton abundances at the stations sampled.

However it was present as 30 and 37 individuals m^{-3} at Windward Edge and California Bank, respectively. *F. carinata* (MANOVA, P= 0.001) seemed to have similar distribution (increase in the numbers of this species as distance offshore increased) but it was only observed at South East Cay, Windward Edge and California Bank. It was not observed at Harbour Shoal Beacon over all the sampling occasions.

Using the Jaccard Community Coefficient (JCC), the zooplankton community at the stations increased in similarity from Harbour Shoal Beacon (HSB) towards California Bank (CB). HSB was the least similar compared to the other stations with similarities of 38% and less (Table 3). The highest community similarities were observed between CB and WE (66% similarity). Communities at South East Cay (SEC) and Windward Edge (WE) showed 63% similarity while SEC and CB were 46% similar (Table 4). This pattern was almost identical to the phytoplankton community.

TABLE 3
Mean Jaccard Community Coefficient values comparing the zooplankton community at the different stations investigated

	HSB	SEC	WE	CB
HSB	1			
SEC	0.38	1		
WE	0.36	0.63	1	
CB	0.35	0.46	0.66	1

DISCUSSION

Comparison of water quality and plankton across areas spanning coastal bays or harbors and offshore, oceanic banks are rare as intensive plankton and water quality sampling requires relatively short intervals between collecting and processing events. Alternatives include availability of large enough vessels for shipboard analysis or restricting attention to few parameters (Moore & Sander, 1979). This study achieved comparative analysis of 11 physicochemical parameters, 13 zooplankton parameters and five phytoplankton parameters sampled from different depths at stations up to 22km apart across an expected eutrophication gradient.

Thus it was expected that the physicochemical parameters would show severe changes from the eutrophic waters at Harbour Shoal Beacon (HSB) at the mouth of Kingston harbor to South East Cay (SEC), Windward Edge (WE) and California Bank (CB) 22km away, along the predicted eutrophication gradient. However, with the exception of Extinction coefficient and Salinity, the change in water quality parameters with increasing distance off shore was not as severe as expected. In

TABLE 4
Mean abundances of numerically dominant zooplankton taxa and potential indicator species at the four stations

TAXA	SPECIES	MEAN ABUNDANCES- Nos m^{-3}			
		HSB	SEC	WE	CB
Cladocera	*Penilia avirostris*	278.39	3.99	10.28	0.27
Calanoida	*Clausocalanus sp.*	0	45.28	154.05	9.9
	Paracalanus parvus	734.64	88.9	48.88	73.84
	Undinula vulgaris	19.08	87.07	40.6	85.22
Cyclopoida	*Farranula carinata*	0	4.82	34.08	40.37
	Oithona nana	192.54	119.69	6.34	5.88
Harpacticoida	*Microsetella sp.*	4.27	9.35	30.69	37.18
Decapoda	*Lucifer faxoni*	23.91	0.55	0.39	2.76
Larvae	*Copepod nauplii*	1 438.16	495.78	507.42	842.14
Mollusca	Bivalve	1 113.53	71.69	36.31	5.24
	Gastropod	63.59	68.15	83.96	52

fact the gradually declining nutrient gradient was disrupted by values at the furthest station (CB) being higher than those from its next nearest neighbor. This pattern was also demonstrated for the zooplankton parameters: species richness, numbers of *L. faxoni, Paracalanus parvus* and copepod nauplii. Values at California bank for these parameters indicated unexpected enrichment of the area. Offshore banks and shelf areas may receive enrichment from upwelling which is aided by horizontal circulation patterns like gyres that concentrate nutrients and retain planktonic communities (Genin, 2004; Rakhesh, Raman & Sudarsan, 2006). Such circulation is said to lead to increased numbers in especially larval forms, phytoplankton and other plankton with limited means of movement (Carleton, Brinkman & Doherty, 2001).

While it was unexpected for the offshore bank to have nitrate values as high as at the mouth of Kingston Harbour, upwelling has been shown to promote significant enrichment of surface waters (Caldeira et al., 2002). Nevertheless, it is important to note that nutrient values between the eutrophic Kingston harbor and relatively pristine offshore sites were not as different as expected; clearly indicating the deficiency in relying on nutrients as indicators in such conditions.

The identification of indicator species and groups from the plankton was more reliable at characterizing different water masses (McGehee, Derner & Warren, 2004; Fehling et al., 2012; Tseng, Dahms, Chen & Hwang, 2013). Netplankton (>20µm) is known to be dominant in high nutrient waters because of the low surface area to volume ratio causing them to be best suited and therefore allowing them to persist in high nutrient concentrations (Hopcroft, 1988; Webber, 1990), such as is available at HSB. Contrastingly, the picoplankton size class, having a high surface area to volume ratio would dominate oligotrophic areas such as South East Cay, Windward Edge and California Bank (Hopcroft, 1988; Webber, 1990). The last size fraction, the nanoplankton, are known to remain fairly consistent whether near or far from the coast (Vant & Safi, 1996). This is corroborated by the findings of Webber and Roff (1996) where small picoplankton dominated nutrient poor oceanic waters and netplankton in coastal waters nutrient rich waters.

The taxonomic richness (number of zooplankton species and phytoplankton genera) did not follow the expected gradient as lowest number of species occurred at both Harbour Shoal Beacon and California Bank. Furthermore, while total abundances (zooplankton Nos. m^{-3} and Chlorophyll *a* l^{-1}) followed the expected gradient, individual species and groups such as copepod nauplii showed secondary increases at the station located furthest offshore due to enrichment associated with the changes in circulation associated with the submerged bank.

While abundances may be unpredictable, community composition has been shown to be better when identifying distinct water masses (Campbell et al., 2008). Thus greater percentage similarity was expected and obtained from stations closer to each other along the gradient. Even in cases where the nutrient concentrations were similar, (e.g. Harbor Shoal Beacon and California Bank), the planktonic communities were most different and reflected the differing conditions of the associated water mass. This is also supported by the dominant species (indicators) in each water body. In terms of the phytoplankton, coastal and oceanic water bodies were separated into two general groups with, the coastal stations having dinoflagellattes (also shown by Matsuoka, Joyce, Katoni & Matsuyma, 2003) such as: *Gonyaulax, Gyrodinium and Perdinium* being dominant while oceanic stations having diatoms such as: *Navicula, Nitzschia, Rhixosloenia and Thallassionema* being dominant; irrespective of nutrient levels.

Throughout the study, zooplankton groups were dominated by copepods and larvae which accounted for more than 70% of the abundances at each station. However, copepods were expected to be the dominant group as was previously reported by other authors (Youngbluth, 1980; Moore & Sander, 1979; Webber & Roff, 1995; Dunbar & Webber, 2003). The larval group contained representatives from different groups notably copepod nauplii, fish eggs and echinoderms. The high larval presence at the offshore stations (California Bank and Windward Edge), was further evidence that they are productive areas with reduced flushing and water retention processes that lead to increased numbers of especially larval forms with limited means of movement (Cowen & Castro, 1994; Carleton et al., 2001).

Within each group/taxa a few species displayed high abundances and occurrence at the stations and therefore have the potential for use as indicators of different water masses/conditions. *L. faxoni* has been identified as an indicator of Kingston Harbour waters in previous studies (Lindo, 1991; Webber et al., 1996; Dunbar & Webber, 2003). *L. faxoni*, clearly displayed highest numbers at the Harbour station but did not have lowest mean values at the furthest offshore station. The distribution of the species appears to be less affected by salinity levels and more by nutrients.

The Cladoceran, *P. avirostris* has often been paired with *L.* faxoni. As shown in the present investigation, it also tends to have highest numbers at the harbor station and low numbers at offshore areas. *P. avirostris* has been previously reported in high abundances in the Kingston Harbour and at its mouth (Moore & Sander, 1979; Dunbar & Webber, 2003; Webber et al., 2005). The distribution of the species appears to be affected by salinity concentrations and food availability. Moraitou-Apostolopoulou and Kiortsis (1973) found that higher salinities and pelagic nature of the waters had an effect on *P. avirostris'* distribution, thereby limiting its presence to areas with shallow low-salinity waters.

The copepod *Microsetella sp.* was the dominant harpacticoid at the offshore stations and Moore and Sander (1979) reported this species as only occurring at stations outside of the Harbour and while Webber et al. (1996) did not report it from their study of the Port Royal Cays, it was found offshore Discovery Bay, north coast of Jamaica (Webber & Roff 1995). The cyclopoid, *F. carinata* was important at the offshore stations, while being absent from the Harbour Shoal Beacon. This species has also been found to be important in oceanic waters off the north coast at Discovery Bay, Jamaica by Webber & Roff (1995). *Microsetella* sp. and *F. carinata* therefore could be indicators of offshore waters.

Larvae followed the general trend of highest numbers at the Harbour mouth; however the numbers at station California Bank were second highest. Moore and Sander (1979) had reported relatively low mean numbers (135m^{-3}) at their offshore station, a magnitude lower than reported by the present study. In using a single mesh (~200µm) for their study they would have underestimated copepodites by a factor of three to six, and also underestimated copepods by a factor of five (Webber & Roff, 1995). The relatively high larval abundance at California Bank would suggest a mechanism or processes that retain larvae associated with this area. Similar effects have been seen by Heywood, Barton & Simpson (1990) and Hernández-León (1990), where they found an increase in the biological production and attributed it to the presence of an offshore bank.

In general there was a change in biological parameters with increasing distance from the harbor towards the open sea. Based on the indices investigated, the identification of a gradient of conditions with different levels of eutrophication was partially achieved with confirmation that Harbour Shoal Beacon was the most eutrophic site and Windward Edge most oligotrophic. South East Cay, due to its position on the south coast shelf, should be classified as mesotrophic (Vollenweider et al., 1998) along with California Bank. California Bank while having oceanic planktonic communities, is not oligotrophic, but is influenced by processes that reflect mesotrophic conditions hence its pairing with South East Cay. The findings of this study indicate that accurate characterization of water masses and their trophic status must involve a range of physicochemical and biological parameters.

RESUMEN

Comunidades planctónicas de la costa sudoriental jamaiquina; una comparación de puerto, estante y áreas oceánicas. Pocos estudios han comparado la calidad de agua y plancton a lo largo de un gradiente de eutrofización en el Puerto Kingston con aguas oceánicas en Jamaica. Para comparar la comunidad de plancton a lo largo del gradiente de nutrientes esperado, muestreamos cada dos semanas en cuatro estaciones, desde el eutrófico Puerto Kingston hasta el Banco oceánico California. Evaluamos el fitoplancton de agua entera en botellas de molde tipo Niskin usando la biomasa total y y zooplancton por arrastres verticales con redes de plancton de tres tamaños de malla diferente: 64µm, 200µm y 600µm. La biomasa total de fitoplancton mostró una fuerte caída al aumentar la distancia desde el puerto Kingston (1.0µg L-1 en el Puerto Shoal Beacon a 0.2µg L-1 en el Banco California). Géneros característicos estuarinos como *Ceratium, Gonyaulax, Gyrodinium* y *Rhizosolenia* dominaron en las muestras del Puerto Kingston mientras que géneros característicos de costa afuera como *Asterionelliopsis, Navicula, Nitzschia, Rhizosolenia* y *Thalassionema* dominaron en el Banco California. Las densidades más altas de fitoplancton (valores promedio de 34 174 células L-1) se encontraron en la boca del puerto. Valores promedio de zooplancton oscilaban entre un máximo (5 858.5m-3) en el Puerto Shoal Beacon (HSB) a un mínimo (2 124.19m-3) en el Banco California (CB), 171 especies del zooplancton fueron identificadas, de los cuales los copépodos dominaban con 76 especies. En general, se identificaron 75 especies del zooplancton en HSB, 107 de los Cayos Port Royal (SEC), 110 del borde de la plataforma expuesta (WE) y 95 del Banco oceánico (CB). Las formas larvarias eran numéricamente dominantes con nauplios de copépodos, huevos de peces y larvas de equinodermos que ocurren en todos los sitios. La dominancia de especies individuales fue utilizada para caracterizar las masas de agua. *Lucifer faxoni* y *Penilia avirostris* fueron indicativos de las aguas del puerto y *Microsetella sp.* y *Farranula carinata* fueron identificados como indicadores de aguas costa afuera. Taxones seleccionados de de zooplancton, como *L. faxoni, Paracalanus parvus* y nauplios de copépodos, a pesar de mostrar un decline gradual con la distancia desde el puerto de Kingston a la otra estación costa afuera, aumentan su abundancia en la estación más lejana, Banco California. Banco California es claramente una zona que experimenta un enriquecimiento que a veces puede ser tan alto como las áreas cerca de la costa, pero la comunidad planctónica es única y similar únicamente a las estaciones costa afuera. Para ser confiable, la caracterización de masas de agua debe implicar una serie de parámetros físico-químicos y biológicos.

Palabras clave: Plancton, costa sur-este, calidad de agua, Puerto Kingston, Jamaica.

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Marine Protected Area monitoring in the nearshore waters of Grenada, Eastern Caribbean: benthic cover and fish populations

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Received 07-IX-2013 Corrected 23-II-2014 Accepted 24-III-2014

Abstract: Grenada is highly dependent on coral reefs as a source of food and to support tourism. Local and global environmental stressors threaten these reefs. Legislation was created for this MPA in 2001, permanent mooring buoys were deployed in 2009 and enforcement of fishing restrictions began in 2010. Initiatives to address point and nonpoint source pollution from the land have recently begun, aimed at reducing stress on reef area. This study documents benthic cover and fish populations associated with reefs in a Marine Protected Area (MPA) along Grenada's southwest coast from 2008 through 2012. Both Point Line Intercept and Photo Quadrat methods were used to assess benthic cover along permanent 30m transects (8 in and 12 outside the area) annually. Fish and *Diadema antillarum* urchin relative abundance were determined based on 2m wide belt surveys along the same transects. The predominant substrate cover was algae, ranging from 41% in 2009 to 74.2% in 2011. A general trend of increasing algal cover was noted. Combined annual survey results prior (2008-2010) and after controls were implemented (2011-2012) showed a significant increase in algal cover. The predominant algal form was macroalgae comprising 65.4% - 90.8% of total algae. Live hard coral percent cover ranged from 8.7% to 21.1%. Little annual variation was observed in percent live coral cover. Branching corals (34.1% - 52.3% of total living hard coral) were the most common. Of the 19 living hard coral species identified, *Porites porites* (21%-23%) and *Porites astreoides* (20%) dominated percentage composition. *Madracis mirabilis* contributed 21% of total live hard coral outside the MPA but only 8.7% in the MPA. Of the 63 species of fish identified in the study areas *Chromis spp.* (71.5% - 46%) was the dominant group. Wrasse had a significant increase from 6.9% in 2008 to 21.5% in 2010 inside the MPA with a similar increase peaking in 2011 outside the MPA. There was a noticeable (though not statistically significant) increase in piscivorous fishes in the MPA in 2012. This is a promising indication that fishing restrictions in the MPA may be having an effect. *Diadema antillarum* density was low, ranging from 4.58 to 0.21 urchins/100m^2 outside and 0.28 to 0.10 urchins/100m^2 inside despite a stocking attempt in the area in 2011. Rev. Biol. Trop. 62 (Suppl. 3): 273-286. Epub 2014 September 01.

Key words: benthic cover, reef fish, monitoring, Grenada, Eastern Caribbean, marine protected area.

The Reefs at Risk Revisited report (Burke, Reytar, Spalding & Perry*,* 2011) documents Grenada as a country with high exposure to reef threats and high reef dependence. Many countries have established Marine Protected Areas (MPAs) to conserve coral reef systems thereby addressing problems associated with coral community decline (Kelleher, 1999; Guarderas, Hacker & Lubchenco*,* 2008; Graham, Barrett & Stuart-Smith, 2009; Selig & Bruno, 2010; Alvarado, Cortés, Esquivel & Salas, 2012; Crabbe, 2013). It is hoped that by protecting these areas they will recover and serve as a source of biodiversity for adjacent communities (Kelleher, 1999). In addition, MPAs help raise community awareness of the economic value of coral reefs and provide opportunities to educate the public about the threats to coral communities (Angulo-Valdes & Hatcher, 2010; Sala et al., 2013).

Since tourism is the primary industry of Grenada and the nearshore reefs are important tourist attractions, the Grenadian government established legislation for the Moliniere-Beausejour MPA on the southwest coast of the island in 2001 (Byrne, 2007; Turner, 2009). Permanent mooring buoys were established in 2009 and in 2010 warden patrols began enforcing newly established fishing and anchoring restrictions. Annual monitoring of fish and coral communities within Grenada's MPA and at similar coral communities outside the MPA began in 2008 (Anderson et al., 2012). Monitoring is an essential component of the success of this MPA (Convention on Biological Diversity, 2012). The biological data collected over the past five years can be used to inform adaptive management of the Moliniere-Beausejour MPA. The current study provides a detailed analysis of substrate cover including relative abundance of coral species as well as two years of monitoring data since implementation of MPA restrictions.

METHODS AND MATERIALS

Study Area: The Moliniere-Beausejour MPA is located along Grenada's southwest coast. Two study sites are in the MPA (Dragon Bay, 12°5'6.00"N, 61°45'45.36"W and Flamingo Bay, 12°5'30.36"N, 61°45'30.60"W) and three sites on nearby reef areas outside the MPA (Northern Exposure Shallow, 12°1'57.30"N, 61°46'14.28"W; Northern Exposure Deep, 12°2'22.14"N, 61°46'4.74"W and Quarter Wreck, 12°1'40.98"N, 61°47'0.84"W). Water depth at the study sites ranged from 5.2m-12.2m. All sites were established in 2008; in water surveys were conducted during May or June each year.

Methods: Both Point Line Intercept (PLI) and Photo Quadrat (PQ) methods were used to assess substrate type inside and outside the Moliniere-Beausejour MPA. Relative abundance of major substrate types along with fish species and *Diadema antillarum* were estimated based on a revision to the Crosby and Reese (1996) PLI method developed by Crosby and Bruckner in 2002. Three algal forms were identified in the sampling protocol: macro algae, turf algae and coralline algae. In addition live hard coral was grouped into branching, massive, plate and encrusting forms. Four 30m parallel permanent transects were set up at each of the five sampling sites. Substrate type was recorded at points at 50cm intervals along the 30m transects. Fish species and *D. antillarum* observed within a two meter wide belt along the transect tape and throughout the water column during a 10 minute scan were recorded. In order to enhance the reliability of these observations digital photographs were taken with a Canon EOS Digital Rebel XTI, with EF-S 60mm f/2.8 Macro USM lens and dual Ikelite DS160 strobe lights each 50cm along the transect tape immediately after the PLI transects were completed. An "L" shaped PVC pipe attached to the camera housing was used to maintain a 60cm distance from the substrate and provide a standard scale for size calibration. CPCe v.3.6 and v.4.0 (Kohler & Gill, 2006) was used to estimate substrate cover types in a 20cm by 20cm square within each photo. The substrate under eight randomly generated points was identified providing a total of 480 points per transect. An approximately six minute video scan of each transect at each study site was also made with a Sony HDR-SR8 in an Amphibico housing to provide a general perspective of the coral community.

Coral species encountered along transects were identified and relative abundance determined based on occurrence within 50cm by 30cm rectangles created on 2011 transect photographs using CPCe v.3.6. Scleractinian corals were identified to species level and octocorals were identified to genus unless picture quality would not allow sufficient detail for identification. Identifications were based on Humann (1993) and Sprung (1999).

Statistical Analysis: For the photo quadrat, point line intercept, and fish data a Repeated Measure Analysis of Variance (ANOVAR) with two factors, time and protection, was used to determine if the category varied by year or location (inside and outside of the MPA). All data was tested for normality, equal variance, and sphericity, and an ArcSine Root or Log transformation was used to satisfy the assumptions of normality and equal variance. A Greenhouse-Geisser correction was used for data that did not meet the assumption of sphericity. When significant differences were detected a follow up one-way ANOVA for time and a T-Test for protection were used to determine when the differences occurred. If the data did not meet the assumptions of equal variance or normality, despite transformations, the ranked values were analyzed instead. Non-normally distributed data, if deviation from normality was not severe, was still analyzed as ANOVA tests are robust to deviations from normality (Sokal & Rohlf, 1995). Additionally, before (2008-2010) and after (2011-2012) analysis using a T-Test or a non-parametric Wilcoxon test was done on the various categories to determine if enforcement measures may have had an effect. For the 2011 coral species abundance data a non-parametric Wilcoxon test was also used to determine significant differences between a particular coral species inside and outside the Marine Protected Area.

RESULTS

Substrate: Algae was the dominant substrate cover at survey sites inside and outside the MPA. Both the Point Line Intercept (PLI) and Photo Quadrat (PQ) survey methods showed a trend of increasing algal cover reaching a peak in 2011 (Fig. 1). Combining survey results prior to implementation of MPA controls

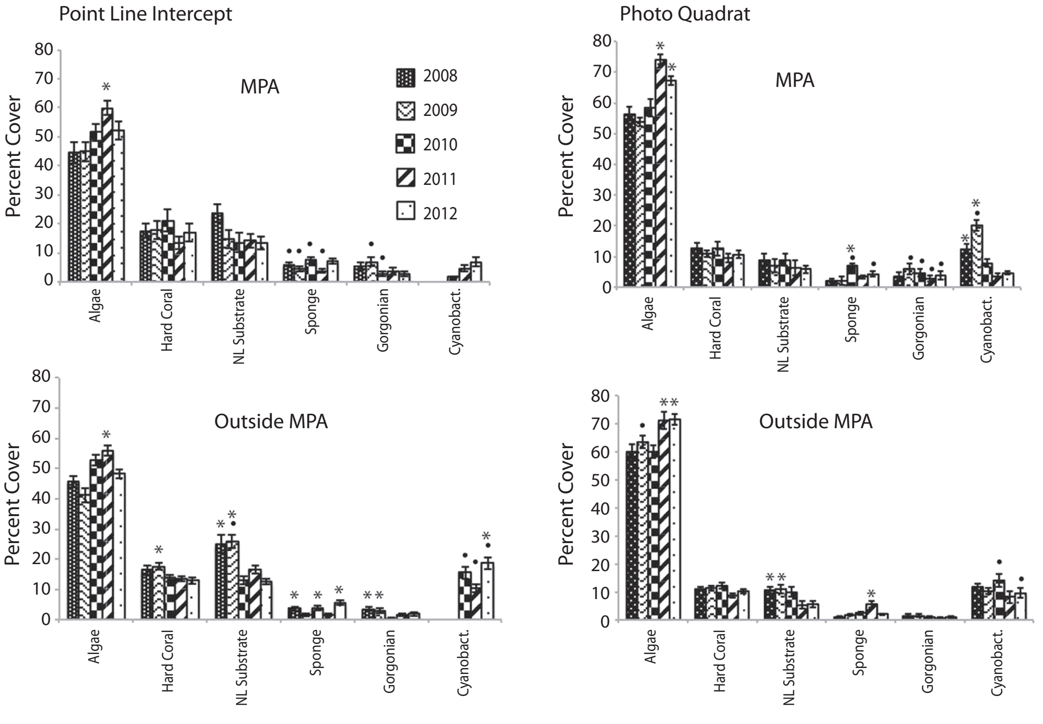

Fig. 1. Mean percent substrate cover with standard error bars based on Point Line Intercept and Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada's southwest reefs during 2008-2012. (*) Significant annual difference (ANOVAR; p<0.05) (Ÿ) Significant difference between inside and outside the MPA for that year (T-Test; p<0.05).

(2008-2010) and comparing this to combined data after MPA controls were implemented (2011-2012) showed a significant increase in algal cover for both PLI and PQ after controls were implemented both inside and outside the MPA (Table 1) (T-Test, p<0.05). Algal cover ranged from 41.1% (SE=2.3, n=60) outside the MPA in 2009 to 74.2% (1.6, 40) inside the MPA in 2011 and was not significantly different (T-Test, p>0.05) inside and outside the MPA except in 2009 PQ surveys (T-Test, p<0.05). Three algal forms were identified in the sampling protocol: macro algae, turf algae and coralline algae. Macro algae dominated ranging from 65.4% (3.1, 60) to 90.8% (1.6, 40) of the total algae found (Table 2). Both PLI and PQ surveys indicated an increasing trend for macro algae across the years although these differences were not statistically significant (ANOVAR, p>0.05). A significant difference between percent composition of macro algae inside and outside the MPA was seen only in 2011 (T-Test, p<0.05) when it reached its highest level of 90.8% in the MPA while outside the MPA it was 75.3% (2.2, 60). Percent composition of macro algae inside and outside the MPA was not significantly different (T-Test, p>0.05) after implementation of MPA controls relative to prior to implementation however it was significantly higher in the MPA in both time frames (Table 3) (T-Test, p<0.05). Turf algae had significant annual variation (ANOVAR, p<0.05) with the highest percent composition of 27.2% (6.2, 60) occurring during 2009 outside the MPA. That same year turf algae was significantly less (T-Test, p<0.05) inside the MPA only reaching 8.5% (1.7, 40) of total algae found. The contribution of turf algae to total algal composition since 2009 has been less than 7% at all sites (Table 2). The combined years comparison revealed that the proportion of turf algae decreased significantly after implementation of controls in the MPA (T-Test, p<0.05). Outside the MPA turf algae also decreased however this was not significant (Wilcoxon, p=0.089), although it was very close to being significant. Photo Quadrat results did show significantly less turf algae outside the MPA after fishing controls were implemented in the MPA (Table 3) (T-Test, p<0.05). Percent cover of coralline algae was significantly higher in 2008 and 2009 than in 2010 through 2012 (ANOVAR, p<0.05) in the PQ surveys. Percent contribution of coralline

TABLE 1

Mean percent substrate cover and standard error based on point line intercept and photo quadrat surveys inside and outside Marine Protected Areas along Grenada's southwest reefs before (2008-2010) and after (2011-2012) implementation of MPA control measures

Point Line Intercept Survey

		n	Coral	SE	Algae	SE	NL Substrate	SE	Gorgonian	SE	Sponge	SE	Cyano-bacteria	SE
MPA	Pre	24	18.8	1.8	47.0	2.0	17.2	2.0	$^{+}$5.0	0.8	$^{+}$6.0	0.6	1.6	0.4
MPA	Post	16	15.2	1.9	*56.0	2.1	13.8	1.6	3.2	0.7	5.4	0.7	*5.8	1.0
NPA	Pre	36	*15.9	0.8	46.6	1.4	*21.3	1.6	2.3	0.4	2.9	0.4	$^{+}$15.5	2.1
NPA	Post	24	13.2	0.6	*52.1	1.4	14.5	1.0	1.6	0.3	3.6	0.6	$^{+}$14.5	1.5

Photo Quadrat Survey

		n	Coral	SE	Algae	SE	NL Substrate	SE	Gorgonian	SE	Sponge	SE	Cyano-bacteria	SE
MPA	Pre	24	12.1	1.0	56.3	1.3	8.2	1.2	$^{+}$4.7	0.8	$^{+}$3.7	0.6	*13.5	1.4
MPA	Post	16	10.1	1.0	*70.8	1.4	6.0	1.3	$^{+}$3.3	0.8	3.8	0.5	4.1	0.5
NPA	Pre	36	*11.6	0.5	$^{+}$61.2	1.3	*10.5	0.9	1.3	0.2	1.8	0.2	12.1	1.0
NPA	Post	24	9.4	0.6	*71.3	1.8	5.5	0.9	0.8	0.2	*3.7	0.7	$^{+}$8.8	1.4

(*) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between pre-implementation of MPA control measures and post-implementation. ($^{+}$) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between inside and outside the MPA.

TABLE 2

Percent Composition and standard error of algal forms based on Point Line Intercept and Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada’s southwest reefs during 2008-2012

	2008		2009		2010		2011		2012	
PLI – Algae Form	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA
Macro	77.8	75.3	86.6	69.3	78.0	70.2	90.8+	75.3	82.2	75.2
S.E.	3.7	4.2	2.2	6.4	5.3	2.7	1.6	2.2	2.7	2.3
Turf	15.1	14.8*	8.5	27.2*+	3.0	2.1	0.0	2.9	5.7	6.4
S.E.	2.6	3.5	1.7	6.2	1.2	0.5	0.0	1.3	1.7	1.0
Coralline	7.2	9.9	4.9	3.5	19.0*	27.7*	9.2	21.9*+	12.1	18.4*+
S.E.	1.5	1.8	1.2	1.0	4.5	2.7	1.6	2.8	1.3	1.6
PQ - Algae Form										
Macro	70.5	68.8	69.5	65.4	78.8	74.2	87.1*	88.6*	82.2	79.9
S.E.	1.9	2.6	3.0	1.4	3.3	3.6	2.3	1.8	4.3	1.4
Turf	1.5	3.6*	0.8	0.7	4.3*	6.6*	0.1	0.4	2.9	2.9*
S.E.	0.6	1.0	0.4	0.3	1.8	1.8	0.1	0.2	0.9	0.5
Coralline	28.0*	27.6*	29.7*	33.9*	16.9	19.1	12.8	11.0	14.8	17.2
S.E.	2.4	2.9	3.3	1.4	1.6	2.1	2.3	1.8	3.5	1.1

(*) Indicates a significant annual difference (ANOVAR; p<0.05). (+) Indicates a significant difference between inside and outside the MPA (T-Test; p<0.05).

TABLE 3

Percent Composition and standard error of algal forms based on Point Line Intercept and Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada’s southwest reefs before (2008-2010) and after (2011-2012) implementation of MPA control measures

Point Line Intercept Survey

		n	Macro	SE	Turf	SE	CCA	SE
MPA	Pre	24	$^{+}$80.8	2.3	*8.9	1.5	10.4	2.0
MPA	Post	16	$^{+}$86.5	1.9	2.8	1.1	10.7	1.1
NPA	Pre	36	71.6	2.7	14.7	2.9	13.7	2.1
NPA	Post	24	75.2	1.6	4.7	0.9	$^{+}$*20.1	1.6

Photo Quadrat Survey

		n	Macro	SE	Turf	SE	CCA	SE
MPA	Pre	24	72.9	1.8	2.2	0.7	*24.9	1.8
MPA	Post	16	*84.7	2.4	1.5	0.6	13.8	2.1
NPA	Pre	36	69.5	1.6	*3.6	0.8	*26.9	1.6
NPA	Post	24	*84.3	1.4	1.6	0.4	14.1	1.2

(*) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between pre-implementation of MPA control measures and post-implementation. ($^{+}$) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between inside and outside the MPA.

algae in the PLI surveys for 2008 and 2009 were much lower than the PQ results for the same transects possibly due to under estimates by the divers. This shows the benefit of photo quadrat sampling on the same transects as the PLI surveys. The coralline algae contribution inside and outside the MPA was significantly higher before MPA controls were implemented based on PQ data (T-Test, p<0.05) however PLI results showed that coralline algae was significantly higher after MPA controls outside the MPA (Table 3) (Wilcoxon, p<0.05).

Live hard coral percent cover (Fig. 1) ranged from 8.7% (0.8, 60) outside the MPA in 2011 to 21.1% (3.9, 40) inside the MPA in 2010 with little annual variation inside or outside the MPA (ANOVAR $p>0.05$). Percent cover for live hard coral was somewhat greater inside than outside the MPA but this difference was not significant (T-Test, $p>0.05$). Combined year comparisons show in both PLI and PQ results that percent live hard coral cover did not change significantly in the MPA since implementation of control measures (T-Test, $p>0.05$). In addition there was no significant difference between live hard coral cover inside and outside the MPA (T-Test, $p>0.05$). Interestingly, live hard coral cover decreased significantly after MPA controls outside the MPA (Table 1) (T-Test, $p<0.05$). Branching coral was the predominant form of coral found on the transects ranging from 34.1% (5.3, 40) to 52.3% (5.4, 60) of all coral. The percent composition of this coral form varied little from year to year and comprised a slightly greater portion of the hard coral outside the MPA compared to within the MPA (Table 4). Combined annual results before and after implementation of MPA controls (Table 5) showed that the percent composition of branching coral did not change significantly (T-Test, $p>0.05$). Massive coral percent composition on the other hand was significantly greater inside than outside the MPA (T-Test, $p<0.05$) before but not after controls were implemented based on both the PLI and PQ surveys (Table 5). Massive and encrusting coral were similar in percent composition of the total hard coral community with no significant annual variation (ANOVAR, $p>0.05$) except for a significantly higher percent composition (T-Test, $p<0.05$) seen outside the MPA in 2012 compared to 2008 (Table 4). Percent composition of massive coral was significantly higher in the MPA in 2008 (T-Test, $p<0.05$) than outside the MPA but the difference declined somewhat through the years to the point that massive coral percent composition was higher outside the MPA in the 2012 PLI survey (Table 4).

A total of 22 coral taxa were identified (19 hard coral species and three octocoral genera) in the nearshore waters of Grenada. In the MPA *Porites porites* and *Porites astreoides* dominated the surveys (Table 6) making up

TABLE 4

Percent composition and standard error of hard coral forms based on Point Line Intercept and Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada's southwest reefs during 2008-2012

	2008		2009		2010		2011		2012	
PLI Coral Form	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA	MPA	nonMPA
Massive	24.1+	9.0	31.9	23.4	30.8	24.0	21.6	16.6	22.9	28.8*
S.E.	5.3	1.6	5.1	3.5	5.8	4.5	5.8	4.8	2.6	6.1
Branching	36.6	38.2	44.9	47.8	41.9	50.5	42.7	40.4	44.4	52.3
S.E.	7.2	5.2	4.8	4.8	9.6	5.2	8.4	5.2	6.9	5.4
Encrusting	34.2	49.6*	19.4	23.2	21.3	21.5	32.0	36.7	27.5	16.6
S.E.	9.9	5.7	1.9	3.5	7.6	2.7	8.3	4.5	7.4	2.7
PQ Coral Form										
Massive	43.3+	27.6	33.2	27.7	35.9	24.5	33.2	31.7	37.3	30.1
S.E.	4.4	4.3	4.3	4.4	2.7	4.2	4.7	5.2	2.6	4.6
Branching	38.9	46.9	35.9	50.1	40.1	44.7	36.8	41.2	34.1	45.3
S.E.	6.1	7.1	6.4	4.4	6.4	4.9	7.2	5.7	5.3	5.5
Encrusting	16.3	24.7	24.3	20.3	23.6	28.1	24.5	20.2	24.1	22.5
S.E.	3.0	4.6	6.0	2.3	4.9	3.7	7.1	2.7	4.5	2.4

(*) Indicates a significant annual difference (ANOVAR; $p<0.05$). (+) Indicates a significant difference between inside and outside the MPA (ANOVAR; $p<0.05$).

TABLE 5
Percent composition and standard error of hard coral forms based on Point Line Intercept and Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada's southwest reefs before (2008-2010) and after (2011-2012) implementation of MPA control measures

Point Line Intercept Survey

		n	Massive	SE	Branching	SE	Encrusting	SE
MPA	Pre	24	$^{+}$28.9	3.1	41.2	4.2	25.0	4.3
MPA	Post	16	22.2	3.1	43.5	5.2	29.7	5.4
NPA	Pre	36	18.8	2.2	45.5	3.0	31.4	3.2
NPA	Post	24	22.7	4.0	46.3	3.9	26.7	3.3

Photo Quadrat Survey

		n	Massive	SE	Branching	SE	Encrusting	SE
MPA	Pre	24	$^{+}$37.5	2.3	38.3	3.5	21.4	2.7
MPA	Post	16	35.3	2.7	35.4	4.3	24.3	4.1
NPA	Pre	36	26.6	2.4	47.2	3.1	24.3	2.1
NPA	Post	24	30.9	3.4	43.3	3.9	21.3	1.8

(*) Indicates a significant difference (T- Test; $p<0.05$ or Wilcoxon; $p<0.05$) between pre-implementation of MPA control measures and post-implementation. ($^{+}$) Indicates a significant difference (T- Test; $p<0.05$ or Wilcoxon; $p<0.05$) between inside and outside the MPA.

TABLE 6
Mean frequency of occurrence of coral species and standard error based on Photo Quadrat surveys inside and outside Marine Protected Areas along Grenada's southwest reefs during 2011

Taxon	MPA	SE	non-MPA	SE	Taxon	MPA	SE	non-MPA	SE
Colpophyllia natans	0.5	0.15	0.1*	0.06	*Madracis formosa*	5.6*	0.49	2.3	0.28
Dichocoenia stokesi	0.1	0.08	0	0.00	*Madracis mirabilis*	8.7	0.72	21*	1.03
Diploria labyrinthiformis	0.4	0.17	0.1	0.05	*Porites porites*	21	0.98	23	0.98
Diploria strigosa	0.8	0.15	0.7	0.18	*Agaricia agaricites*	1.8*	0.25	0.3	0.09
Meandrina meandrites	0.5*	0.10	0.1	0.05	*Agaricia lamarcki*	0.3*	0.11	0	0.00
Montastraea annularis	0.4	0.15	2.5*	0.37	*Millepora alcicornis*	0.5	0.13	1.2*	0.23
Montastraea cavernosa	5.3*	0.52	1.2	0.19	*Millepora complanata*	1.4	0.30	1.4	0.23
Montastraea faveolata	2.9	0.37	5.5*	0.47	*Porites astreoides*	20	0.94	20	0.81
Siderastrea siderea	7.3*	0.55	2.9	0.38	*Pseudopterogorgia*	11*	0.65	3	0.35
Dendrogyra cylindrus	0	0.03	0.1	0.09	*Gorgonia*	0.8	0.15	0.7	0.19
Eusimilia fastigiata	0.3	0.12	0.1	0.05	*Erythropodium*	0.1	0.08	0.1	0.05
					Unknown Coral	7.1	0.57	11	0.65

(*) Indicates a significant difference between MPA (n=478) and nonMPA (n=714) sites (Wilcoxon test; ChiSquare approximation $p<0.05$).

21% (1.0, 478) and 20% (0.9, 478) of the live coral cover respectively and no significant difference in percent composition outside the MPA (Wilcoxon, $p>0.05$) was found. *Madracis mirabilis* was also a major coral species outside the MPA making up 21% (1.0, 714) of the live coral cover however it was significantly lower (Wilcoxon, $p<0.05$) at 8.7% (0.7, 478) in the MPA. Massive corals *Montastraea cavernosa* and *Siderastrea siderea* occurred more frequently in the MPA (Wilcoxon, $p<0.05$) while *Montastraea annularis* and *Montastraea faveolata* occurred more often outside the MPA (Wilcoxon, $p<0.05$). Soft coral, *Pseudopterogorgia* spp., was more prevalent in the MPA where it made up 11% (0.7, 478) of the total substrate cover compared to the 3% (0.4, 714) outside the MPA (Wilcoxon, p<0.05). The species *Dichocoenia stokesi* and *Agaricia lamarcki* were only found in the MPA.

Fish: Of the 63 species of fish observed along transects inside and outside the MPA (Table 8) *Chromis* spp. was the dominant group (Fig. 2). Through the five years of the study the relative composition of *Chromis* spp. declined from 71.5% (4.2, 40) of the total fish recorded to 46.0% (4.9, 40) in the MPA. Outside the MPA *Chromis* spp. also declined from 2008 through 2011 but increased to nearly the 2009 level in 2012. None of these annual variations were statistically significant (ANOVAR, p>0.05). The proportion of Wrasses increased significantly in the MPA from 6.9% (1.5, 40) in 2008 to 21.5% (4.4, 40) in 2010 (ANOVA p<0.05) but declined in 2011 and 2012. Outside the MPA the proportion of wrasses increased significantly from 6.9% (1.6, 60) in 2008 to 20.4% (3.9, 60) in 2011 (ANOVA, p<0.05) but declined to 12.8% (2.7, 60) in 2012. Percent composition of territorial Damselfishes has remained fairly constant across years in the 10% range (ANOVAR p>0.05). Parrotfishes and Surgeonfishes also remained steady from year to year around the 5% (ANOVAR, p>0.05) and 1% (ANOVAR, p>0.05) range respectively in the MPA. A similar annual pattern for Parrotfishes and Surgeonfishes was seen outside the MPA; however in 2008 (T-Test, p<0.05) and 2011 (T-Test, p<0.05) percent composition of Parrotfishes was significantly higher outside compared to inside the MPA (Fig. 2). Analysis of combined annual results prior to implementation of fishing controls and after implementation showed no significant change for the major groups of fishes observed along transects inside and outside the MPA (T-Test, p>0.05). The only exception to this was a significant increase in wrasse outside the MPA after implementation of fishing controls (T-Test, p<0.05) (Table 7).

The fish observed along transects were grouped based on their feeding habits following Sandin, Sampayo and Vermeij (2008). Planktivores, comprised mainly of Blue and Brown Chromis as well as Bicolor Damselfish, dominated the feeding groups' percent composition (Fig. 3). Percent composition of planktivores was significantly greater inside than outside the MPA in 2011 and significantly higher in 2008 and 2011(T-Test, p<0.05). Herbivores, made up of Parrotfishes, territorial Damselfishes, and Surgeonfishes, ranked second among the percent composition of feeding groups and were significantly greater outside the MPA in 2008 (T-Test, p<0.05) and 2011 (T-Test, p<0.05). There was a large increase in the piscivore feeding group in the MPA during 2012; however this increase was not significant

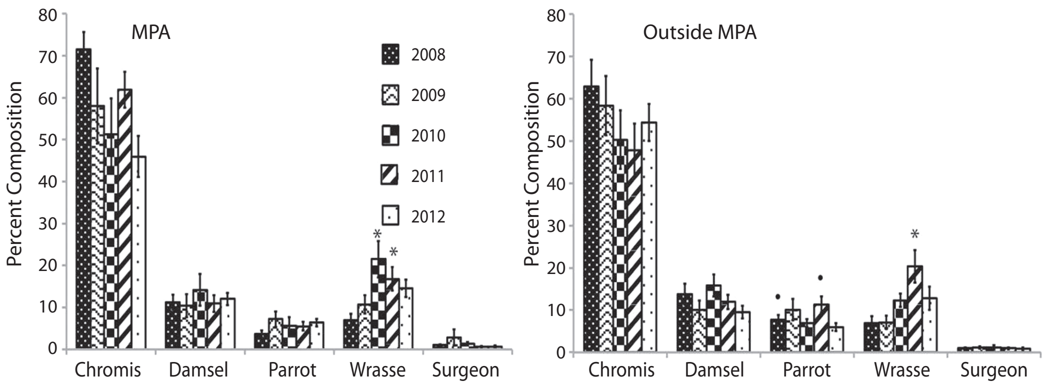

Fig. 2. Mean percent fish composition with error bars (SE) based on belt transect surveys inside and outside Marine ProtectedAareas along Grenada's southwest reefs during 2008-2012. (*) Indicates a significant annual difference (ANOVAR; p<0.05) (Ÿ) Indicates a significant difference between inside and outside the MPA (T-Test; p<0.05).

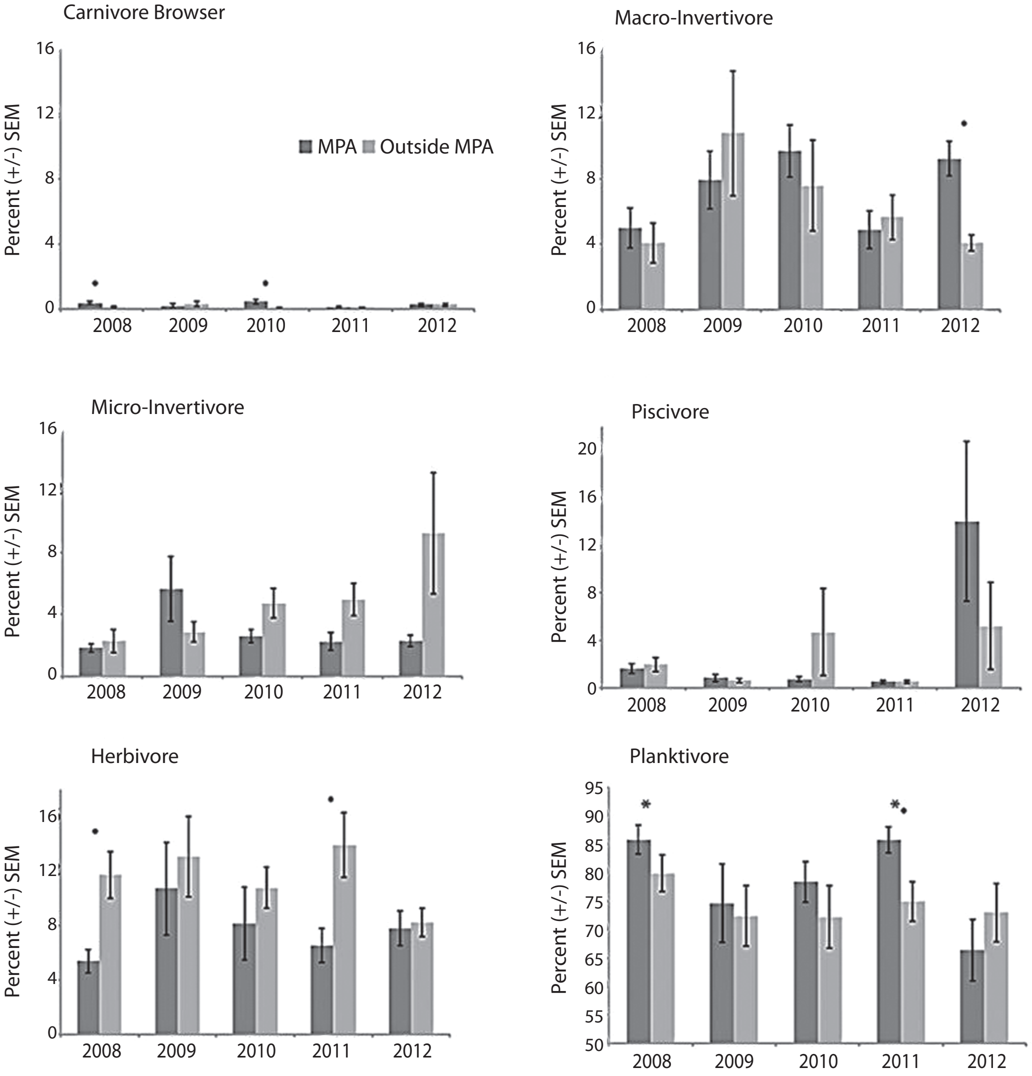

Fig. 3. Mean percent composition of fish feeding groups with error bars (SE) based on belt transect surveys inside and outside Marine Protected Areas along Grenada's southwest reefs during 2008-2012. (*) Significant annual difference (ANOVAR; p<0.05) (^{Ÿ}) Significant difference between inside and outside the MPA (ANOVAR; p<0.05).

TABLE 7

Mean percent fish composition with error bars (SE) based on belt transect surveys inside and outside Marine Protected Areas along Grenada's southwest reefs before (2008-2010) and after (2011-2012) implementation of MPA control measures

		n	Chromis	SE	Damsel	SE	Parrotfish	SE	Wrasse	SE	Surgeon	SE
MPA	Pre	24	60.3	4.5	11.9	1.6	5.5	1.0	13.1	2.1	1.8	0.7
MPA	Post	16	53.9	3.8	11.5	1.2	5.9	0.7	15.7	1.7	0.6	0.1
NPA	Pre	36	57.2	3.9	13.2	1.4	8.3	1.0	8.8	1.0	1.1	0.2
NPA	Post	24	51.1	3.8	10.7	1.1	8.6	1.2	*16.6	2.5	0.9	0.2

(*) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between pre-implementation of MPA control measures and post-implementation. ($^{+}$) Indicates a significant difference (T- Test; p<0.05 or Wilcoxon; p<0.05) between inside and outside the MPA.

TABLE 8

Fish species observed during surveys at five sampling locations over Grenada’s southwest coastal reefs during 2008-2012

- **Acanthuridae**
  - *Acanthurus coeruleus*
  - *Acanthurus chirurgus*
  - *Acanthurus bahianus*
  - *Acanthurus* spp.
- **Apogonidae**
  - *Apogon townsendi*
  - *Apogon* spp.
- **Aulostomidae**
  - *Aulostomus maculatus*
- **Balistidae**
  - *Monacanthus* spp.
- **Blenniidae**
  - *Blennidea* spp.
- **Bothidae**
  - *Bothus lunatus*
- **Carangidae**
  - *Carangoides ruber*
  - *Decapterus macarellus*
- **Cirrhitidae**
  - *Amblycirrhitus pinos*
- **Chaetodontidae**
  - *Chaetodon capistratus*
  - *Chaetodon striatus*
  - *Chaetodon* spp.
- **Diodontidae/Tetraodontidae**
  - *Canthigaster rostrata*
- **Gobiidae**
  - *Coryphopterus glaucofraenum*
  - *Coryphopterus hyalinus*
  - *Elacatinus genie*
  - *Coryphopterus lipernes*
- **Muraenidae**
  - *Echidna catenata*
- **Haemulidae**
  - *Haemulon chrysargyreum*
  - *Haemulon flavolineatum*
  - *Haemulon* spp.
- **Holocentridae**
  - *Myripristis jacobus*
  - *Holocentrus rufus*
  - *Holocenthus coruscus*
  - *Holocentrus adscensionis*
- **Grammatidae**
  - *Gramma loreto*
- **Labridae**
  - *Thalassoma bifasciatum*
  - *Clepticus parrae*
  - *Halichoeres bivittatus*
  - *Bodianus rufus*
  - *Halichoeres garnoti*
  - *Xyrichtys* spp.
- **Lutjanidae**
  - *Lutjanus synagris*
  - *Lutjanus mahogoni*
  - *Ocyurus chrysurus*
  - *Lutjanus* spp.
- **Mullidae**
  - *Pseudupeneus maculatus*
  - *Mulloidichthys martinicus*
- **Ophichthidae**
  - *Myrichthys breviceps*
- **Ostraciidae**
  - *Acanthostracion quadricornis*
  - *Acanthostracion polygonius*
- **Priacanthidae**
  - *Priacanthus arenatus*
- **Pomacentridae**
  - *Holacanthus tricolor*
  - *Chromis cyanea*
  - *Chromis multilineata*
  - *Stegastes partitus*
  - *Abudefduf saxatilis*
  - *Stegastes leucostictus*
  - *Stegastes diencaeus*
  - *Stegastes planifrons*
  - *Microspathodon chrysurus*
- **Scaridae**
  - *Scarus vetula*
  - *Sparisoma aurofrenatum*
  - *Sparisoma viride*
  - *Scarus* spp.
- **Sciaenidae**
  - *Equetus lanceolatus*
  - *Equetus punctatus*
- **Scorpaenidae**
  - *Scorpaena plumieri*
- **Serranidae**
  - *Cephalopholis fulva*
  - *Cephalopholis cruentata*
  - *Serranus tigrinus*
  - *Hypoplectrus* spp.
  - *Hypoplectrus guttavarius*
  - *Hypoplectrus chlorurus*
- **Synodontidae**
  - *Synodus intermedius*

due to the high variation in the data (ANOVAR, $p>0.05$). Combining percent composition of fish feeding groups results revealed that carnivorous microinvertivore feeders were significantly more abundant outside the MPA than inside after implementation of controls in the MPA (T-Test, $p<0.05$). Herbivorous fishes were significantly more abundant outside the MPA than inside before and after implementation of MPA controls (Table 9) (T-Test, $p<0.05$).

Diadema antillarum: Density of *Diadema antillarum* has been consistently greater outside than inside the MPA during 2008 through 2012. Density ranged from 4.58 urchins/$100m^2$ (2.3; 24) outside the MPA in 2008 to 0.1

TABLE 9
Mean percent composition of fish feeding groups with error bars (SE) based on belt transect surveys inside and outside Marine Protected Areas along Grenada's southwest reefs before (2008-2010) and after (2011-2012) implementation of MPA control measures.

		n	Carnivore Browser	SE	Carnivore Macro-invertivore	SE	Carnivore Micro-invertivore	SE	Carnivore Piscivore	SE	Herbivore	SE	Planktivore	SE
MPA	Pre	24	0.3	0.1	7.6	0.9	3.4	0.8	1.1	0.2	8.1	1.5	79.6	2.8
MPA	Post	16	0.2	0.1	7.1	0.9	2.3	0.3	7.3	3.7	7.2	0.9	76.0	3.8
NPA	Pre	36	0.2	0.1	7.5	1.7	3.3	0.5	2.4	1.2	$^{+}$11.9	1.2	74.8	2.8
NPA	Post	24	0.2	0.1	4.9	0.7	$^{+}$*7.1	2.0	2.9	1.9	$^{+}$11.1	1.4	73.9	3.0

(*) Indicates a significant difference (T- Test; $p<0.05$ or Wilcoxon; $p<0.05$) between pre-implementation of MPA control measures and post-implementation. ($^{+}$) Indicates a significant difference (T- Test; $p<0.05$ or Wilcoxon; $p<0.05$) between inside and outside the MPA.

TABLE 10
Mean *Diadema antillarum* density (urchins/100m^2) with error bars (SE) based on belt transect surveys inside and outside the Marine Protected Area along Grenada's southwest reefs during 2008-2012.

	MPA			Outside MPA		
	n	Mean Density	SE	n	Mean Density	SE
2008	8	0.28	0.19	12	4.58	2.30
2009	8	0.73	0.46	12	2.29	0.81
2010	8	0.10	0.12	12	0.21	0.11
2011	8	0.10	0.12	12	0.49	0.29
2012	8	0.10	0.12	12	1.04	0.55

urchins/100m^2 (0.1; 16) in the MPA during the 2010 - 2012 surveys. There is a general decline in density across the years (Table 10).

DISCUSSION

Nearshore coral reefs are suffering from local as well as global environmental impacts. Local impacts such as overfishing, nutrient and soil runoff from farms, municipal pollution and damage from tourist activities combine with the impacts of global climate change to cause degradation of coral communities (Gardner, Côte´, Gill, Grant & Watkinson, 2003; Burke & Maidens, 2004; Knowlton & Jackson, 2008; Burke et al., 2011; Jackson et al., 2012). Changes in global climate have resulted in ocean temperatures high enough to cause bleaching and stress to corals (Baker, Glynn & Riegl, 2008; Bruckner & Hill, 2009; Cantin et al., 2010; Eakin et al., 2010; Buddemeier, lane & Martinich, 2011; Riegl, Berumen & Bruckner, 2013). Local impacts such as increased nutrient levels have now been shown to increase sensitivity of corals to bleaching (Wiedemann et al., 2013). Increased CO_2 levels in the atmosphere drive higher CO_2 levels in ocean water reducing pH that in turn hampers formation of the calcium carbonate skeletons of some coral species (Ries, Stanley & Hardie, 2006, Fine & Tchernov, 2007; Riegl, Bruckner, Coles, Renaud & Dodge, 2009). Marine Protected Areas have the potential to offer some relief from the local stressors thereby increasing potential resilience of the coral community to impacts associated with climate change (Riegl et al., 2009; Selig & Bruno, 2010; Riegl et al., 2013). The purpose of this study is to monitor the coral reef community in Grenada's MPA as various management practices are implemented.

The five years of data compiled in this study to date confirm concerns that Grenada's nearshore reefs are at risk as indicated in Burke et al. (2011). The general increase in macro algal cover and low percent live coral cover are clear indicators of continued local as well as global stresses. High relative percent of macro algae compared to turf and coralline algae both inside and outside the MPA are indicators of high nutrient levels and overfishing (Littler & Littler, 2007; Sandin et al., 2008). The greater proportion of branching corals compared to massive corals and the high relative percent of non-framework building corals (Gardner et al., 2003) such as *Porites porites, Madracis mirabilis*, and *Porites astreoides* (Table 4) are not indicative of a resilient coral reef system. The predominance of planktivorous fishes and low percent composition of piscivores are likely a result of selective overfishing and nutrient loading (Knowlton & Jackson, 2008; Sandin, 2008; Jackson et al., 2012).

Grenada's Moliniere-Beausejour MPA encompasses an important portion of the reefs along Grenada's southwest coast and improvement in the reef community in the MPA has the potential for improving all of the coral reef communities along the southwest shore (Angulo-Valdes & Hatcher, 2009; Crabbe, 2013; Sala et al., 2013). Fishing restrictions and required usage of permanent mooring structures have been implemented in the MPA. The MPA is patrolled and information campaigns highlighting the role and importance of the MPA have targeted fishermen as well as the general public on the island. An attempt to reduce macro algae in the MPA by introducing *D. antillarum* in 2011 (Nimrod, 2012) did not result in a detectible increase in urchin density during surveys in 2011 or 2012 (Table 10) and in fact *D. antillarum* density in the MPA was actually lower in 2010 through 2012 than in the previous two years. Comparison of combined annual survey data before MPA controls were implemented (2008-2010) to surveys after implementation (2011-2012 show that algal cover on the reef has increased significantly both inside and outside the MPA. This algal increase along with some reduction in live hard coral cover suggests that protection measures have not yet impacted the benthic reef community. To date no significant changes in the benthic or fish community have been recorded in the MPA. It is interesting to note however that there was an increase in piscivores and a slight decline in planktivores in the MPA in 2012 (Fig. 3, Table 9). These results may be an indication that additional measures need to be taken to enhance the MPA. Measures implemented thus far target fishing and physical damage to the reef. Since excess nutrient runoff from shore is a potential driver of algal growth this may be an important issue to be addressed by all concerned with marine resources.

Studies of local nutrient runoff from point and nonpoint sources on local farmland and municipal areas are under development. In addition the government of Grenada Fisheries Division will soon be implementing a modified version of the Great Barrier Reef Marine Park Authority 'Reef Guardian' educational program for groups including farmers (pers. comm. C. Andrew 2013). It is hoped that follow through on these initiatives may help to reduce the stresses posed to this coral community.

This ongoing nearshore monitoring study is focused on those reefs used most extensively by Grenada's dive and snorkel industry. It is hoped that the data collected will assist in raising public awareness of conditions on the reefs and also assist MPA managers in applying effective management practices. Enhanced reefs in the nearshore waters of Grenada's southwest shore could result in a boost to the island's economy through increased interest in dive tourism. With appropriate regulation of tourist and local user activities this area will be a sustainable resource for Grenada.

ACKNOWLEDGMENTS

Funding for this project was provided by the Fischer Family Foundation and Gary Stimac and is greatly appreciated. Thanks are also offered to Jacob Krause, Jillian Groeschel, Kyle Foster, Svetlana Bornschlegl, Victoria Krueger, Thomas Dietrich, Ben Hermanson, Laurelyn Dexter, Angela Majeskie, Allison

Page, and Angela Blasezyk, Andrew Dunlop, Nate Sorum, Joe DuFore, Courtney Moll, Arielle Schildback, Heather McLain and Henry Tews for data collection. Billie Harrison of the Milwaukee County Zoo is thanked for expert field work.

RESUMEN

Monitoreo en aguas cercanas al área marina protegida en la costa de Granada, Caribe Oriental: cobertura bentónica y poblaciones de peces. Granada es muy dependiente de los arrecifes coralinos como fuente de alimento y apoyo al turismo. Factores estresantes locales y globales amenazan con estos arrecifes. La legislación fue creada para esta área protegida en el 2001, boyas de amarre fueron colocadas en 2009 y las restricciones a la pesca comenzaron a implementarse a partir del 2010. Iniciativas para reducir el estrés por contaminación terrestre, de fuentes puntuales y no-puntuales, en la zona comenzaron recientemente. Este estudio documenta la cobertura bentónica y poblaciones de peces asociados a los arrecifes del área marina Protegida (MPA) a lo larfo de la costa suroeste de Granada del 2008 al 2012. Se utilizaron los métodos de Punto Línea Intercepción (PLI) y Cuadrantes Fotográficos (PQ) para evaluar anualmente la cobertura bentónica a lo largo de transectos permanentes de 30m (ocho dentro y 12 fuera del MPA). La abundancia relativa de peces y del erizo negro *Diadema antillarum* a través de censos visuales de 2m de ancho a lo largo de los mismos transectos lineales. La cobertura de sustrato estuvo dominada por algas con 41% en 2009 y 74.2% en 2011. Se notó una tendencia general de aumento en la cobertura algal. La combinación de los resultados antes de las encuestas (2008-2010) y después de la implementación de los controles del MPA (2011-2012) mostró un aumento significativo en la cobertura algal. La forma algal predominante fue macroalgas que consta el 65.4% y el 90.8% del total de algas. El porcentaje de cobertura de coral durovarió entre un 8.7% y un 21.1%. Se observó una pequeña variación anual en el porcentaje de cobertura de coral vivo. Los corales ramificados (34.1%-52.3% del total de corales duros) fueron la forma de coral más común encontrada durante el estudio. De las 19 especies de corales duros identificados, *Porites porites* (21% - 23%) y *Porites astreoides* (20%) dominaron el porcentaje de composición. *Madracis mirabilis* contribuyó en un 21% del total de corales duros fuera del MPA pero solo un 8.7% en el MPA. De las 63 especies de peces identificadas en el área de estudio *Chromis spp.* (71.5% - 46%) fue el grupo dominante. Los lábridos (Labridae) mostraron un aumento significativo de su abundancia de un 6.9% en 2008 a un 21.5% en 2010 dentro del MPA con un pico de incremento similar en el 2011 fuera de la MPA. Hubo un aumento notable (aunque no significativo estadísticamente) en los peces piscívoros dentro del MPA en 2012. Esto es una indicación prometedora de que las restricciones de pesca en la MPA pueden estar dando efecto. La densidad de *Diadema antillarum* fue baja, osciló entre 4.58 y 0.21 erizos/100m^2 fuera del MPA y entre 0.28 y 0.10 erizos/100m^2 dentro del MPA a pesar de la existencia de un programa de repoblación de la especie llevado a cabo en el 2011.

Palabras clave: cubierta bentónica, peces de arrecife, monitoreo, Granada, área protegida del Caribe, Marina oriental.

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Capacity building and policy development in Belize marine protected areas, an example for Caribbean integrated coastal management

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Received 01-VIII-2013 Corrected 04-II-2014 Accepted 24-III-2014

Abstract: Sustainability science can, through capacity building, allow for integrated stakeholder management of the vital Caribbean marine ecosystems. We did a capacity building exercise in two major coral reef areas in Southern Belize. The key outcome was a six-month personal/professional action plan developed by each participant about tactics for leading, educating and supporting issues regarding sustainable development and tactics for collaboration to influence policy decisions. Our results can be applied across the Caribbean. Rev. Biol. Trop. 62 (Suppl. 3): 287-291. Epub 2014 September 01.

Key words: hurricanes, bleaching, MPAs, climate change, global warming, Belize, Jamaica.

Against a backdrop of natural and anthropogenic insults, an important question is: how can management practices maintain sustainable coral reef ecosystems? Integrated Coastal Zone Management (ICZM) is a complex worldwide governance issue requiring an integrated or coordinated approach. It involves many relevant stakeholders and policy initiatives need to be developed over long time scales. Ideally, marine ecosystems (i.e., corals and seagrass beds) should be closely linked to terrestrial ecosystems such as mangroves and coastal forests. In developing management policies, education and training to enhance human skills and institutional capacity in resource management is critical (Wescott, 2002). Both developed and developing countries have used capacity-building programs (Kaplan, Liu & Hannon, 2006; Rogers, Johnson, Warner, Thorson & Punch, 2007). While many, if not all, of these programs involve building competencies and empowerment in local communities, few of them involve policy makers or government officials (Mequanent & Taylor, 2007). Partnerships can be vital for ICZM, particularly where government policies link to local stakeholders (e.g., beach clean-up groups and marine wildlife associations) to produce collaborations that can involve people with vested interests in the coastal ecosystem (e.g., fishers, tour operators) and in ongoing management frameworks.

The effective application of ICZM to coral-reef ecosystems should address a number of themes including:

1. Use of ecosystem and economic parameters to quantify the needs of marine reserves.
2. Development of tactics for leading, educating, and supporting issues regarding sustainable development of coral reef ecosystems.
3. Incorporation of all relevant stakeholders into the formulation of policy issues pertaining to marine resource management zoning plans.

We therefore undertook a capacity-building exercise around Marine Protected Areas (MPAs) which involved both local Belizean

NGO community workers and a government fisheries officer, so that community engagement could be directly interfaced with fisheries operations and policy. Our methodology involved the development of personal action plans to facilitate the future of sustainable MPAs in the MesoAmerican Barrier Reef system. Our approach meant that each individual produced plans that reflected not only their own priorities, but were tailored to their own abilities. Team discussion meant that personal plans were interlaced throughout the group, so that the whole became greater than the sum of the parts.

MATERIALS AND METHODS

Capacity building: We undertook the capacity building exercise in respect of two MPAs in Southern Belize. There are two major coral reef areas in Southern Belize, the Sapodilla Cayes Marine Reserve (SCMR, a World Heritage Site), and the Port Honduras Marine Reserve (PHMR). The SCMR is a 125km^2 reserve and has had a collaborative agreement with the Belize Fisheries Department and the Toledo Association for Sustainable Tourism and Empowerment (**TASTE**) to manage the area since its declaration in 1996. The PHMR is a 414km^2 reserve, and has been managed by the Toledo Institute for Development and Environment (**TIDE**) since its declaration in January 2000.

The capacity building team consisted of one officer from the Belize Fisheries Department, three senior officers from NGOs involved in managing Belize MPAs (TIDE, TASTE and Friends of Nature), and a Facilitator (the author of this paper) from the UK. These individuals were chosen because they had direct contact with both NGOs (Non-governmental organisations) and CBOs (Community-based organisations), and the government Fisheries Department, thus maximising exposure of capacity building while keeping the numbers of participants within workable limits. Daily meetings, lasting between 1-2h, took place on Lime Caye in the SCMR, Abalone Caye in the PHMR, and in Punta Gorda Town, over a 10-day period in August 2007. Discussions, led by the Facilitator employed a modified nominal group technique (Sample, 1984) to identify priorities related to personal action plans. Four rounds were employed; round one was based on the Delphi technique and further rounds on the nominal group technique approach (McCance, Fitzsimons, Keeney, Hasson & McKenna, 2007). Specifically, after initial meetings which revolved around frank discussions on the interface been the Fisheries Department and MPA management by NGOs, each participant developed a personal action plan to facilitate and improve the sustainability of the MPAs in Southern Belize. There was repeated iteration of these plans between the participants, and the final production of a policy for sustainable management of both the marine reserves in the Sapodilla Cayes and in Port Honduras.

RESULTS

Capacity building outcomes: The key outcome was a six-month Personal/Professional Action Plan developed by each Belizean participant outlining how they will personally and professionally strive to meet the capacity-building objectives above, and influence policy development. Specifically these plans involved:

a. Tactics for leading, educating and supporting issues regarding sustainable development in Southern Belize; and
b. Tactics for collaboration with other stakeholders to collectively influence policy decisions in Southern Belize.

Discussion among the participants and facilitator as described in the Field methodology section resulted in the generation of a series of tactics to be adopted around a number of themes *viz*: Organisation and management, Education, Support and Policies (Crabbe et al., 2010). Table 1 identifies a set of twelve management operational needs identified by the participants as their united action plan that

TABLE 1

1. Ecosystem zonation redesignated to balance stakeholders' wishes and evidence-based fisheries catches.
2. A community-based research program developed via participants. This involved local fishers, with qualitative and/or quantitative research methods.
3. Data of high accuracy recorded. Quantitative ecosystem data needs to be verified statistically.
4. Co-management plans between NGOs, communities and fisheries departments to address problems of illegal fishermen from states or countries outside the governance of the MPAs. This is a significant problem in reef areas close to Belize.
5. Regular public meetings of stakeholders fostered, as well as regular education events. Action plans were developed and monitored by staff and stakeholders alike.
6. Effectiveness of zoning monitored and quantified. This relates to fishing practices as well as ecosystem health.
7. Alternative livelihoods for fishers (e.g., in the tourist industry) fostered and maintained. Government agencies were involved in linking tourism and economic development.
8. Tourists monitored and encouraged sustainably. All stakeholders were involved, with penalties for unsustainable practices.
9. Effective management linked to the country's economy. This is helped in Belize as fishing, and tourism are both important parts of the country's gross domestic product (GDP).
10. NGOs and MPAs link together. In areas where different NGOs are responsible for MPA management, as in the MesoAmerican Barrier Reef, and where MPAs are distant from one another, it was helpful to link both NGOs and MPAs so that a greater area of reef could be managed
11. Regular information to all stakeholders, from the politicians to the local communities, maintained. Communication linked to the communities served (e.g. some oral, some printed, some via internet).
12. Management plans passed into law. The involvement of government officers –e.g., fisheries officers– as partners is key to this important outcome, to ensure appropriate policing if resources are made available.

involved partnerships among government, non-governmental organizations (NGOs), and communities to improve ICZM. Each individual member then implemented their action plans and the united action plan with the communities that they represented.

DISCUSSION

Marine Reserves are an important tool in sustainable management of the Belizean coral reefs (Cho, 2005; Williams & Polunin, 2000). The need for case studies in building integrated coastal management capacity has been powerfully made (Jorge, 1997; McDuff, 2001; Wescott, 2002). Normally representatives of all stakeholders (including fishermen, dive-boat operators, etc) would be included in such a capacity-building exercise. Our particular process was chosen as it represented key stakeholders in the MPAs of Belize, while being an efficient way of engaging a Facilitator from abroad. Targeting a government ministry worker and policy maker is a relatively new approach in this area. Our study group members were highly focused and motivated to improving management of the Belize MPAs, and were strongly committed to both short- and long-term acceptance of the study group's goals for sustainability and resource management by stakeholder groups. One reason for this was the experience and responsibilities of the individuals concerned – selection as to who was in the group was a key operational factor. However two groups were missing from the capacity-building exercise – someone from the political arena, and someone from the University of Belize. We feel that it will be important in the future to involve both these sectors, the former to ensure that policy development becomes law, and the latter to ensure the sustainable monitoring of the reefs. Political engagement is of particular interest, as unlike the Great Barrier Reef, where management is the responsibility of a single country, Australia, the Mesoamerican Barrier Reef is managed by Mexico, Belize, Guatemala and Honduras, all countries which have different management policies.

Our capacity building case study has produced new ideas to improve organisation, management, education, support, and policy development in MPAs in Southern Belize. In addition, we suggest that MPAs need to share regulation, enforcement and conservation, underpinned by scientific research. A major challenge for the participants in this exercise will be to maintain iterations among and between their constituent groups to ensure continued sustainability of both the reef and the fishing practices.

The involvement of a Fisheries officer in our capacity building has resulted in direct transfer of information from the communities to the Government department. The Facilitator has also directly communicated the outcomes of our study to the Director of Fisheries. The personal action plans that were produced have been implemented, taken back into their constituent communities, and the NGOs TASTE and Friends of Nature have been incorporated into a single NGO, which spans several MPAs in Southern Belize. Previously, there were areas between MPAs that were not monitored or policed, resulting in much illegal fishing. Our approach is also part of a wider picture in marine resource management in Belize, where, for example, communities and fishermen are being exhorted not to catch parrotfish (*Scaridae*), as grazing by that species is critical to reef resilience and restoration (Mumby, Hastings & Edwards, 2007). In summary, our approach is part of a complex relationship (Gray & Hatchard, 2008) linking an ecosystem-based approach to fisheries management with comprehensive stakeholder participation.

Although MPAs are important conservation tools, their limitations in mitigating coral loss from acute thermal stress events suggest that they need to be complemented with policies aimed at reducing the activities responsible for climate change (Eakin et al., 2010). One way forward is to have networks of MPAs (Keller et al., 2009), and they could be more effective in conjunction with other management strategies, such as fisheries regulations and reductions of nutrients and other forms of land-based pollution. Developing MPAs as part of an overall climate change policy for a country (Söderholm 2012) may be the best way of integrating climate change into MPA planning, management, and evaluation.

ACKNOWLEDGMENTS

I thank the Earthwatch Institute and the Oak Foundation (USA) for funding the Capacity Building, and Burton Shank (Conservation International) for essential help with the GPS coordinates in Belize. Also thanks to Charley Hitchcock and Dennis and Sandra Garbutt for their vital organisational support during the Belize project.

RESUMEN

Desarrollo de capacidades y desarrollo de políticas en áreas marinas protegidas de Belice, un ejemplo para la gestión integrada de la costa del Caribe. La ciencia de la sostenibilidad puede, a través del desarrollo de capacidades, permitir la gestión integrada de los actores interesados en estos ecosistemas marinos vitales del Caribe. Realizamos un ejercicio de desarrollo de capacidades en dos importantes arrecifes de coral al sur de Belice. El resultado clave fue el desarrollo de un plan de acción personal/profesional de seis meses para cada participante sobre técnicas para liderar, educar y apoyar los problemas acerca del desarrollo sostenible y técnicas para influir en decisiones políticas. Nuestros resultados se pueden ejecutar a lo largo de todo el Caribe.

Palabras clave: huracanes, blanqueo, cambio climático, calentamiento global, Belice, Jamaica.

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Application of the Soil and Water Assessment Tool (SWAT Model) on a small tropical island (Great River Watershed, Jamaica) as a tool in Integrated Watershed and Coastal Zone Management

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Received 17-X-2013 Corrected 07-II-2014 Accepted 24-III-2014

Abstract: The Great River Watershed, located in north-west Jamaica, is critical for development, particularly for housing, tourism, agriculture, and mining. It is a source of sediment and nutrient loading to the coastal environment including the Montego Bay Marine Park. We produced a modeling framework using the Soil and Water Assessment Tool (SWAT) and GIS. The calculated model performance statistics for high flow discharge yielded a Nash-Sutcliffe Efficiency (NSE) value of 0.68 and a R^2 value of 0.70 suggesting good measured and simulated (calibrated) discharge correlation. Calibration and validation results for streamflow were similar to the observed streamflows. For the dry season the simulated urban landuse scenario predicted an increase in surface runoff in excess of 150%. During the wet season it is predicted to range from 98 to 234% presenting a significant risk of flooding, erosion and other environmental issues. The model should be used for the remaining 25 watersheds in Jamaica and elsewhere in the Caribbean. The models suggests that projected landuse changes will have serious impacts on available water (streamflow), stream health, potable water treatment, flooding and sensitive coastal ecosystems. Rev. Biol. Trop. 62 (Suppl. 3): 293-305. Epub 2014 September 01.

Key words: Soil and Water Assessment Tool, Integrated Coastal Zone and Watershed Management, GIS.

Increasing population along with increasing pressure on land for food, expansion, and the need for infrastructure facilities have given rising alarm to conflicting demands on finite land and water resources (Biswas, Sudhakar & Desai, 2002). Additionally, anthropogenic land use changes tend to result in various geomorphic and hydrologic changes. These include changes in the spatial and temporal aspects of flood peaks, and in the extent and type of soil erosion (Magilligan & Stamp, 1997).

To adequately handle the stresses to our natural resources from climate change (e.g., flooding) and 'burgeoning populations' innovative methods have been conceptualized over the years. As it relates to challenges at the watershed scale, various management policies have been formulated under several titles; the most common being integrated watershed management, integrated environmental management, integrated water management, adaptive management and integrated coastal zone management (Margerum, 1999; Hooper, 2003; Ferreyra & Beard, 2007).

The primary focal point of watersheds is the river systems. Rivers provide the hydrologic link and as such represent the key management unit within a watershed, particularly in tropical island states and other equatorial regions. Rivers provide the link between upland regions and coastal zones and the regions surrounding them. By receiving water inputs from the land through infiltration and groundwater inputs, they convey the excesses from precipitation to areas such as seas, oceans, and lakes. Therefore, the importance of a river's ecological health is of paramount importance as it reflects the status of the land surrounding it and indicates the potential impact of practices within the watershed (particularly upper watershed management areas) (Hooper, 2003; Jakeman & Letcher, 2003; Ferreyra & Beard, 2007).

In an effort to achieve environmental sustainability, an integrated watershed and coastal zone management (IWCZM) approach must be incorporated, particularly as it relates to coastal zones irrespective of their definition by geographic or political boundaries. It is critical that an ecosystem-based approach to management is taken that will ensure a holistic management that integrates the impacts within the watershed and the resultant effect cumulatively on our coastal zones (Nobre et al., 2010).

According to the Coral Reef Alliance, coral reefs are among the world's most productive ecosystems (Goreau & Hayes, 2008). They are a major natural resource providing coastal protection, fisheries, and tourism income. The survival of coral reefs is largely dependent on a set of environmental parameters including low nutrient and sediment levels. Therefore, the management of watersheds plays a vital role in their survival because they are easily altered through land use changes (e.g., agriculture, degree of deforestation, and the extent of coastal development) that affect the quantity and quality of water flowing through a watershed and into the coastal zone. Effective management of watersheds, in conjunction with the coastal zone, can therefore improve the protection of the health of our coral reefs, wetlands, and the people that rely on them (OECD, 1993; NRCA, 2001; OECS, 2002).

The location of the island, its geography and geology make Jamaica susceptible to several natural hazards such as earthquakes, landslides, hurricanes, floods and droughts. The country has also acknowledged the increasing importance of climate change due to the high vulnerability attributed to the high concentration of development and infrastructure within the coastal zone. Coupled with this, human induced pressures on ecosystem goods and services are significant and highlighted within the major national development plan, Vision 2030 (PIOJ, 2009).

The current study examines the applicability of the Soil, Water and Assessment Tool (SWAT) on a tropical island watershed to evaluate the ability of the model to predict stream flow, and impacts of landuse changes on stream flow to allow for better understanding of how these tools can aid in water resources management. The following objectives were established:

- Calibration and validation of the hydrologic component of SWAT model in the Great River Watershed;
- Investigation of fluctuations in annual and seasonal stream flows and other hydrological parameters due to three projected landuse scenarios.

The Great River Watershed is located in the northwestern section of the island of Jamaica and is one of 26 watersheds in the island. The Great River is approximately 74km (46mi) long with an area of 327.27km^2 and has five major tributaries: Brown's River, Sevens River, Quashies River, Lambs River and Roaring River (Hayman, 2001; ARD, 2003). The Great River Watershed (GRW), similar to most watersheds in Jamaica, is considered to be in a state of environmental and economic decline. Agriculture, the major economic activity, faces many challenges, and as returns on investment decline, management is reduced. With reduced management comes less attention to natural resource conservation. Although there are numerous small communities scattered throughout the watershed, a large number of squatter-type settlements exist. These settlements generally lack adequate facilities for solid waste and sewage disposal (NRCA, 1997; Hayman, 2001; STATIN, 2001).

Regular monitoring of water quality within the watershed is not routinely carried out and as such monitoring data are inconsistent (Hayman, 2001; Greenaway, 2004). The water quality throughout the watershed is generally good with the exception of fecal coliform contamination triggered by human and animal fecal waste. The most recent assessment conducted from April 2002 to July 2003 by the University of the West Indies (Greenaway, 2004) suggested a river system in good health with relatively low nutrient (primarily nitrogen and phosphorous) and high dissolved oxygen levels. During the wet season when flow is fairly high nitrate levels were often detectable. Although soil erosion potential is moderate to high in the upper watershed, fairly low suspended sediment loads were observed outside adverse weather patterns such as tropical storms and hurricanes with significant precipitation. Flood plumes into the coastal zone were only observed during these episodes. No pesticide contamination was detected in the water samples taken during that period (Greenaway, 2004).

There are relatively few peer-reviewed, published SWAT model applications in tropical regions (Gassman, Reyes, Green & Arnold, 2007; Oestreicher, 2008). This is primarily due to the diversity of soils, species and climate of these regions in comparison to those of temperate zones. The model is very flexible and can be applied to a wide range of different environmental conditions (Arnold & Fohrer, 2005). The SWAT model, a freeware, was developed by the USDA-Agricultural Research Service to assist with assessment of watersheds ranging in sizes from small (a few hundred square kilometers) to large watersheds (several thousand square kilometers) (Neitsch, Arnold, Kiniry, Williams & King, 2002). One advantage of SWAT is the integration of the basin-scale model with GIS providing much improved modelling linkages within a management basin (Srinivasan & Arnold, 1994). SWAT has several components including: hydrology features, landuse, soil and slope attributes, and an improved weather generator, among other factors. The model is complete with documentation for equations and algorithms, a user manual describing model inputs and outputs, and an ArcGIS interface manual (Arnold & Fohrer, 2005; Neitsch, 2005; Santhi, Srinivasan, Arnold & Williams, 2006; Setegn, Srinivasan & Dargahi, 2008). This study focuses on the climate, land management and hydrology components.

Although the model has significant advantages, it is important to recognize that limitations exist. SWAT unfortunately is lacking in relation to the spatial representation of the hydrological response units within sub-basins (Gassman et al., 2007). The impacts on the predictions of evapotranspiration, percolation and soil water content are significantly affected despite the increase in spatial heterogeneity experiences with using large sized sub-basins. Generally, it is found that surface runoff is not significantly impacted by having larger and less sub-basins (Tripathi, Raghuwanshi & Roa, 2006). Additionally, SWAT incorrectly models infiltration into aquifers in hard rock areas by assuming unlimited capacity for water infiltration (Garg, Karlberg, Barron, Wani & Rockstrom, 2012, Batchelor, 2013). Despite these limitations, SWAT has been applied in tropical regions as support system for environmental management decision and policy making (Oestreicher, 2008). Oestreicher in his study identified several studies where the application of the SWAT model was met with acceptable performance. These included the modelling of the effects of hypothetical land-use change scenarios (primarily deforestation and reforestation of croplands) on flow, sediment, and nutrient yields in Honduras, Costa Rica, Brazil, Kenya, and China.

Of the two main classes of hydrological models identified in the literature: lumped and distributed models; the former is considered generally not spatially explicit largely representing a collection of changes in watershed land-use while the latter is more spatially explicit and highlight aspects such as surface runoff control factors. Despite the greater data requirement of the latter model, which includes SWAT, there is increased and improved forecasting ability of hydrological processes (Ward & Robinson, 2000; Evelyn, 2009). Several watershed modelling software have been developed and are universally accepted such as the Better Assessment Science Integrated Point and Nonpoint Sources (BASINS), Modelo

Hidrodinâmico (MOHID), SWAT, Water Quality Analysis Simulation Program (WASP), and Watershed Modelling Systems (WMS) among others (Erturk et al., 2006). Despite the vast wealth of models, the diversity and cost-effective approach, as well as the significantly large and growing model extensions has increased SWAT's application worldwide in developed and developing countries in a wide range of watershed sizes and conditions. In many cases these applications are requirements of government agencies evaluating the impacts of different scenarios such as climate and land-use change (Wang & Yin, 1997; Gassman et al., 2007; Zhang, Srinivasan & Hao, 2007; Graiprab, Pongput, Tangtham & Gassman, 2010).

MATERIALS AND METHODS

In order to setup SWAT various inputs are required. These include: the Digital Elevation Model (DEM), soil data, landuse data, stream network layers, weather data (rainfall and temperature) and stream discharge data. A 56m DEM, supplied by Mona GeoInformatics Institute (UWI-Mona, Jamaica), was used to determine the slope and flow direction, which was used to determine sub-basin outlets and areas contributing discharge to the outlets. Spatial datasets and input files were organised according to guidelines by Neitsch et al. (2002). Land-use/Land-cover data were supplied by the Forestry Department of Jamaica. Weather data (daily rainfall and daily temperature) were supplied by the Meteorological Service of Jamaica for the period 1998-2006. Of the eight available stations only four stations had complete data to undertake this study greater than 5 years between the period 1960 and 2010. The decision criteria required using the longest complete dataset exceeding 5 years for as many stations as possible. Minor pre-processing of data was done to format the data according to SWAT's input style. Stream network and soil data were supplied by the Water Resources Authority of Jamaica (WRA). Additional data layers were supplied by the Natural Environment and Planning Agency (NEPA). All digital datasets were projected to the Lambert Conformal Conic Projection, and the projected coordinate system used was the JAD 2001 Jamaica Grid.

The SWAT 2005 model was used through the ArcSWAT interface embedded in the ArcGIS software. This allows one to employ all available tools of ArcGIS in handling spatial datasets. SWAT allows for the discretisation of a watershed by dividing it into multiple sub-watersheds, which can then be further subdivided into hydrologic response units (HRUs) that consist of homogeneous land use, management, and soil characteristics (Neitsch, 2005). ArcGIS was used to calculate: basic hydrologic information for the model (i.e., surface slope, water flow paths), the position and size of the HRUs, and the necessary files to be used by SWAT (Winchell, Srinivasan, di Luzio & Arnold, 2007; 2009). The model, through the two phases (land and stream routing), simulates the routines for evapotranspiration, surface runoff, infiltration, percolation, return flow, groundwater flow, channel transmission losses, channel routing, and plant water use processes among others (Arnold, Srinivasan, Muttiah & Allen, 1999).

The modeling process generated 30 HRUs that represent the entire GRW. Calibration of the model was performed by comparing the simulated discharge with the monitoring (measured) discharge data in situ. The measured data were divided into two time periods covering the period 1998 to 2006 and represented complete data for the longest time period with the most meteorological stations in the watershed. The period 1998 to 2002 was selected for calibration and the period 2002 to 2006 for validation.

Calibration of the discharge was achieved by adjusting the input parameters. The top ten parameters were selected based on ranking achieved from the sensitivity analysis conducted. Adjusting the selected parameters allowed for a better match of measured and simulated discharges. The most sensitive parameters were used to calibrate the model for the GRW. The first year data (1998) was used as start-up/

warm-up in the calibration process and was therefore not included in the final model simulations. No formal optimisation procedure during calibration exists and therefore subjective decisions were generally made in calibrating the model (Santhi et al., 2006). Modifications of values were made by replacement, by addition of an absolute change or by a multiplication of a relative change. A parameter is never allowed to go beyond the model embedded predefined parameter range. Sensitivity tests and preliminary model run were carried out in order to identify the most sensitive model parameters. To avoid over parameterization, only the most sensitive parameters (top 10 ranked) were adjusted in model calibration.

Land use scenarios used in this study were designed to offer management planning for the protection of the watershed by assessing the potential impact of land use changes on hydrological parameters such as surface runoff, stream flows, and potential evapotranspiration. Land use scenarios were designed around real macro development possibilities within the watershed. Three scenarios were designed as follows: (1) an increase in agriculture to meet the projected demand of an increasing population and also to support the tourism industry with locally grown produce, (2) an increased conservation strategy by increasing the forest cover, and (3) increased urbanization of the watershed in line with long-term development plans to increase residential, tourism and commercial activities with new and improved road network. Though hypothetical each scenario mapped defines a potential maximum change in landuse that is realistic in nature. These three major landuse scenarios were designed by making changes to the SWAT reclassified landuse/land-cover map.

RESULTS

Watershed modelling & streamflow: The measured and simulated monthly discharges (Fig. 1) showed that the SWAT model mirrored

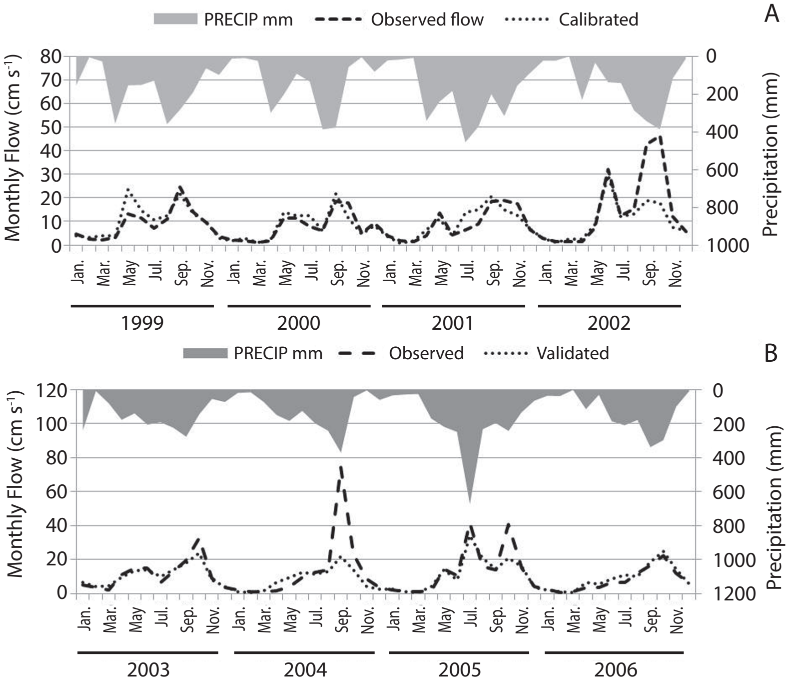

Fig. 1. Performance of Model under Calibration (A) and Validation (B) modes with influence from monthly rainfall data.

the measured monthly flow very closely. The mean calibrated measured monthly flow volume was 10.18cm s^{-1} (std. dev.= 9.94) slightly lower than the mean simulated monthly flow volume of 10.25cm s^{-1} (std. dev.= 7.06). The model was run during the validation period on the basis of the parameters from the calibration process only. The mean validation measured monthly flow volume was 11.50cm s^{-1} (std. dev.= 13.32), slightly higher than the mean simulated monthly flow volume of 10.66cm s^{-1} (std. dev.= 7.72).

The calculated model performance statistics for discharge yielded a Nash-Sutcliffe Efficiency (NSE) value of 0.68 and a R^2 value of 0.70 suggesting a fairly good correlation between measured and simulated (calibrated) discharge. The validation period similarly demonstrated good model performance. The NSE value of 0.61 and R^2 value of 0.67 also suggests a fairly good correlation.

Landuse scenarios modelling – Impact on stream flow: The land-use change scenarios performed reasonably well in comparison to the simulated baseline when calculated for mean monthly stream flow (Fig. 2). Simulated mean annual stream flow was less than measured stream flow using the validated period with a range of 10.67cm s^{-1} (agriculture) to 10.86cm s^{-1} (urban). These changes represented a 5.5% (urban) to 7.17% (agriculture) reduction in annual mean stream flow when compared with the baseline measured flow at the single discharge gauge station located approximately 3km from the river sea interface. The simulated land-use changes suggest no noticeable impact on mean stream flow with no more than a 3% increase for the dry season (December to April) and a 2% increase for the wet season shown for the urban scenario when compared with the simulated baseline.

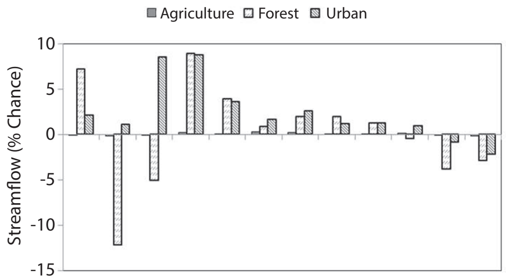

Fig. 2. Variability in mean simulated monthly stream flow as a percentage of baseline.

Although changes in simulated stream flow are fairly small in real values, the percent change in stream flow during the dry season for the forest and urban land-use scenarios are more exaggerated, ranging from an increase of 5% to 9% primarily during the dry season. Interestingly, the forest land-use scenario reflected similar fluctuations in reduction in stream flow during the same period particularly in the months of February and March while the agriculture scenario showed little or no change from the baseline throughout both dry and wet seasons.

Land-use scenarios modelling – Impact in stream nutrients: Simulated agriculture and urban land-use changes produced consistent increases in organic nutrients for most months with the greatest increase (106%) being predicted under simulated urban land use changes in March. The greatest increase in organic nitrogen for the agriculture land-use change was observed for the dry season month of January (~56%) when stream flow is lower and outside the main growing season of April-May. Increases exceeded 12% for all months in the year. Increases of 20-40% were also observed for wet season months of May to September when average monthly stream flow increases (Fig. 3).

Simulated agriculture and urban land-use changes produced consistent increases in organic phosphorous for each month with urban land use changes in March having the highest % change. Increases of 28-48% were also observed for wet season months of May to November for organic phosphorous within the stream (Fig. 4). Similar to organic nitrogen, phosphate contributions to stream flow were greatest during low-flow period.

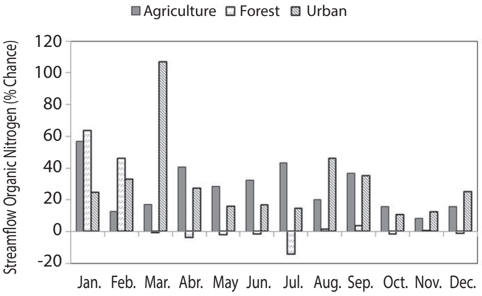

Fig. 3. Variability in mean simulated monthly organic nitrogen as a percentage of baseline.

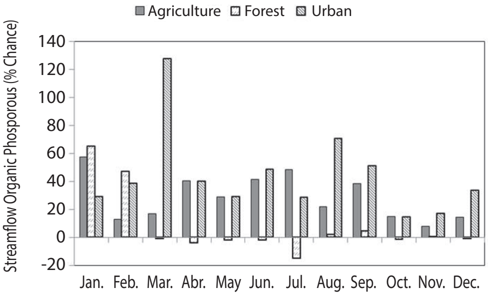

Fig. 4. Variability in mean simulated monthly organic phosphates as a percentage of baseline.

Land-use scenarios modelling – Impact on surface runoff to streams: Increase in surface runoff were generally observed for all three land-use changes, however forest land-use change recorded marginal decreases in some dry season months. While agriculture land-use scenario projected small increases in surface runoff contribution to stream flow ranging from 3.13% to 12.70%, forest land use change contributions ranged from -5.1% to 52%. The urban land-use scenario unlike the others projected greater monthly increases in surface runoff contributions. During the dry season the increase in surface runoff was in excess of 150% for the urban scenario. During the wet season the increase in surface runoff had a range of 98% to 234% (Fig. 5).

DISCUSSION

Despite the slight over-estimation at some peaks, the SWAT watershed model was able to adequately match the measured flow. Peak flows tend to be over-predicted for calibrated discharge; this difference may be attributed to rapid discharge during and following periods of storm events. Validation of the model is important in instilling confidence in the suitability and applicability of the model. The storm events may not be well captured due to the location from which rainfall station data used in the simulations was acquired. It is possible that the under-estimation is in part due to the model's assumption of uniform soil texture and land use in the watershed that is not a real world scenario. The under-prediction observed in this study has been reported in other studies for rainy periods (Tripathi, Panda & Raghuwanshi, 2003; Gassman et al., 2007). However, the statistical evaluations for both calibration and validation can be considered

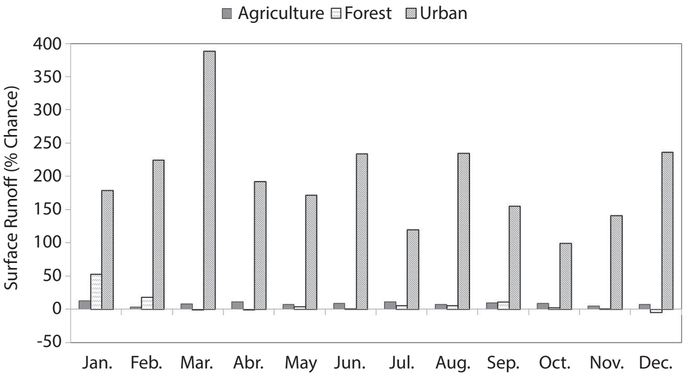

Fig. 5. Variability in mean simulated monthly surface runoff as a percentage of baseline.

to be satisfactory based on the criteria outlined by Moriasi et al. (2007). Therefore, based on the statistics returned, the SWAT model can be considered an effective tool in simulating the hydrology of tropical island watershed such as the Great River Watershed in Jamaica, although the simulated results, though realistic, can only be considered as experimental and ongoing and not conclusive or final.

Stream flow is projected to be impacted most with an increased urban landscape. An increase in the forest and agricultural land-use change does not suggest any real measureable increases in stream flow. Simulated agriculture land-use change has less of an impact and may be attributed to the regions within the watershed where substantive simulated changes were made. The lower-reach had little or no change in agriculture land-use, significant changes were made to the mid- and upper-reach, particularly the upper reach in the southern portion of the watershed. The southern section of the watershed has numerous ridges and potentially impacts on the distribution of rainfall to a greater extent than is experienced in the mid- to lower-reach. An increase in forest cover may have a more pronounced effect on stream flow in the dry season when evapotranspiration is expected to be highest. The modeled urban scenario revealed the very real possibility of surface runoff increasing to levels that may become disastrous. The drive to increase the agricultural component of the watershed may be setback due to a reduction in available water and soil moisture content, an increase in surface runoff, and a reduction in forest cover that provides the microclimate needed. The potential impacts to life and property are very significant.

Little or no data were available for hydrological parameters throughout most of the watershed. Where available the data were often incomplete due to faulty or non-functional equipment. No adequate historical land-use maps for the watershed were available to observe change in land-use over a prolonged period of time to compare with the macro changes in the hypothetical scenarios. A better spatial coverage of functioning rain gauges would afford a much better modelling effort to accurately gauge the impact of rainfall on land-use and its subsequent impact on stream flow. The results obtained from the model can be used exclusively or as an input of river flow and loads to the other models such as the MOHID estuarine models. As such, the model can be utilized to focus on possible interactions between coastal and riverine ecosystems and the social environment through incorporating three key activities: the nutrient loads generated from land based activities transported by surface waters and groundwater, use of coastal fauna associated with income generating activities such as fishing and dredging, and site specific key features arrived at in consultation with stakeholders and resource managers.

Nutrient contamination is a very important aspect of water quality monitoring in rivers and coastal environments globally. In Jamaica, the impact of nutrient contamination has been evident in some rivers and along the coast particularly in areas with coral reefs (Hayman, 2001; Greenaway, 2004; Espeut, 2012). This is evidenced by instances of fish kills, coral reef damage, and eutrophication. Levels of nutrients within stream flow suggest potential nutrient contamination with simulated land-use change scenarios, and are corroborated by existing data from the National Water Commission for the GRW during the period 2006-2010 showing elevated levels of nitrates and phosphates at the point of extraction, as well as water quality data within the river at various sections (Hayman, 2001; Greenaway, 2004). The dataset indicates several instances of coliform tests exceeding the standard of 300MPN/100ml as well as the domestic limit of 0MPN/100ml for potable water. Recorded spikes of 221 and 19.4mg PO_4 L^{-1} were recorded in June 2008 and October 2009 as well as nitrates routinely at or near the upper limit standard of 7.5mg PO_4 L^{-1}. Land-use change influences suggest local water balance and quality will be significantly impacted as suggested in the literature (Heathwaite & Johnes, 1996; Fohrer, Möller & Steiner, 2002; Heuvelmans et al., 2005; Abbaspour et al., 2007). This is easily proved when the sources of organic nitrogen within the watershed such as sewage from pit latrines, agriculture, urban, and rural developments are taken into consideration. Greenaway (2004) found occasionally elevated levels near the mouth of the river; however, concentrations were frequently elevated at some mid to upper reach stations. These locations are typical of small farm holdings with cattle. This corresponds well with findings in the 2001 Ridge to Reef report (Hayman, 2001). There are no centralized sewerage systems within the watershed, and an increase in residential homes is expected to impact on this and other water quality parameters.

Phosphorus is generally present in stream flow as dissolved or particulate matter, and is a vital plant nutrient and possibly the most limiting nutrient to plant growth in fresh water. It is rarely found in significant concentrations in surface waters. As such, its presence in fresh water systems may lead to extreme algal growth, hence eutrophication (Hayman, 2001; Fohrer et al., 2002; Greenaway, 2004; Qi et al., 2009). Sources of phosphorous are similar to those identified above for nitrogen. In urban and rural settings, the use of detergents is a major source. Within the GRW, washing of clothes and personal effects such as cars is a common occurrence as well as bathing in rivers and streams. The increase in organic nitrogen projected is understandable particularly in the agriculture scenario due to the possibility of increased use of fertilizers. In regards to organic phosphorous, an increase in urban component will likely yield an increase in use of soaps and detergents and other commercial products that would increase the phosphorous component particularly in runoff.

Many bodies of freshwater are currently experiencing influxes of phosphorus and nitrogen from outside sources. The increasing concentration of available phosphorus allows plants to assimilate more nitrogen before the phosphorus is depleted. Thus, if sufficient phosphorus is available, elevated concentrations of nitrates will likely lead to algal blooms (Dunne & Leopold, 1978; Easton et al., 2008; Harden, Foster, Morris, Chartrand & Henry, 2009). Algal blooms observed throughout the watershed were more noticeable in the dry season. However, in most instances, these blooms were related to areas prone to low or no flow where stagnant standing bodies of water occur until a rain event that disperses the generated plant material. Interestingly, Hayman (2001) and Greenaway (2004) have both recommended a systematic monitoring of nutrient levels throughout the watershed, particularly the central sections that are utilized for citrus orchards and coffee farms as well as an agricultural research station.

Predictably, surface runoff is projected to increase greatly once the land cover is dominated by hard surface which is a characteristic of urbanization or where forested land cover has reduced allowing for greater sheet flow where agriculture is not dominated by tree crops. This is well represented using the simulated urban land-use scenario wherein surface runoff increases nearly three-fold the baseline to a high of mean annual of 19.88 mm of water. Although an increase is projected for simulated increase in forest cover, the change is marginal in real terms. Simulating varied land-use changes on a greater spatial scale may result in even greater surface runoff for urban land-use changes.

The reduced surface runoff potential for agriculture and forest scenarios may translate to reduced flooding incidences but may have impact on water availability, quality (increased concentrations) and sustenance of critical habitats. An increase of the projected magnitudes for the urban scenario will no doubt increase water availability but depending on how that increase is delivered spatially, it could be a significant environmental and socio-economic impact risk. Such increases bring with it the potential for flooding and transference of pollutants to sensitive areas and ecosystems such as flood plains and coral reefs.

The significant increase in surface water observed for the urban scenario may have huge impacts on stream health that will negatively impact on the treatment services of potable water. This is required bearing in mind the expected increase in population, and also the projected increase in tourism related services such as hotels and eco-adventure tours. Improved watershed management is recognized as a critical area of need in Jamaica. These improvements are geared towards providing reliable and adequate supplies of clean water for agriculture, industry, tourism, urban and rural populations, as well as for ecosystem sustainability. This is well documented in a review of the watershed (Hayman, 2001; ARD, 2003).

Future watershed hydrologic changes due to land conversion are expected to be site-specific, and climate variability is an important factor controlling basin hydrologic processes (Qi et al., 2009). Agricultural activities on steep slopes have long been recognized as the single most important cause of the degradation of watersheds in Jamaica (NRCA, 1999; Hayman, 2001).

The increase run-off in urban areas (particularly residential) and maintenance and potential increase in agriculture within the GRW has and will impact significantly on the dynamics of suspended sediments and nutrient contribution to stream flow. The GRW is dependent on the episodic and seasonal flows to maintain watershed health. Suspended sediment transport is greatest during these events. The temporal pattern of these events (short duration and heavy flow) aids greatly in the removal of material reducing the likely entrainment of material along the stream flow.

Based on these dynamics it is possible that there is an efficient system of material transport and limited impact from channel sedimentation and de-nitrification processes (Brodie & Mitchell, 2005). However, with an increase in nutrients particularly from any increases in agriculture and urban landscape coupled with potential reduction in rainfall, it is likely that without proper management this natural resource could be negatively impacted for future use.

The integrated watershed and coastal zone management approach must be used to tackle issues such as watershed health, stream water quality, coastal zone and sensitive habitat sustainability in the context of various resource managers. There must be a concerted effort to ensure that these managers are all speaking from the same platform. Presently, resource managers typically utilize software that are restricted to particular agencies with a difficult process of translating to the needs of each other. The application of resources that are freely available, proven in the field in developed and developing countries, and have produced robust results should be made available as part of our planning arsenal to ensure all agencies are able to interact in a cohesive manner. SWAT is one such tool that Jamaica can take advantage of; particular in light of the fact that it is embedded in GIS. GIS is a tool most of our resource managers already make, as it's the national spatial planning platform. Despite the coarse nature of model setup the SWAT model has provided valuable quantitative information on the effectiveness of climate and land-use changes, the need to monitor and make predictions on improving water quality, and highlight the potential costs associated with implementing these improvements.

The performance of the SWAT model using the Nash Sutcliffe Coefficient (E) and the Coefficient of Determination (R^2) provided confidence that the model is adequate for use in tropical island watersheds with karts networks. Model predictions are as accurate as the mean of the measured stream flow data with the E values indicating the model is particularly sensitive to low flows but still performs fairly well to peak flows. This research has developed a reasonably calibrated SWAT model for the Great River watershed, given the limited availability of monitoring data and the scope of the study. This tool is available and applicable for use in the remaining 25 watersheds. It has the capability to model water quality, land-use change, climate change and other critical aspects of watershed health at various scales and should therefore be incorporated into Jamaica's national systems as a potential planning tool.

The modelled urban scenario revealed the very real possibility of surface runoff increasing to levels that can be considered catastrophic. The drive to increase the agricultural component of the watershed may be set-back due to a lack of water, a reduction in soil moisture content, an increase in surface runoff and a reduction in forest cover that provides the micro-climate needed. The potential impacts to life and property are very significant and should be further evaluated.

Although this research puts forward impact to watershed based on projected macro changes in land use with projected climate change, it should be highlighted that it is very much theoretical. There is still large uncertainty in predicting future impacts due to climate and land-use changes. The pace at which technology will be developed to arrest the increasing threat of climate change is still unknown. Similarly, the importance of development (economic and social) must be factored and may even be a greater limiting factor. The dynamic shifts in land-use beyond the extent of this study should be investigated to account for the significant climate change projections and their potential impact on land-use changes in watershed.

ACKNOWLEDGMENTS

The authors would like to thank the Inter-American Institute for Global Change Research (IAI) (Project Number: CRN-II-2061) for the financial support. National Meteorological Service and Water Resources Authority of Jamaica are gratefully acknowledged for providing data.

RESUMEN

Aplicación de la herramienta de evaluación de suelo y agua (modelo SWAT) en una isla tropical pequeña (Gran Cuenca del Río, Jamaica) como una herramienta en la gestión integral de cuencas y manejo de la zona costera. La gran cuenca del Río Grande, ubicada en el noroeste de Jamaica, crítico para el desarrollo, particularmente para vivienda, turismo, agricultura y minería. Es una fuente de sedimentos y nutrientes de recarga para el ambiente costero incluyendo el Parque Marino Bahía Montego. Proponemos un marco integrado de modelado utilizando la herramienta de evaluación de suelo y agua (SWAT) y SIG. Las estadísticas de rendimiento del modelo calculadas para la descarga de alto flujo rindió una eficacia de Nash-Sutcliffe (NSE) de 0.68 y un R^2 de 0.70 sugiriendo una buena medición y correlación de descarga simulada (calibrada). Los estados insulares con frecuencia toman decisiones basándose en los impactos de la cuenca. Esto requiere un profundo entendimiento y análisis de factores como los recursos hídricos, uso del suelo/cobertura, sedimentos y nutrientes de recarga entre otros factores a nivel de cuenca. Con financiamiento del Instituto Interamericano para la investigación del Cambio Global (IAI) se examinó la aplicación del modelo de acceso libre en una cuenca jamaiquina. Los resultados de la calibración y validación para caudales fueron similares a los observados en los caudales respectivos, según lo indicado por la eficacia de Nash-Sutcliffe y el coeficiente de determinación. La calibración y validación de los resultados para el caudal son similares a los observados en el caudal. Durante la estación seca el escenario simulado en el uso de suelo urbano predijo un aumento de la escorrentía superficial superior al 150%. Durante la estación lluviosa el aumento de la escorrentía superficial se prevé que alcance desde 98 a 234% lo que representa un riesgo significativo de inundaciones, erosión y otros problemas ambientales. El modelo sugiere que cambios en los usos proyectados de suelo tendrán serios impactos sobre la disponibilidad de agua (caudal), salud de la cuenca, tratamiento de agua potable, inundaciones y ecosistemas costeros sensibles.

Palabras clave: Herramienta de Evaluación de Suelo y Agua, zona costera integrada y manejo de cuencas, SIG

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