



Building capacity in coral reef
science: An anthology of
CRTR scholars' research 2010

Acknowledgements

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Cover photos: (top left) Inspecting the nets, Bolinao Reef Flat, Philippines (Photo: M King); (top right) Jess Melbourne-Thomas recording research data (Photo: M Flavell); (bottom) Panda clownfish and three-spot damselfish, Schumann Island, Papua New Guinea (Photo: S Planes); (middle left) Courtney Couch and Mark Dondi Arboleda researching coral disease.



The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program is a leading international coral reef research initiative that provides a coordinated approach to credible, factual and scientifically-proven knowledge for coral reef management.

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Preface

The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program is all about building the necessary science and applying it in ways that will make our management of coral reefs more effective than it unfortunately is. Coral reefs are the brunt of many human assaults – overfishing, pollution, inappropriate development, the list goes on. Even tourism can love reefs to death. Now that we have created a world with a rapidly changing climate, the pressures on coral reefs are even greater, and growing worse daily. If we want the substantial economic benefits that coral reefs provide through their fishery products, their immensely valuable environments for tourism, and their storm protection services for coastlines, and if we want a world enriched by the incredible biotic richness and the sheer beauty of coral reefs, then we have to start now to manage our impacts on them far better than we have in the past. That means a more rigorously scientific approach to management, using the latest information on how reefs respond to the things we do to them, and management by people well-equipped to understand that science, and to work in close collaboration with reef scientists in adaptive management programs.

During Phase One, through 2009, the CRTR project supported the development of new research in several critical areas of coral reef science. This included recruiting the large team of scientists that participated in the six working groups, and directly supporting a number of graduate students and postdoctoral researchers who worked with them. In this way the science would grow, and the next generation of coral reef experts would also be built. That cohort of students and postdocs has been one of the main products of Phase One – they come from throughout the world, have proved to be a talented crew, and, for the most part, want to remain involved in coral reef science and management into the future. This anthology of some of their work is a tribute to these future coral reef scientists and managers. To them I say, “We have given your generation some enormous challenges, unfairly enormous perhaps, but hopefully, through your participation in CRTR, we have provided some of the tools, some of the network of mentors and collaborators, and some of the insights you will need to meet those challenges. It is going to be difficult over the next few decades, but coral reefs are intrinsically worth looking after. Do what you can, as individuals and as a group, to help humanity make the necessary corrections, in order to build a better world – one with reefs in it.”



Peter F. Sale
Chair, Connectivity Working Group
CRTR Project



Angela Mojica looking for urchins.



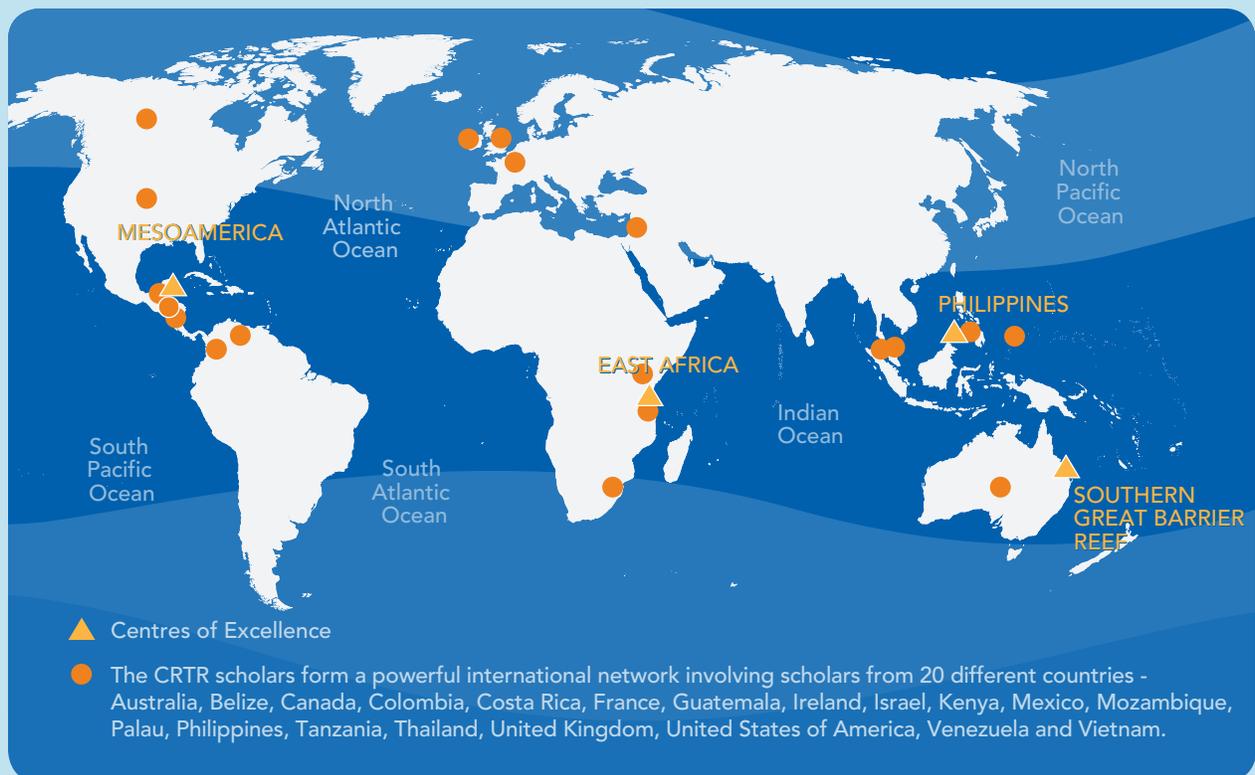
University of the Philippines graduation ceremony, April 2010. Left to right: Dexter dela Cruz, Maria Vanessa Baria, Professor Ed Gomez, Kareen Vicentuan, Rollan Geronimo. Photo: Patrick Cabaitan

The Future Leaders Network

Since the commencement in December 2004 of Phase One of the CRTR Program, there has been a concerted effort to build scientific capacity amongst the next generation of coral reef researchers. Throughout the past five years this has been achieved through the provision of scholarships (at the Masters, PhD and Postdoctoral levels), and through support to students for attendance to targeted workshops and conferences, fieldwork and other activities related to their studies.

In 2007, the Program, in recognition of this network of researchers, brought together all Masters and PhD students, and Postdoctoral fellows in a week-long workshop. The aims were to foster and encourage the network, to build linkages across the countries and areas of research represented, and to exchange information and knowledge with their peers.

From this gathering, the CRTR Program's 'Future Leaders Network' was established and has continued to grow both in terms of numbers, and in the expertise supported. The network now encompasses over 60 scholars from across 20 countries, all of whom are continuing to work or undertake research in coral reefs to provide a secure future for these valuable ecosystems.



Introduction: linking coral reef research across nationalities and disciplines

Jess Melbourne-Thomas and Deb Cleland

This anthology provides a snapshot of research conducted by students and early career researchers under the first phase of the Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program. This talented and diverse group of scholars were first brought together at a Future Leaders' Forum at the University of Queensland in December 2007. During a week-long program of workshops, presentations and field trips we were challenged to make our research count through effective communication and by establishing strong, collaborative research networks. For many of us, one of the more resounding messages from this forum was the challenge set by Professor Peter Sale (Chair of the CRTR Connectivity Working Group): to rouse ourselves and "get angry" about the "unfairly enormous challenges given to our generation" to ensure the survival of coral reefs.

Instead of "getting angry" (or depressed), we decided to work together to build and maintain a Coral Reef Future Leaders network that would help us meet the challenge put to us by Professor Sale. Many of the scholars who took part in the forum in 2007 met again in Florida in July 2008 at the 11th International Coral Reef Symposium. It was in Florida that the idea for an anthology highlighting both the variety in our respective research topics, and the strength of collaborations within the network was first raised. This publication is the result of that first spark of an idea, and of the continued support of the CRTR Executive Officer Melanie King in fostering links within the student network, for which we are endlessly grateful.

Our anthology contains 17 articles contributed by scholars on an aspect of their studies over the first five-year phase of the CRTR Program. These articles demonstrate research and capacity building for a broad range of reef systems, and address important knowledge gaps about how coral reefs function and how we might manage them better. The articles fall under three broad themes:

1. Understanding local-scale ecological processes Articles under this theme address knowledge gaps in our understanding of the local-scale processes of recruitment and coral disease dynamics, and describe the design and application of models in exploring local-scale thresholds for coral-algal phase shifts.

2. Reef dynamics and management actions at regional scales Under the second theme, contributed articles examine the implications of connectivity, disease, thermal stress and human impacts for coral reef dynamics at regional scales in Meso-America, East Africa and the Philippines.

3. New techniques for understanding and managing coral reef systems This theme encompasses articles that explore novel approaches to understanding fundamental processes in coral reefs and that describe a range of techniques for addressing complex management issues for threatened reef ecosystems.

This 'taster' of the research achievements of CRTR scholars during the first phase of the program clearly demonstrates the importance of our findings for building capacity through understanding the major drivers of reef degradation and developing novel techniques to improve coral reef management. It shows how a diverse group of early career researchers are addressing Professor Sale's challenge in "doing what we can, as individuals and as a group, to help humanity make the necessary corrections, in order to build a better world – one with reefs in it."

Understanding local-scale ecological processes 1



Suzanne N. Arnold

Coral survivorship in the gardens of good and evil



Suzanne Arnold was born in Falmouth, Massachusetts in the U.S.A. During an undergrad semester abroad, she completed a Marine Ecology Program in Zanzibar, Tanzania. It was this experience that spurred her interest in coral reef ecosystems and the people who are dependent upon them. She received Master of Science degrees in Marine Biology and Marine Policy in 2007 from the University of Maine, and is currently a doctoral candidate in Marine Biology at the University of Maine under the direction of Professor Bob Steneck. The thrust of her dissertation examines the spatial and temporal scales at which coral recruitment operates.



Terra-cotta coral settlement tiles are used to track the settlement and survivorship of corals and the succession of benthic organisms in these critical nursery habitats.
Photo: Jeanne Brown

Coral survivorship in the gardens of good and evil

Suzanne N. Arnold

University of Maine, School of Marine Sciences

Coral mortality has increased in recent decades, making coral recruitment more important than ever before in sustaining coral reef ecosystems and contributing to their resilience. Successful recruitment requires the survival of coral offspring through sequential life history stages. Larval availability, successful settlement, and post-settlement survival and growth are all necessary for the addition of new coral individuals to a reef and ultimately the maintenance or recovery of coral reef ecosystems. This review summarizes the state of the science of the final stage, and perhaps critical bottleneck, to successful recruitment, coral post-settlement survival.

Post-settlement ecology

Corals, and most benthic marine organisms, suffer high rates of mortality soon after settlement because they are small and vulnerable. Post-settlement processes from the time corals settle (i.e., attach to the benthos) to recruitment (i.e., survive to some later phase) determines much of coral demography (Vermeij and Sandin, 2008). This concept is consistent with the tenet of clonal population biology that states as clonal organisms grow the probability of their death declines but the probability of injury increases (Hughes and Jackson, 1985). Thus, the two rates of early post-settlement mortality and growth can strongly influence the local abundance of corals.

Post-settlement mortality

Coral recruits can die from a myriad of causes including chronic disturbances such as competition and predation and pulse disturbances such as bleaching and disease. However, the chronic disturbances probably drive most post-settlement mortality and thus are serious impediments to reef recovery. Caribbean reefs are a case in point, with incidences of recovery much lower than Indo-Pacific reefs as a result of setbacks from chronic disturbances (Connell et al., 1997).

Algae, encrusting invertebrates, and sediment have all been shown to have deleterious effects on newly settled corals (Rylandsdam, 1983). Settling corals, with limited stores of energy to invest in competitive interactions, are particularly vulnerable when faced with a well-developed benthic community structure and limited space (Jackson and Buss, 1975; Sebens, 1982; Connell et al., 1997). However, the *mechanisms*, or causes, of reduced growth and mortality of newly settled larvae, recruits, and juveniles have, for the most part, only recently been investigated.

Encrusting invertebrates (particularly sponges) can be especially inhospitable for newly settled corals. In cryptic habitats, newly settled corals are likely to lose out by overgrowth of fast-growing heterotrophic groups such as sponges, bryozoans, and bivalves (Vermeij, 2005). Aerts and van Soest (1997) determined the impact of sponges on coral survival to be greatly species specific. Physical, chemical, and biological properties of benthic invertebrates may inhibit coral growth and survival. Some studies used chemical extracts of sponges (Sullivan et al., 1983; Pawlik et al., 2007) to show that allelopathy can negatively impact adult corals. Coral recruits are even more susceptible to stress, yet surprisingly few studies have examined secondary metabolites for their impact on the early life history stages of corals. A field study by Maida et al. (1995) suggested that allelopathy reduced recruitment of corals adjacent to the octocorals *Sinularia flexibilis* and *Sarcophyton glaucum*, and both the live octocorals and settlement plates with dichloromethane extracts of *S. flexibilis* inhibited coral settlement and survival. More long-term, small spatial scale (millimeters to centimeters) studies are needed to determine the effect of benthic invertebrates on post-settlement survival (Edmunds et al., 2004; Vermeij, 2006).

1. Understanding local-scale ecological processes

Areas of high algal biomass are known to be poor nursery habitats for settling corals (Birkeland, 1977; Bak and Engel, 1979; Harriott, 1983; Vermeij and Sandin, 2008; Vermeij et al., 2009; Birrell et al., 2008). There are several mechanisms by which algae may be deleterious to corals. Algae may interfere with larval settlement by simply preempting available settlement space (Mumby et al., 2006; Box and Mumby, 2007). At least one species of turf algae alone (without sediment) has reduced settlement of corals in laboratory experiments (Birrell et al., 2005). More direct physical interactions including algal shading, abrasion, or basal encroachment can result in reduced coral growth or increased mortality (Lirman, 2001; McCook et al., 2001). Shading by the encrusting brown algae *Lobophora variegata* over six months caused a 50% increase in mortality of juvenile *Agaricia agaricites* (less than 20 mm diameter), and the mere presence of *L. variegata* around the coral reduced colony growth by 60% (Box and Mumby, 2007). However, shading by *Dictyota pulchella* resulted in no direct mortality but caused a 99% decrease in coral growth. Other studies have determined that *Lobophora variegata* (in the absence of grazing) is a superior competitor to Caribbean corals, including *A. agaricites*, *A. lamarcki*, *Meandrina meandrites*, *Mycetophyllia aliciae*, and *Stephanocoenia michelinii* and at least one species of Pacific coral, *Porites cylindrica* (De Ruyter van Steveninck et al., 1988; Jompa and McCook, 2003). Thus, it is likely that community phase shifts to high algal biomass decrease recruitment by reducing larval settlement and post-settlement survival (Hughes and Tanner, 2000; Kuffner et al., 2006).

Reduced coral recruitment in algal-dominated reefs (Edmunds and Carpenter, 2001; Birrell et al., 2005) is thought to be in part the consequence of chemically induced mortality or the increased biomass of fleshy algae actually functioning as a reservoir for coral pathogens (Littler and Littler, 1997; Nugues et al., 2004). Bak and Borsboom (1984) proposed that the reduction in water flow adjacent to macroalgae could cause increased coral mortality through changes in the flow regime and increased allelochemical concentrations. Most recently, enhanced microbial activity caused by algal exudates has been proposed as a mechanism of competition (Smith et al., 2006; Vermeij et al., 2009). Kline et al. (2006) determined that elevated levels of dissolved organic carbon, which can occur in areas of high algal biomass, increased the growth rate of microbes living in the mucopolysaccharide layer of corals. These studies all suggest that the detrimental effect of algae on corals could be mediated by several properties of macrophytes.

On modern reefs, algal-related post-settlement mortality probably decreases the population density of coral recruits. Vermeij (2006) compared his recruitment study in Curacao from 1998 to 2004 to that of Van Moorsel (1989) from 1979 to 1981, using the same method in the same location. Recruit densities on the topsides of settlement panels in the more recent study were 5.16 times lower and recruitment on the undersides was 1.14 times lower than the 1979–1981 study. Macroalgae had replaced CCA as the dominant topside space occupier, creating a less-suitable habitat for coral recruitment compared to the crustose algae that had dominated the same site roughly 20 years earlier. In places where *Diadema* urchin recovery and grazing have reduced algal abundance, the population density of juvenile corals has increased (Edmunds and Carpenter, 2001; Aronson et al., 2004; Macintyre et al., 2005).

While herbivory can improve the recruitment potential by keeping reefs relatively free of algae, it can also be a potential cause of mortality for newly settled corals. Grazing rates on exposed outer surfaces of shallow reefs are extremely high, exceeding thousands of bites per square meter per day (Carpenter, 1986; Steneck and Dethier, 1994; Steneck and Lang, 2003). Bites, especially from parrotfish that graze deeply into carbonate substrates, would easily kill a newly settled coral. Few studies have documented recruit mortality resulting from fish grazing (Mumby et al., 2006), although it has been suggested as the cause of the low number of recruits observed on the top surface of settlement plates (Adjeroud et al., 2007). The herbivorous sea urchin *Diadema antillarum* was shown to be a significant agent of mortality for newly settled corals (Sammarco and Carleton, 1981). The highest mortality of newly settled corals is likely to occur on outer exposed surfaces where algal growth rates and herbivore grazing rates are greatest and rates of sedimentation are highest. In shallow reef habitats where algal growth and herbivory rates are greatest, coral recruitment is greater in subcryptic microhabitats (Bak and Engel, 1979). However, which microhabitats increase post-settlement survival has rarely been tested (but see Babcock and Mundy, 1996).

Post-settlement growth rates

Given the vulnerability of small size classes, the adaptive advantages of rapid growth rates are obvious. Coral recruit survival is not merely a function of the attributes of the settlement substrate but also of the coral's ability to resist overgrowth by neighboring encrusting invertebrates and algae (Richmond, 1997). As new corals grow, their mortality rates decline (Vermeij and Sandin, 2008), and they are less likely to be overgrown by competitors (Hughes and Jackson, 1985). Often, however, the slow growth rates of newly settled corals make this a losing battle, and early post-settlement mortality is generally high (Figure 1; Bak and Engel, 1979; Edmunds, 2000; Vermeij and Sandin, 2008). Even in a controlled environment, laboratory studies showed that a coral that remains less than 3 mm in diameter for two or three months has only a 20% chance of survival (Rylaarsdam, 1983). Field studies report a huge amount of variance in early post-settlement mortality. Babcock (1985) found post-settlement survivorship over the first three to six months ranged from 16% to 71%, whereas more recently Box and Mumby (2007) determined a monthly estimated mortality rate for *Agaricia agaricites* to be 3.5% per month. Annual juvenile coral survivorship estimates range from 0% to 77% (Smith, 1992; Wittenberg and Hunte, 1992; Maida et al., 1994; Smith, 1997; Edmunds, 2000).

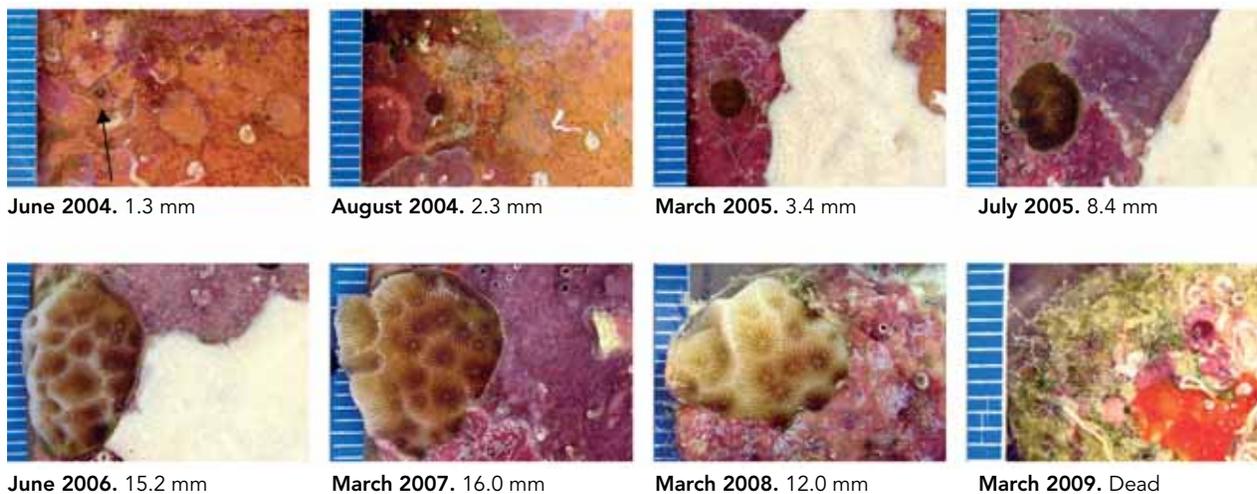


Figure 1. A time series of the growth of *Agaricia* sp. settled on a terracotta tile in Bonaire over 5 years. After March 2007, this recruit is being overgrown by the coralline alga *Titanoderma prototypum*, a known settlement-facilitating species, illustrating just how hazardous the settlement environment can be. One segment on the scale bar is 1 mm. (All photographs by Suzanne Arnold.)

Different species of corals have distinctly different rates of growth and ability to recover following a disturbance (Wakeford et al., 2008). Specifically, some of the Indo-Pacific acroporid corals (e.g., *Acropora tenuis*) are extremely “weedy” and are capable of growing nearly 6 cm in 1.5 years (Omori et al., 2008); this translates to an average growth rate of 3.2 mm/month compared to the much slower growth rates reported for *Oxypora* sp. as ranging between 0.2 and 0.5 mm/month (Babcock and Mundy, 1996).

Settlement habitat also influences growth rates of newly settled corals. Subcryptic habitats protect coral recruits from stresses and disturbances common on outer reef surfaces, but they will invariably have lower productivity potential. Diameters of *Platygyra* sp. and *Oxypora* sp. settlers increased one-quarter to one-half as fast in cryptic undersides than they did on upper exposed surfaces for the two species, respectively (Babcock and Mundy, 1996). Importantly, however, new recruits that selected subcryptic microhabitats had higher survivorship despite their slower growth rates (Babcock and Mundy, 1996).

Conclusion – roles of biodiversity and life history

Globally, many Indo-Pacific reefs have higher rates of settlement, recruitment, and recovery from disturbances, which could be the result of higher biodiversity in the region. In contrast, Caribbean reefs may have evolved a strategy of low recruitment and considerable clonal growth, with low post-settlement mortality for its few reef-building acroporid corals. However, are Caribbean reefs today following the paths of forests and other marine ecosystems in their shift to weedy, stress-tolerant species? (see Knowlton, 2001). Currently, weedy, brooding species such as *Agaricia* spp. and *Porites* spp. are the thrust behind the current rates of coral recruitment in the Caribbean. A recovery such as seen in Palau following the 1998 bleaching event, where sexual recruitment and remnant regrowth were equal contributors (Golbuu et al., 2007), has yet to be recorded in the Caribbean. Success stories of Caribbean recoveries led by broadcast spawning species, such as the major framework builders *Acropora* and *Montastrea*, are scarce (but see Idjadi et al., 2006). Because of the algal phase shift in the Caribbean (Hughes, 1994), acroporid reefs have become hostile to the rare acroporid recruits, and they have lost their receptivity for reattachment of encrusting fragments (Williams et al., 2008). Furthermore, the massive, slow-growing coral *Montastraea annularis*, also a broadcast spawner and framework builder in the Caribbean, has very low rates of recruitment (Hughes and Tanner, 2000) and thus requires long adult life to establish its dominance.

Thus, it seems that Caribbean reefs were built by corals that have been successful since the Pleistocene (Pandolfi and Jackson, 2006) with a strategy of low recruitment, considerable clonal growth, and low post-settlement mortality. However, that strategy may not be broadly viable today, given the global climate trajectory (Hoegh-Guldberg et al., 2007) and patterns of human activities. While Indo-Pacific reefs are not immune to declines in rates of coral recruitment in recent years (Wakeford et al., 2008), the higher biodiversity and range of recruitment and post-recruitment strategies (e.g., high rates of growth) allow reefs there to be more resilient. The relative importance of sexual versus asexual reproduction to recovery in the Caribbean needs to be addressed by long-term observations with particular focus on recovery following large-scale disturbances such as major storms and bleaching events.

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References

- Adjéroud, M., L. Penin, and A. Carroll. 2007. Spatio-temporal Heterogeneity in Coral Recruitment around Moorea, French Polynesia: Implications for Population Maintenance. *Journal of Experimental Marine Biology and Ecology*, 341:204–218.
- Aerts, L.A.M., and R. W. M. van Soest. 1997. Quantification of Sponge/Coral Interactions in a Physically Stressed Reef Community, NE Colombia. *Marine Ecology Progress Series*, 148:125–134.
- Aronson, R.B., I. G. Macintyre, C. M. Wapnick, and W. O. O'Neill. 2004. Phase Shifts, Alternative States, and the Unprecedented Convergence of Two Reef Systems. *Ecology*, 85:1876–1891.
- Babcock, R. 1985. Growth and Mortality in Juvenile Corals: The First Year. *Proceedings of the 8th International Coral Reef Symposium*, 2:1197–1202.
- Babcock, R., and C. Mundy. 1996. Coral Recruitment: Consequences of Settlement Choice for Early Growth and Survivorship in Two Scleractinians. *Journal of Experimental Marine Biology and Ecology*, 206:179–201.
- Bak, R. P. M., and J. L. A. Borsboom. 1984. Allelopathic Interaction between a Reef Coelenterate and Benthic Algae. *Oecologia (Berlin)*, 63:194–198.
- Bak, R. P. M., and M. S. Engel. 1979. Distribution, Abundance and Survival of Juvenile Hermatypic Corals (Scleractinia) and the Importance of Life History Strategies in the Parent Coral Community. *Marine Biology*, 54:341–352.
- Birkeland, C. 1977. The Importance of Rate of Biomass Accumulation in Early Successional Stages of Benthic Communities to the Survival of Coral Recruits. In *Proceedings of the 3rd International Coral Reef Symposium*, Miami, pp. 15–21.
- Birrell, C. L., L. J. McCook, and B. L. Willis. 2005. Effects of Algal Turfs and Sediment on Coral Settlement. *Marine Pollution Bulletin*, 51:408–414.
- Birrell, C. L., L. J. McCook, B. L. Willis, and G. A. Diaz-Pulido. 2008. Effects of Benthic Algae on the Replenishment of Corals and the Implications for the Resilience of Coral Reefs. *Oceanography and Marine Biology: An Annual Review*, 46:25–63.
- Box, S. J., and P. J. Mumby. 2007. Effect of Macroalgal Competition on Growth and Survival of Juvenile Caribbean corals. *Marine Ecology Progress Series*, 342:139–149.
- Carpenter, R. C. 1986. Partitioning Herbivory and Its Effects on Coral Reef Algal Communities. *Ecological Monographs*, 56:343–363.
- Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-Year Study of Coral Abundance, Recruitment, and Disturbance at Several Scales in Space and Time. *Ecological Monographs*, 67:461–488.
- de Ruyter van Steveninck, E. D., L. L. Van Mulekom, and A. M. Breeman. 1988. Growth Inhibition of *Lobophora variegata* (Lamouroux) Womersley by Scleractinian Corals. *Journal of Experimental Marine Biology and Ecology*, 115:169–178.
- Edmunds, P. J. 2000. Patterns in the Distribution of Juvenile Corals and Coral Reef Community Structure in St. John, US Virgin Islands. *Marine Ecology Progress Series*, 202:113–124.
- Edmunds, P. J., J. F. Bruno, and D. B. Carlton. 2004. Effects of Depth and Microhabitat on Growth and Survivorship of Juvenile Corals in the Florida Keys. *Marine Ecology Progress Series*, 278:115–124.
- Edmunds, P. J., and R. C. Carpenter. 2001. Recovery of *Diadema antillarum* Reduces Macroalgal Cover and Increases Abundance of Juvenile Corals on a Caribbean Reef. *Proceedings of the National Academy of Sciences of the United States of America*, 98:5067–5071.
- Golbuu, Y., S. Victor, L. Penland, D. Idip, C. Emaurois, K. Okaji, H. Yukihiro, A. Iwase, and R. van Woesik. 2007. Palau's Coral Reefs Show Differential Habitat Recovery Following the 1998 Bleaching Event. *Coral Reefs*, 26:319–332.

1. Understanding local-scale ecological processes

- Harriott, V. J. 1983. Reproductive Seasonality, Settlement, and Post-settlement Mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. *Coral Reefs*, 2:151–157.
- Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatzioiols. 2007. Coral Reefs under Rapid Climate Change and Ocean Acidification. *Science*, 318:1737–1742.
- Hughes, T., and J. B. C. Jackson. 1985. Population Dynamics and Life Histories of Foliose Corals. *Ecological Monographs*, 55:141–166.
- Hughes, T. P. 1994. Catastrophes, Phase-Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, 265:1547–1551.
- Hughes, T. P., and J. E. Tanner. 2000. Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals. *Ecology*, 81:2250–2263.
- Idjadi, J. A., S. C. Lee, J. F. Bruno, W. F. Precht, L. Allen-Requa, and P. J. Edmunds. 2006. Rapid Phase-Shift Reversal on a Jamaican Coral Reef. *Coral Reefs*, 25:209–211.
- Jackson, J. B. C., and L. Buss. 1975. Allelopathy and Spatial Competition among Coral Reef Invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 72:5160–5163.
- Jompa, J., and L. J. McCook. 2003. Contrasting Effects of Turf Algae on Corals: Massive *Porites* spp. Are Unaffected by Mixed-Species Turfs, But Killed by the Red Alga *Anotrichium tenue*. *Marine Ecology Progress Series*, 258:79–86.
- Kline, D. I., N. M. Kuntz, M. Breitbart, N. Knowlton, and F. Rohwer. 2006. Role of Elevated Organic Carbon Levels and Microbial Activity in Coral Mortality. *Marine Ecology Progress Series*, 314:119–125.
- Knowlton, N. 2001. The Future of Coral Reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 98:5419–5425.
- Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. Beach. 2006. Inhibition of Coral Recruitment by Macroalgae and Cyanobacteria. *Marine Ecology Progress Series*, 323:107–117.
- Lirman, D. 2001. Competition Between Macroalgae and Corals: Effects of Herbivore Exclusion and Increased Algal Biomass on Coral Survivorship and Growth. *Coral Reefs*, 19:392–399.
- Little, M. M., and D. S. Little. 1997. Disease-Induced Mass Mortality of Crustose Algae on Coral Reefs Provides Rationale for the Conservation of Herbivorous Fish Stocks. *Proceedings of the 8th International Coral Reef Symposium*, 1:719–724.
- Macintyre, I. G., P. W. Glynn, and F. Hinds. 2005. Evidence of the Role of *Diadema antillarum* in the Promotion of Coral Settlement and Survivorship. *Coral Reefs*, 24:273.
- Maida, M., J. C. Coll, and P. W. Sammarco. 1994. Shedding New Light on Scleractinian Coral Recruitment. *Journal of Experimental Marine Biology and Ecology*, 180:189–202.
- Maida, M., P. W. Sammarco, and J. C. Coll. 1995. Effects of Soft Corals on Scleractinian Coral Recruitment. I: Directional Allelopathy and Inhibition of Settlement. *Marine Ecology Progress Series*, 121:191–202.
- McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition Between Corals and Algae on Coral Reefs: A Review of Evidence and Mechanisms. *Coral Reefs*, 19:400–417.
- Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. *Science*, 311:98–101.
- Mumby, P. J., and R. Steneck. 2008. Coral Reef Management and Conservation in the Light of Rapidly Evolving Ecological Paradigms. *Trends in Ecology and Evolution*, 23:555–563.
- Nugues, M. M., G. W. Smith, R. J. Van Hooindonk, M. I. Seabra, and R. P. M. Bak. 2004. Algal Contact as a Trigger for Coral Disease. *Ecology Letters*, 7:919–923.
- Omori, M., K. Iwao, and M. Tamura. 2008. Growth of Transplanted *Acropora tenuis* 2 Years after Egg Culture. *Coral Reefs*, 27:165.
- Pandolfi, J. M., and J. B. C. Jackson. 2006. Ecological Persistence Interrupted in Caribbean Coral Reefs. *Ecology Letters*, 9:818–826.
- Pawlik, J. R., L. Steindler, T. P. Henkel, S. Beer, and M. Ilan. 2007. Chemical Warfare on Coral Reefs: Sponge Metabolites Differentially Affect Coral Symbiosis In Situ. *Limnology and Oceanography*, 52:907–911.
- Richmond, R. H., 1997. Reproduction and Recruitment in Corals: Critical Links in the Persistence of Reefs. In *Life and Death of Coral Reefs*, ed. C. E. Birkeland, pp. 175–198. New York: Chapman & Hall.
- Rylandsdam, K.W. 1983. Life Histories and Abundance Patterns of Colonial Corals on Jamaican Reefs. *Marine Ecology Progress Series*, 13:249–260.
- Sammarco, P. W., and J. H. Carleton. 1981. Damselfish Territoriality and Coral Community Structure: Reduced Grazing, Coral Recruitment, and Effects on Coral Spat. In: *Proceedings of the 4th International Coral Reef Symposium*, 2:525–535.
- Sebens, K. P. 1982. Competition for Space: Growth Rate, Reproductive Output, and Escape in Size. *American Naturalist*, 120:189–197.
- Smith, J. E., M. Shaw, R. A. Edwards, D. Obura, O. Pantos, E. Sala, S. A. Sandin, S. Smriga, M. Hatay, and F. L. Rohwer. 2006. Indirect Effects of Algae on Coral: Algae-Mediated, Microbe-Induced Coral Mortality. *Ecology Letters*, 9:835–845.
- Smith, S. R. 1992. Patterns of Coral Recruitment and Post-settlement Mortality on Bermuda's Reefs: Comparisons to Caribbean and Pacific Reefs. *American Zoologist*, 32:663–673.
- . 1997. Patterns of Coral Settlement, Recruitment and Juvenile Mortality with Depth at Conch Reef, Florida. *Proceedings of the 8th International Coral Reef Symposium*, 2:1197–1202.
- Steneck, R. S., and J. C. Lang. 2003. Rapid Assessment of Mexico's Yucatan Reef in 1997 and 1999: Pre- and Post-Mass Bleaching and Hurricane Mitch (Stony Corals, Algae and Fish). *Atoll Research Bulletin*, 496:294–317.
- Steneck, R. S., and M. N. Dethier. 1994. A Functional Group Approach to the Structure of Algal-Dominated Communities. *Oikos*, 69:476–498.
- Sullivan, B., D. J. Faulkner, and L. Webb. 1983. Siphonodictidine, a Metabolite of the Burrowing Sponge *Siphonodictyon* sp. That Inhibits Coral Growth. *Science*, 221:1175–1176.
- Van Moorsel, G. W. N. M. 1989. *Juvenile Ecology and Reproductive Strategies of Reef Corals*. Leiden: Backhuys Publishers.
- Vermeij, M. J. A. 2005. Substrate Composition and Adult Distribution Determine Recruitment Patterns in a Caribbean Brooding Coral. *Marine Ecology Progress Series*, 295:123–133.
- . 2006. Early Life-History Dynamics of Caribbean Coral Species on Artificial Substratum: The Importance of Competition, Growth and Variation in Life-History Strategy. *Coral Reefs*, 25:59–71.
- Vermeij, M. J. A., and S. A. Sandin. 2008. Density-Dependent Settlement and Mortality Structure: The Earliest Life Phases of a Coral Population. *Ecology*, 89:1994–2004.
- Vermeij, M. J. A., J. E. Smith, C. M. Smith, R. V. Thurber, and S. A. Sandin. 2009. Survival and Settlement Success of Coral Planulae: Independent and Synergistic Effects of Macroalgae and Microbes. *Oecologia*, 159:325–336.
- Wakeford, M., T. J. Done, and C. R. Johnson. 2008. Decadal Trends in a Coral Community and Evidence of Changed Disturbance Regime. *Coral Reefs*, 27:1–16.
- Williams, D. E., M. W. Miller, and K. L. Kramer. 2008. Recruitment Failure in Florida Keys *Acropora palmata*, a Threatened Caribbean Coral. *Coral Reefs*, 27:697–705.
- Wittenberg, M., and W. Hunte. 1992. Effects of Eutrophication and Sedimentation on Juvenile Corals I. Abundance, Mortality and Community Structure. *Marine Biology*, 112:131–138.



Spotlight on:

Mark Dondi Arboleda

PhD student Mark Dondi Arboleda kills corals – but in their own best interests, he is quick to add.

A coral microbiologist, his PhD project focuses on investigating the causes for coral disease by examining the bacterial profiles of healthy and diseased corals. This sometimes involves infecting corals on purpose and assessing their recovery potential under different conditions.

Infection trials have looked at Porites Ulcerative White Spot (PUWS) disease. There is a high incidence of this disease in the Lingayen Gulf (Philippines) region's coral reefs. It is characterised by bleached, round spots 3 to 5 mm in diameter which may either regress or progress to full tissue-thickness ulcerations that join together, occasionally resulting in colony death. The research has demonstrated that a *Vibrio* isolate is a causative agent for this condition. Interestingly fish-farming waste did not have a significant effect on the incidence of, and recovery from, PUWS under experimental conditions.

Spotlight on Southeast Asian scholars

In March 2009, CRTR Program Communications Coordinator Gabrielle Sheehan visited the Southeast Asian Centre of Excellence to help the researchers tell their stories. She interviewed the scholars as a journalist would, to find out about their research and discover what motivates them to study the world of coral reefs. These stories are included in scholar profiles throughout the anthology.



Spotlight on:

Ronald Villanueva

A post-doctoral researcher, Ronald Villanueva spends his time talking a lot about concrete balls and pitching tents underwater. It is not the boy scouts but critical work for the Restoration & Remediation Working Group to assess the efficacy and cost effectiveness of using ReefBalls™ to work better in the coral reef restoration process.

ReefBalls™ have been used around the world to encourage the re-growth and formation of coral reefs, but with mixed results. Their advantages include provision of a standard substrate for coral growth and fish refuges. They are robust and can be accurately placed in target areas. However they are relatively expensive and cumbersome. More needs to be understood about how best to use ReefBalls™ in situ, if their potential as a tool in reef restoration is to be realised.

Ronald's research is examining the use of ReefBalls™ on reefs subject to a range of anthropogenic pressures. He is examining the effect of algal grazing on coral recruitment through introduction of a snail (*Trochus niloticus*) to the trial ReefBalls™ in the Bolinao reef complex, and working out which species of coral grow best on the ReefBalls™ through transplantation experiments. The project also includes augmentation of coral larval supply at a trial site in Palau where a tent is pitched around the ReefBalls™ to ensure a concentrated supply of larvae is exposed to the ReefBalls™ surface.

Jacqueline L. Padilla Gamiño

Coral romance: exploring coral reproduction with a field perspective



Jacqueline is currently a graduate student enrolled in a PhD program in the Department of Oceanography at the University of Hawaii and working in the laboratory of Dr. Ruth Gates at the Hawaii Institute of Marine Biology. Her research focuses on the reproductive ecophysiology of scleractinian corals. Specifically, she is interested in how reproductive patterns (fecundity, fertilization, parental investment per ovum and larval fitness) can be influenced by a coral's exposure to, and ability to adapt and/or acclimatize to new environmental conditions. After her PhD, she is planning to return to Mexico to work as a professor and researcher in the area of Marine Ecophysiology.



Coral romance: exploring coral reproduction with a field perspective

Jacqueline L. Padilla-Gamiño

(UH Sea Grant Supported Graduate Student)

Department of Oceanography, Hawaii Institute of Marine Biology, University of Hawaii, USA

Coral reefs are extremely diverse and very important ecosystems on Earth. Coral reefs can provide protection and shelter for many species (fish, mollusks and other invertebrates) and protect the coast from strong currents, waves and even tsunamis! In order for corals to persist, coral communities depend on the supply and survival of new recruits. Understanding the mechanisms related to the supply and success of new recruits is of vital importance to predict future changes associated with global warming and other anthropogenic effects.

Corals reproduce both asexually and sexually. Asexual modes of reproduction include fission/budding, fragmentation and parthenogenesis (development of an egg without fertilization). Sexual reproduction requires fertilization to occur. Some corals release their gametes (egg and sperm) into the water and fertilization occurs in the water column. These corals are called spawners and can be either gonochronic (male or female) or hermaphrodites (both sexes). In contrast, brooder corals have their eggs fertilized inside the polyps and release larvae. Brooders can also be hermaphrodites or males and females.

Reproduction of corals can be affected by many factors such as sedimentation, nutrients, pollution, habitat destruction, temperature, light, etc. Sedimentation, as a result of both natural processes and human activities, can be one of the main drivers of reef degradation. Increased sediment loading of coastal waters can (1) reduce the area of sea floor suitable for settlement, (2) alter chemical cues for settlement, (3) increase water turbidity that can lead to lower light available for photosynthesis, (4) reduce feeding surfaces responsible for catching prey, and (5) in extreme cases, burying entire coral colonies. Reproduction (fecundity) and early life stages of corals are especially vulnerable to higher sedimentation rates. For example, reduction in water quality by particulate land based pollution negatively can affect rates of survival and settlement of coral larvae and interferes with chemical signals that allow for the synchronous release of gametes. Although, some corals efficiently remove sediments using mucus production and ciliary action, these activities expend metabolic energy, a cost that could potentially limit both reproductive success and growth. In addition, the reduction of photosynthesis due to lower light levels in more turbid waters can significantly lower the energy for development and maturation.

Population growth rates in the coastal zone and the use of coral reef resources have greatly increased in the last decades. Human activities such as farming, coastal development (tourism infrastructure, building or road construction), dredging and deforestation have increased the rate of soil erosion and sediment input into streams. This pressure intensification has had enormous ecological and economical consequences worldwide. Frequent run-off near large streams and re-suspension of sediment are the two main processes causing high sedimentation levels in Hawaiian coastal waters.

My research seeks to understand how coral fecundity and parental investment (adult vs. offspring phenotypes) are affected by different environmental conditions (i.e. sedimentation) in Kane'ohe Bay, Hawaii.

Spatial and long-term temporal variation in coral reproductive capability has not been well studied because of the sporadic nature of reproductive activities in corals and the limited methodological approaches for exploring them. These methods include histology, dissection and observations during the spawning nights. Currently, we are using novel techniques to collect egg-sperm bundles of the coral rice *Montipora capitata*.



Colony of *Favites halicora* spawning at the hatchery, Bolinao Marine Science Laboratory, May 2009 (James Guest)

For the last two years we have collected egg-sperm bundles in the natural environment (in situ) from colonies with different sizes and morphologies. We were able to collect egg-sperm bundles from approximately 38 colonies from different locations during different months and days of the lunar cycle. For this effort we had the participation of 170 volunteers ranging in ages from 10 to 55 years old! It was an amazing experience to join efforts with students, professors and the local community to construct a good data base that will help us to assess coral reproductive dynamics at different temporal and spatial scales.

Currently, I am studying different physiological properties of the collected eggs in order to understand how the offspring is influenced by the parental characteristics (phenotype) and different environmental conditions. This work will help to understand the variability within the eggs, which might compromise the survival and dispersal of coral larvae and the success of new recruits. Because reproductive fitness may be used as a sensitive indicator of stress in corals, the data from this study will also provide a useful tool for future monitoring in Kane’ohe Bay and a tool to design future ecological risk assessments in Hawaii’s coral reef ecosystems.

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Morgan Mouchka & Courtney Couch

The effects of aquaculture effluent on *Porites cylindrica* innate immune function

Morgan graduated Summa Cum Laude with an Honors Bachelor of Science degree from Oregon State University (OSU). As an undergraduate, Morgan conducted thesis research on cnidarian mutualistic symbiosis in the laboratory of Dr. Virginia Weis. After graduating, she became a research assistant in the laboratory of Dr. Jane Lubchenco and Dr. Bruce Menge at OSU where she investigated the ecophysiology of intertidal invertebrates. She is currently a PhD candidate in the Department of Ecology and Evolutionary Biology in the laboratory of Dr. Drew Harvell at Cornell University and is interested in cnidarian innate immunity and its relationship to mutualistic symbioses.

Courtney is currently a PhD candidate in the Department of Ecology and Evolutionary Biology advised by Dr. Drew Harvell. Interested in the effects environmental stress has on coral physiology and coral reef health, Courtney has employed a multidisciplinary approach to understand how corals mount an immune response to pathogens and abiotic stressors. Courtney's doctoral thesis is now focused on the role of environment and viruses in *Porites lobata* growth anomalies on the island of Hawaii. In addition to her graduate research, Courtney has also acted as the coordinator of the CRTR's Coral Disease Working Group since 2007.



Morgan (left) and Courtney (right) grinding coral samples at the Bolinao Marine Laboratory. Photo: Miahnie Pueblos

The effects of aquaculture effluent on *Porites cylindrica* innate immune function

Morgan Mouchka and Courtney Couch

Cornell University, Ithaca, USA

As marine fisheries continue to decline, aquaculture has undergone unprecedented growth to meet global protein demand (Sapkota et al. 2008). In tropical coastal regions, aquaculture is increasingly regarded as a threat to coral reef ecosystems (Loya 2004; Villanueva et al. 2006). The introduction of organic matter from waste feed and metabolic end-products into nearby waters can lead to eutrophication and increased sedimentation, two stressors that are particularly detrimental to coral reefs that normally thrive in clear, oligotrophic waters. The effects of these stressors on coral reefs have been well-studied in the context of terrestrial run-off, and include ecosystem degradation and loss of resilience (Hughes et al. 2003; Fabricius 2005).

Though small in number, few studies examining the effects of effluent on reef-building corals suggest that aquaculture can negatively affect many facets of coral biology. Loya et al. (2004) found that reproductive effort was reduced in *Stylophora pistillata* exposed to fish pen effluent in the Red Sea. In the Philippines, Villanueva et al. (2005; 2006) found that survivorship of juvenile *Seriatopora caliendrum* and *Pocillopora damicornis* was reduced at sites adjacent to fish cages, as was adult *P. damicornis* survivorship, growth, photosynthesis, and larval output. Aquaculture effluent can also alter coral microbial communities. Garren et al. (2009) found that effluent exposure led to shifts in the coral-associated bacterial community of *Porites cylindrica*, and that the duration of these shifts is dependent upon effluent concentration.

To date, the direct effects of aquaculture effluent on coral immunity have not been investigated. To explore this relationship, we transplanted coral fragments from a relatively effluent-free site (Reference site), to sites representing low and high effluent exposure (Far 1 and 2, and Near 1 and 2, respectively) and documented immune protein activity at 5, 10, and 22 days following transplantation. We hypothesized that immune protein activity would be higher in fragments exposed to high effluent for three, not necessarily mutually exclusive reasons. First, coral fragments transplanted to high effluent sites would experience higher bacterial, and viral loads (Garren et al. 2008). Second, coral fragments at high effluent sites might be exposed to potentially novel, pathogenic bacteria (Garren et al. 2009). Third, eutrophication associated with effluent may act to “fertilize” potentially pathogenic microbes (Bruno et al. 2003; Voss and Richardson 2006). We also collected coral fragments with *Porites* ulcerative white spot (PUWS) disease, a common disease on Indo-Pacific reefs (Raymundo et al. 2003), to compare immune protein activity between healthy and diseased fragments. Given the increase in the prevalence and severity of coral disease over the last several decades, a better understanding of the environmental drivers of coral disease and immunity is needed.

Materials and methods

Transplant experimental set up

Fragments were collected on May 20, 2008 from healthy donor colonies of *P. cylindrica* on the outer reef slope of Malilnep Channel. This site was chosen as the reference site based on the relatively healthy nature of the reef ecosystem, continual flushing by fresh seawater from the South China Sea, and its distance from fish cages (~10 km). Fragments were removed from seven colonies and inserted into 5 cm plastic hose. Fragments were then attached to mesh covered PVC frames, attached to iron bars, and anchored to the substrate at five sites: the Reference site plus four additional sites, representing two transects of increasing distance from the fish cages (Fig. 1). Seven *P. cylindrica* fragments with *Porites* Ulcerative White Spots disease (PUWS) and clinically healthy fragments were also collected from the nearshore reef crest at Malilnep Channel, adjacent to the reference site.

Sample collection and preparation



Figure 1. Map of the study area showing the two water quality gradients and reference site. Bolinao, Pangasinan, Philippines.

A fragment from each colony was sampled prior to transplantation, and then at five, ten, and 22 days post-transplantation from each site. Following collection, fragments were flash frozen in liquid nitrogen and stored at -20°C until processing. Crude extracts were prepared by grinding fragments weighing between 2-4 grams in liquid nitrogen with a mortar and pestle, and adding the resulting powder to 1 ml per gram weight protein extraction buffer. Samples were extracted on ice for 45 min before centrifugation and collection of the resulting supernatant. Protein concentration of the extracts was determined using the Bio-Rad DC Protein Assay Kit according to manufacturer's instructions.

Measurements of immune response

The immune response of *P. cylindrica* as a function of treatment was quantified with three colorimetric assays: prophenoloxidase (PPO) activity, superoxide dismutase (SOD) activity, and antibacterial (AB) activity. PPO is an enzyme that initiates the formation of melanin, an important barrier to pathogen spread. SOD is an antioxidant that catalyzes the conversion of the reactive oxygen species, superoxide, into hydrogen peroxide and oxygen. Superoxide is produced via cellular stress and/or pathogen infection and is combated via up-regulation of SOD. The antibacterial assay measures the inhibition of bacteria exposed to coral extracts. Activity of all three assays has been shown to be increased in diseased corals (Mydlarz et al. 2008; Mydlarz et al. in press). SOD activity was measured via the Fluka Analytical SOD Determination Kit according to manufacturer's instructions and PPO and antibacterial activity were measured according to Mydlarz et al. (2008) and Couch et al. (2008), respectively. Enzyme and antibacterial activity were standardized by protein concentration.

Results and discussion

This is the first study to investigate the effects of aquaculture effluent on coral immunity. For all three assays, there were no significant differences in immune protein activity between sites or times for the transplant experiment (Fig. 2, 3, and 4). These results suggest that aquaculture effluent has very little effect on PPO, SOD, and antimicrobial activity. Kramarksy-Winter et al. (2009) compared a suite of cellular responses between *S. pistillata* colonies transplanted near aquaculture sites and those in minimally polluted waters and found that while there were some significant differences between proteins involved in protein metabolic condition, oxidative stress, and xenobiotic responses, no significant differences were found in levels of Hsp70, ubiquitin, MnSOD, glutathione peroxidase, and catalase, proteins that not only play a role in cellular stress, but in immunity as well. It's also possible that our results reflect differences in the temporal scale of the transplantation duration and the coral immune response. Previous studies have shown that many invertebrates mount an immune response within minutes or hours of elicitation (Korner and Schmid-Hempel 2004; Zelck et al. 2005). Therefore, our sampling scheme may have "missed" any increase in immune protein activity associated with effluent exposure, and by day 5, the coral response had relaxed as a result of adaptation to transplantation site.

1. Understanding local-scale ecological processes

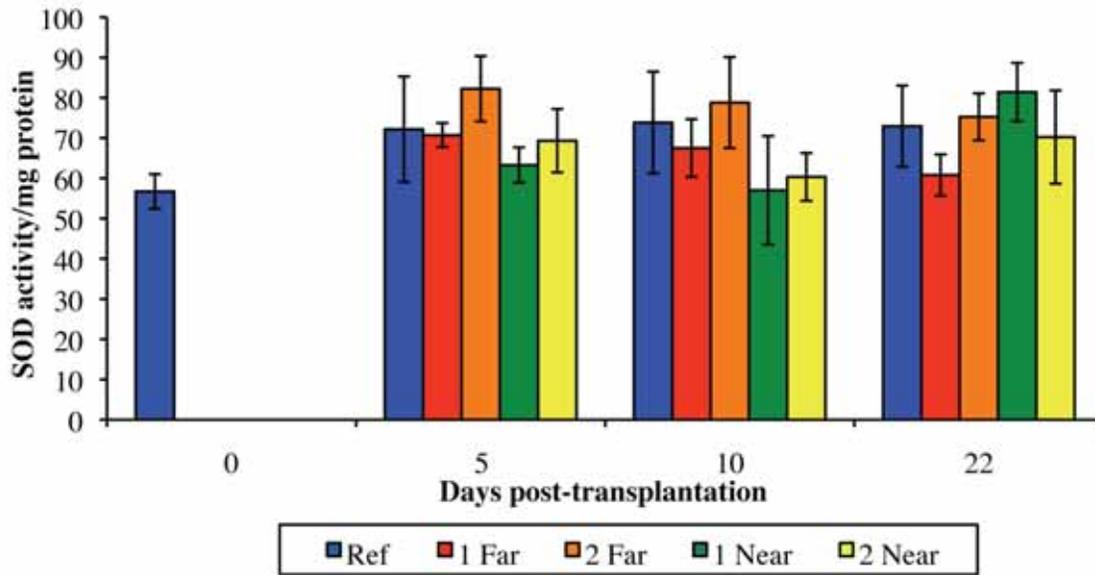


Figure 2. SOD activity of *Porites cylindrica* crude protein extracts at 0, 5, 10, and 22 days post-transplantation at 5 sites representing two gradients of water quality. n=7 fragments per site per sampling period; mean \pm SE. (ANOVA by site by time: 5d $p < 0.378$; 10 d $p < 0.3$; 22d $p < 0.7251$).

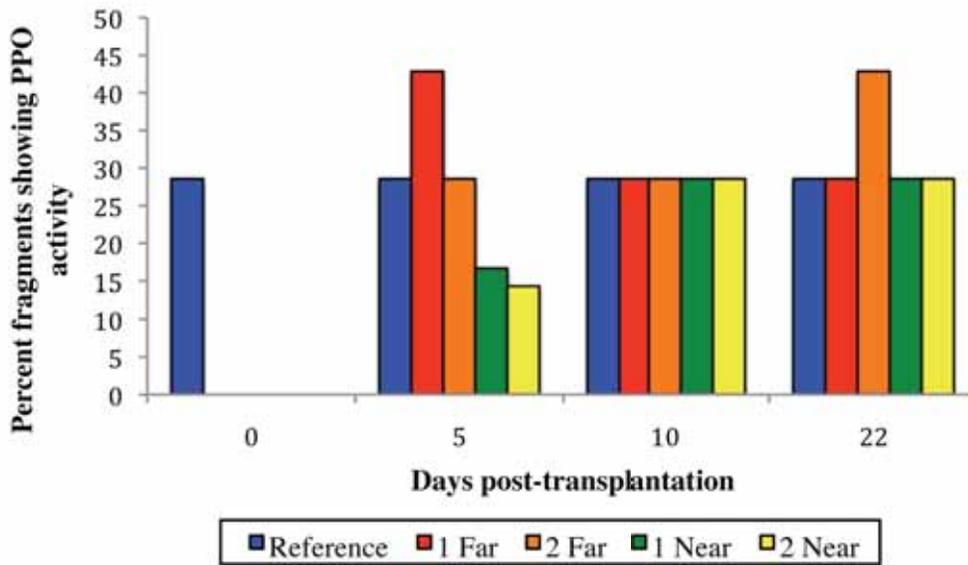


Figure 3. Percent of *Porites cylindrica* fragments that initiated a PPO response at 0, 5, 10, and 22 days post-transplantation at 5 sites representing two gradients of water quality. n=7 fragments per site per sampling period. (Pearson's chi-square test by site by time; 5 d $p < 0.7674$; 10 d $p < 1.00$; 22 d $p < 0.9705$).

1. Understanding local-scale ecological processes

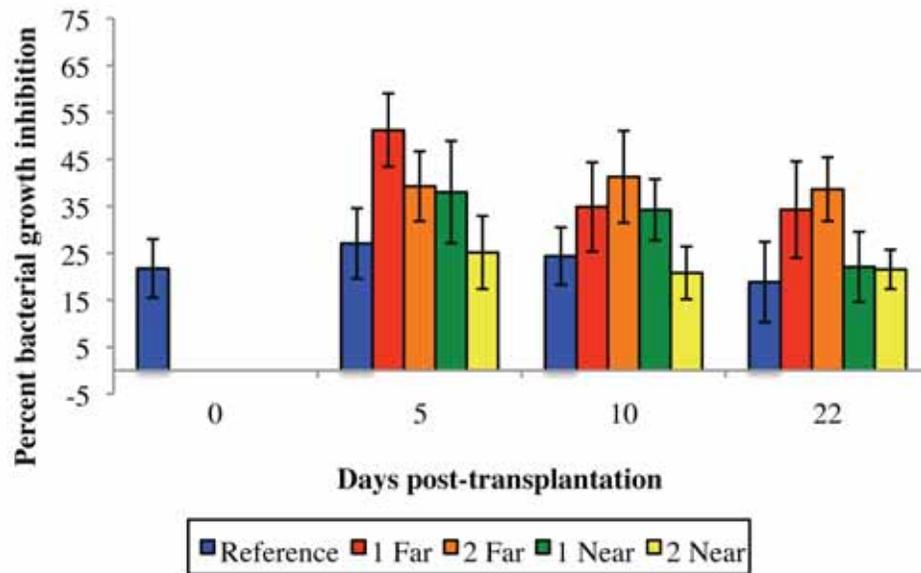


Figure 4. Bacterial growth inhibition of *Porites cylindrica* crude protein extracts at 0, 5, 10, and 22 days post-transplantation at 5 sites representing two gradients of water quality. $n=7$ fragments per site per sampling period; mean \pm SE. (ANOVA by site by time: 5 d $p < 0.2129$; 10 d $p < 0.3351$; 22 d $p < 0.2934$)

This is the first study to document immune protein activity as a function of PUWS infection. Significantly more diseased fragments initiated a PPO response than healthy fragments (Table 1). While not significant, diseased fragments had higher SOD and antibacterial activity, suggesting that future investigations of a larger sample of corals are warranted. Taken together, these data suggest that *P. cylindrica* may up-regulate immune activity as a function of PUWS infection. Both the healthy and diseased fragments were collected from an effluent-free site, and it would be interesting to see the combined response of coral immunity to effluent exposure and infection. Previous studies have documented an increase in disease severity (% tissue loss) with increasing nutrients. Therefore, it is possible that diseased fragments in high effluent sites would show a larger increase immune protein activity to combat increased disease severity. It is also possible, however, that the stress associated with eutrophication and sedimentation in the high effluent sites would compromise host immunity, potentially resulting in death. Future investigation into the role of effluent on coral disease will be critical in making better-informed decisions regarding aquaculture placement and management practices.

Table 1. Immune protein activity of healthy fragments and those infected with *Porites ulcerative white spot* (PUWS) disease collected from Malilnep Channel. $n=7$ fragments. PPO: percentage of fragments that initiated a PPO response (Fisher's Exact Test); SOD: Mean \pm SE superoxide dismutase activity per mg protein (t-test); AB: Mean \pm SE bacterial growth inhibition (t-test).

	Mean \pm St. Error		df	F ratio	p-value
	Healthy	Diseased			
PPO	37.5	100	1	NA	0.028
SOD	56.74 \pm 4.30	65.9 \pm 8.27	1	0.8851	0.369
AB	13.55 \pm 5.36	33.97 \pm 8.86	1	4.5584	0.0541

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References

- Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters* 6: 1056-1061
- Couch CS, Mydlarz LD, Harvell CD, Douglas NL (2008) Variation in measures of immunocompetence of sea fan coral, *Gorgonia ventalina*, in the Florida Keys. *Marine Biology* 155: 281-292
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50: 125-146
- Garren M, Raymundo LJ, Guest J, Harvell CD, Azam F (2009) Resilience of Coral-Associated Bacterial Communities Exposed to Fish Farm Effluent. *Proceedings of the National Academy of Sciences of the United States of America* in press
- Garren M, Smriga S, Azam F (2008) Gradients of coastal fish farm effluents and their effect on coral reef microbes. *Environmental Microbiology* 10: 2299-2312
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg RK, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough J, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933
- Korner P, Schmid-Hempel P (2004) In vivo dynamics of an immune response in the bumble bee *Bombus terrestris*. *Journal of Invertebrate Pathology* 87: 59-66
- Kramarsky-Winter E, Downs CA, Downs A, Loya Y (2009) Cellular responses in the coral *Stylophora pistillata* exposed to eutrophication from fish mariculture. *Evolutionary Ecology Research* 11: 1-21
- Loya Y (2004) The coral reefs of Eilat-past, present and future: Three decades of coral community structure. In: Rosenberg E, Loya Y (eds) *Coral Health and Disease*. Springer-Verlag, Berlin, pp 1-34
- Mydlarz LD, Couch CS, Weil E, Smith GW, Harvell CD (in press) Immune defenses of Healthy, Diseased and Bleached *Montastraea faveolata* during the 2005 Caribbean Bleaching Event. *Diseases of Aquatic Organisms*
- Mydlarz LD, Holthouse SF, Peters EC, Harvell CD (2008) Cellular responses in sea fan corals: Granular amoebocytes react to pathogen and climate stressors. *PLoS One* 3: e1811
- Raymundo LJ, Harvell CD, Reynolds TL (2003) Porites ulcerative white spot disease: description, prevalence, and host range of a new coral disease affecting Indo-Pacific reefs. *Diseases of Aquatic Organisms* 56: 95-104
- Sapkota A, Sapkota AR, Kucharski M, Burke J, McKenzie S, Walker P, Lawrence R (2008) Aquaculture practices and potential human health risks: Current knowledge and future priorities. *Environment International* 34: 1215-1226
- Villanueva RD, Yap HT, Montano MNE (2006) Intensive fish farming in the Philippines is detrimental to the reef-building coral *Pocillopora damicornis*. *Marine Ecology-Progress Series* 316: 165-174
- Villanueva RD, Yap HT, Montano MNE (2005) Survivorship of coral juveniles in a fish farm environment. *Marine Pollution Bulletin* 51: 580-589
- Voss JD, Richardson LL (2006) Nutrient enrichment enhances black band disease progression in corals. *Coral Reefs* 25: 569-576
- Zelck UE, Janje B, Schneider O (2005) Superoxide dismutase expression and H₂O₂ production by hemocytes of the trematode intermediate host *Lymnaea stagnalis* (Gastropoda). *Developmental & Comparative Immunology* 29: 305-314



Spotlight on:

Maria Vanessa Baria

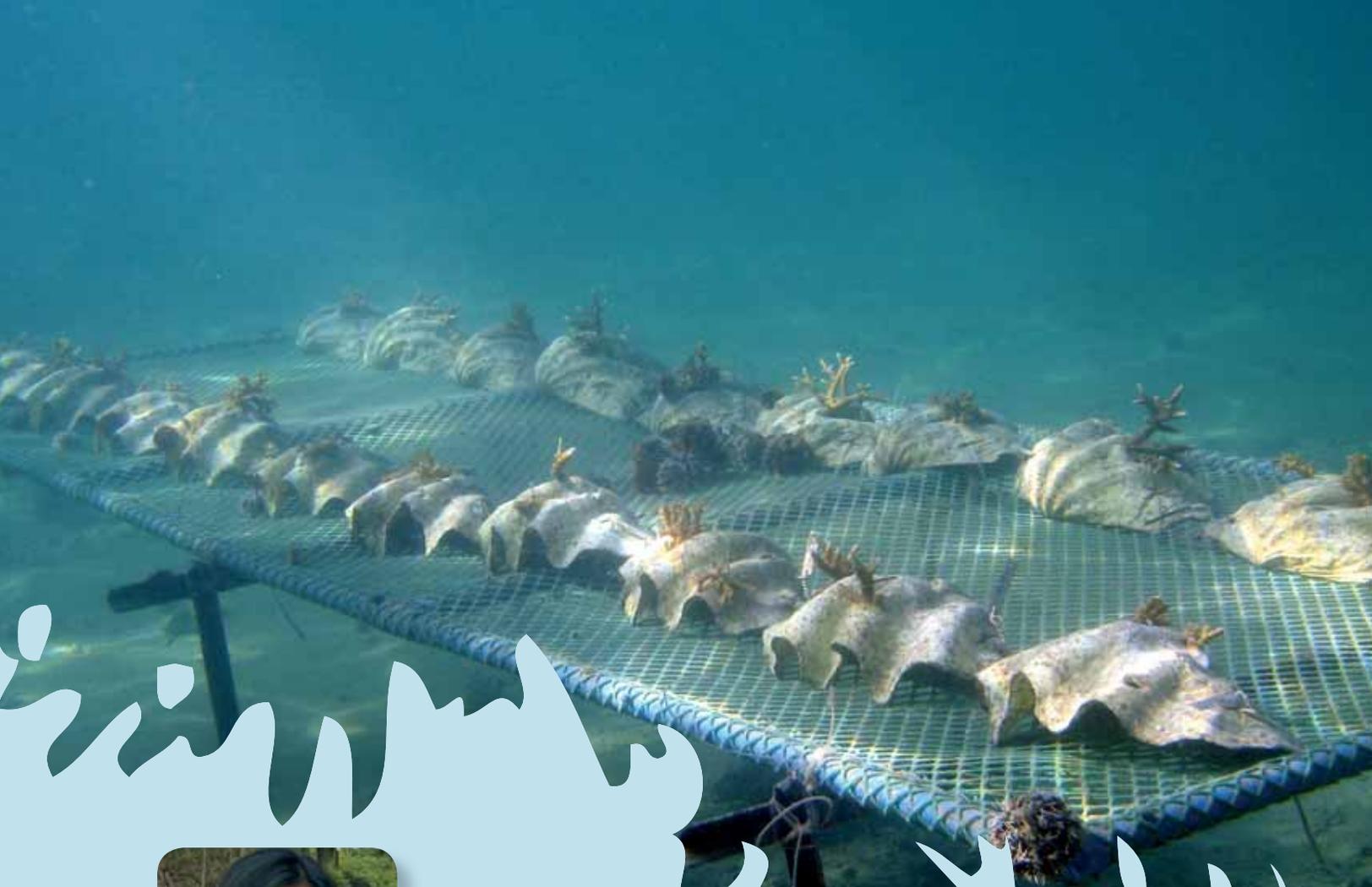
Most mothers keep a careful watch on their babies – this was not so easy for Masters student Maria Vanessa Baria some of whose “babies” live in the middle of Bolinao Lagoon. She proudly acknowledges however that they are thriving, and will one day become parents themselves.

Her research is on coral recruitment and larval rearing for the CRTR Restoration & Remediation Working Group. Her Masters project determined that larval recruitment in the Bolinao-Anda reef complex is not an issue, but problems lie in the long term survival of recruits. Successful larval rearing and subsequent survival on natural reefs is a key goal in restoration of degraded reefs, but methods must be efficient and economically viable. In her lab nursery, Vanessa has successfully reared common local species *A. tenuis*, *A. hyacinthus*, *A. millepora*, *Montastrea colemani*, *Favites halicora* and *Platygyra pini*.

When transplanted to bommies and to semi-caged nurseries in the lagoon, survival rates among species varied. *A. hyacinthus* and *A. millepora* have so far proved to be the most resilient with 100% survival in the nursery and 57% survival on the bommies. Field trials have also proved that in the early development of coral spats, herbivory exclusion cages enhanced juvenile survivorship.

“I call the corals my ‘babies’ because I have been responsible for them, and thought about them so much,” says Vanessa, “but the really important thing is ensuring a sustainable reef so our communities that rely on them can prosper. I am very proud my coral babies have contributed to our store of knowledge.”

Vanessa’s future work will focus on larval rearing of two other species and on trying to establish the best time to outplant nursery-reared juveniles.



Spotlight on:

Kareen Vicentuan-Cabaitan

As an 8-year-old on the beach in the central Philippines, Kareen Vicentuan-Cabaitan performed her first experiment in coral reef science, harvesting a beautiful piece of coral reef and placing it on the beach for closer observation. A return visit revealed a dead lump of coral, just like the ones she had seen underwater. This put a surprised Kareen on the path to discovery – how can we keep the reefs beautiful?

For her Masters project with the Restoration & Remediation Working Group, Kareen looked at the effects of fragmentation and transplantation on the growth, survival and reproduction of *Acropora muricata* and *Hydnophora rigida* to increase understanding of coral recruitment's role in restoration and resilience. Despite setbacks including a significant bleaching event in June 2007 and predation by *Acanthaster planci* (Crown-of-Thorns starfish) at the trial sites, her work, based at Bolinao, has shown fragmentation and transplantation have no significant effect on survival, growth and reproduction in *H. rigida* but have a significant effect on *A. muricata*.

"This information will increase our ability to restore these key species on degraded coral reefs, and hopefully make them beautiful for other little girls to see," says Kareen. She does not recommend her childhood research method however...

Adán Guillermo Jordán-Garza

Is the thin dark line sign on *Montastraea cavernosa* associated with tissue loss and caused by the presence of cyanobacteria?



Adán Guillermo is a Mexican marine biologist from the “Universidad Nacional Autónoma de México” that has received most of his reef-related training at Puerto Morelos, Quintana Roo under the tutelage of Dr. Eric Jordán-Dahlgren. One of his main concerns is the effect of environmental changes (natural and anthropogenic) on the populations of reef-building corals. That is why one of his main research lines has been the effect of diseases on corals of the *Montastraea* genus. With a huge experience on the field, Adán Guillermo is currently pursuing a PhD with Dr. Robert van Woesik in Florida. Given the uncontrolled speed of changes generated by the expansion of our societies and it’s related processes, Adán Guillermo considers that there is a growing necessity for better models that will help understand and manage coral reefs.



Conducting a field experiment on *Montastraea faveolata* colonies with yellow-band syndrome.
Photo: Rosa Rodríguez-Martínez

Is the thin dark line sign on *Montastraea cavernosa* associated with tissue loss and caused by the presence of cyanobacteria?

Adán Guillermo Jordán-Garza and Eric Jordán-Dahlgren

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Abstract

In the last decades there has been a considerable increase in the number of different coral diseases, yet only for a few of them the etiology is solved. Diagnosis is generally based on signs and syndromes observed on the colonies and those can be subjective and uninformative. The thin dark line sign is suspected to cause coral mortality and to be related to other diseases where cyanobacteria are involved as causative agents. By following colonies in the field and using spectral analysis this study shows that the thin dark line was not associated with significant tissue loss and that cyanobacteria were absent on colonies of the Caribbean *Montastraea cavernosa*. The presence of endolithic algae near the surface of the coral skeleton at the colony edge caused the dark line.

Introduction

Since the first observations of coral diseases on the early 1970s, a chronic increase in their prevalence has been documented, with unexpected region-wide epizootics (Harvell et al. 1999; Harvell et al. 2002). For some diseases, the causative agents (i.e. pathogens, environmental parameters) and their effect on coral colonies has been documented (Bruno et al. 2003; Patterson et al. 2002; Kuta and Richardson 2002; Richardson et al. 1998; Ben-Haim and Rosenberg, 2002), but for the majority of the diseases, their etiology is still elusive (Sutherland et al. 2004). Part of the problem is a lack of systematic disease characterization (Work and Aeby, 2006) that has led to subjective descriptions and interpretations, hindering the inferring of causality and the forecast of the effects on coral populations. Coral disease diagnoses are based on the description of visual changes from the normal appearance of coral tissue (Sutherland et al. 2004).

The coloration of scleractinian corals is related to the abundance and pigmentation of the algal symbionts, and to the coral proteins homologous to green fluorescent protein (Kelmanson and Matz, 2003). Variation in pigment concentration among healthy corals may be a normal feature, unrelated to diseases (Apprill et al. 2007). In a stressed coral, however, the expulsion of zooxanthella leads to bleaching or yellowing (Douglas, 2003; Cervino et al. 2004). Darkening of the tissue edge may be related to the external presence of microorganisms, as in the cases of black-band disease and folliculinid ciliates (Croquer et al. 2006; Rutzler et al. 1983). Tissue darkening could also be caused by a coral protein or by the presence of an intracellular microorganism. A sign named thin dark line was described by Jordán-Dahlgren et al. (2005) as a thin line of darkened tissue on the edge of colonies of the genus *Montastraea* on Mexican reefs in the Gulf of Mexico and Caribbean. According to these authors, tissue mortality could be associated with this sign and due to the suspected presence of cyanobacteria they propose it could be an early stage of black band disease. Previously Peters (1984) described a similar sign as the darkening of the edge of colonies of *M. annularis*, *Diploria* spp. and *Siderastrea* spp., next to an accumulation of filamentous and calcareous algae and sediment and accompanied by a variety of microorganisms including ciliates, cyanobacteria, and other bacteria.

The goal of this study was to characterize the potential deleterious effect of the sign by measuring tissue progression, and also to use spectral signatures to investigate the presence of cyanobacteria. (Poryvkina et al. 1993). The coral *M. cavernosa* was used as a model because the thin dark line had a relatively high prevalence and was the main sign affecting the coral colonies at Puerto Morelos back reef in the Mexican Caribbean.

Materials and methods

Seventeen colonies of *Montastraea cavernosa*, with edges bearing the thin dark line (TDL) sign and edges free of any sign, were marked on the back reef of Puerto Morelos, Mexico (Figure 1). To follow the progression of the TDL sign 161 stainless-steel nails (5 cm long) were hammered on the reef substratum near the colony edges (Figure 2). The number of marks (nails) per colony varied depending on colony form and availability of space to place the marks without disturbing the colonies. To assess tissue progression for a year period, the distance between the tissue and the nail was measured with a plastic caliper once in September 2004 and then again in September 2005. Progression rates of tissue with no signs and tissue with signs were compared with a student t-test.

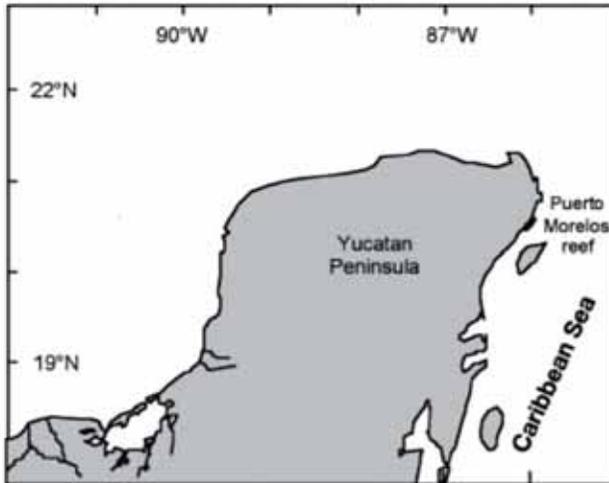


Figure 1. Map of the Yucatan Peninsula showing the location of Puerto Morelos Reef on the Mexican Caribbean Sea.

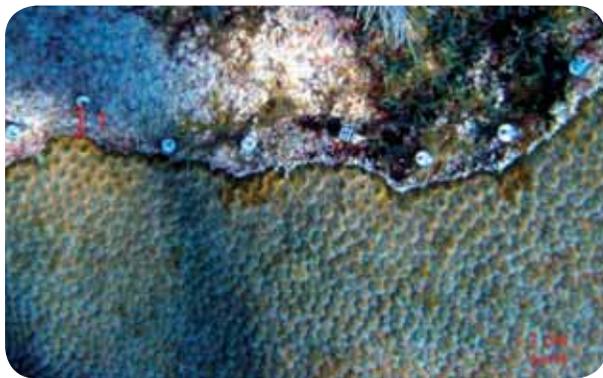


Figure 2. The stainless steel nails were hammered on reef substratum near the colonies edges. The shortest distance nail-edge (1) was measured with a plastic caliper.

Three *Montastraea cavernosa* fragments (around 7 x 5 cm) were obtained using a hammer and chisel. The fragments contained apparently healthy tissue and the TDL sign on their edges. They were kept on seawater and immediately transported to the laboratory to obtain their spectral characteristics. The reflectance spectra of normal appearing tissue and of tissue with the TDL sign were obtained between 400 and 750 nm with 1-nm resolution using a 4800S Lifetime spectrofluorometer (SLM-Aminco) following the technique described in Rodríguez-Román et al. (2006). The normally colored tissue was used for comparison with the sign bearing tissue. After this, the tissue was removed from the coral skeleton with pressured water. A sample of the tissue was observed with an optic microscope (OLYMPUS CH20-NCWHK 10x/18L) and the naked skeleton was also examined.

Results and discussion

No significant differences in tissue progression were found between sign bearing tissue and tissue with no signs ($t= 0.74$, $df= 159$, $p= 0.45$; Levene (1, 159)= 1.038, $p=0.3$). A slight tendency of tissue loss is observed on the tissue with TDL (Figure 3). The mean progression rates for tissue with no signs (-0.016 ± 1.02 mm/month, $MEAN \pm SD$) and TDL bearing tissue (-0.12 ± 0.85) were both close to 0 (no net change); but the high variability observed on both cases reflects the complex interactions of growth and the effect of different factors at the edges of colonies in the absence of major storms during the study period (corallivores, sedimentation, competition; Lang and Chornesky 1990; Lirman 2001).

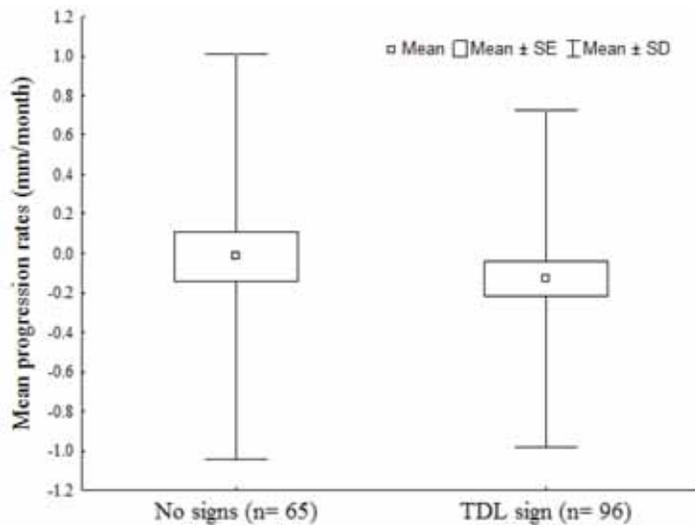


Figure 3. Mean progression rates of tissue with no signs and tissue bearing the thin dark line sign on colonies of *Montastraea cavernosa*.

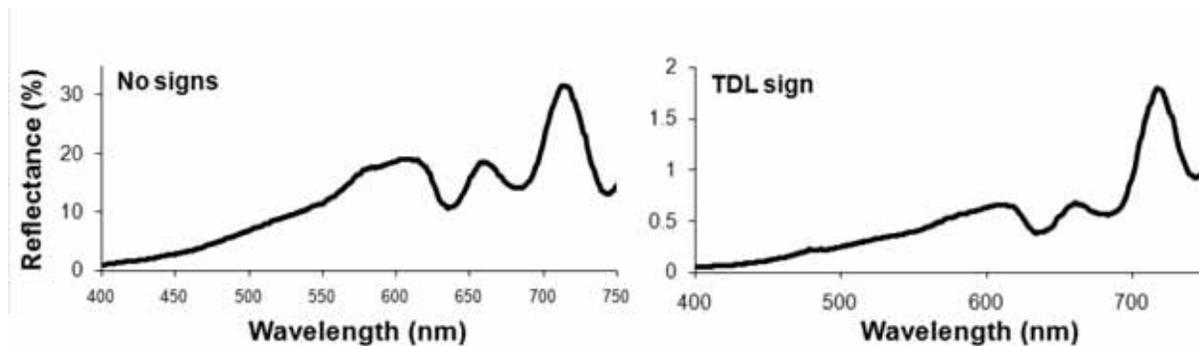


Figure 4. Reflectance spectra of tissue with no signs (left) and tissue with the thin dark line sign (right) on *Montastraea cavernosa*. Note the different scales on the y axis due to different absorption qualities.

Because the presence of cyanobacteria could be at the origin of the TDL sign, reflectance spectra of tissue with and without TDL sign were obtained from the coral fragments. Cyanobacteria contain phycoerythrin and would have caused absorption peaks at 505 and 571 nm (Lesser et al. 2004) but the results did not show the presence of light absorbing organisms or substances at the expected wavelengths (Figure 4). The sign bearing tissue had a reflectance on the PAR (400 to 700 nm) region of the spectrum that was lower than the normal looking tissue, average reflectance of normal tissue was 0.21 ± 0.11 ($MEAN \pm SD$) while TDL tissue had a mean of 0.09 ± 0.08 . This results from the darker appearance of the sign. Microscopic observations of the healthy and TDL sign bearing tissue did not reveal any differences between them or the presence of other organisms. Nevertheless, when the tissue was removed, a dark line of endolithic algae appeared on the skeleton, very close to the surface on the coral edge, right under the location of the sign (Figure 5).

1. Understanding local-scale ecological processes

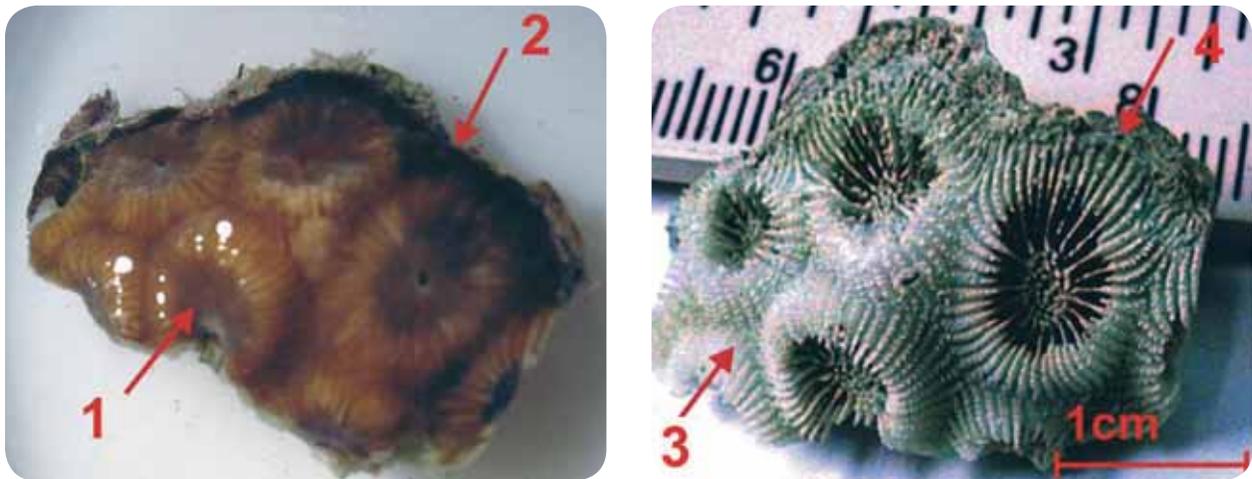


Figure 5. The image to the left shows the thin dark line sign on the living fragment of *Montastraea cavernosa* (1: normal appearing tissue; 2: sign on colony edge). The image to the right shows the same fragment with the tissue removed and the colored border due to the presence of endolithic algae (3: bare skeleton; 4: green pigmented skeleton).

Endolithic algae on corals are mainly from the genus *Ostreobium* sp. (Highsmith, 1981) and have been observed before on colony edges (Lukas, 1973) and, although the author was not sure if the algae penetrated the coral tissue, Peters (1984), observed basophilic sheathed structures apparently associated with *Ostreobium* sp. that appeared to compress the calicoblast layer of tissue and distort the normal structure of this layer.

Rodríguez-Román et al. (2006) showed that, in the presence of a bleaching event, the opacity generated by the endolithic algae could help the recovery process of the colonies. But in this case the presence of the algae could result in a hampered photosynthetic efficiency and reduced growth, as their presence changes the optic properties of the skeleton (Enriquez et al. 2005). Those hypotheses could explain the slight tendency to tissue loss shown when the sign is present.

The study shows the importance of conducting long term observations of colonies affected by signs of unknown or dubitable etiology as their effect on coral colonies might be less acute than expected. Borger (2005) following colonies with dark spot syndrome and not finding a significant tissue loss associated with it, questions the validity of calling the dark spot a disease. Further observations are required in the case of the thin dark line as, even with no significant tissue loss observed, other functions of the colony might be compromised.

Acknowledgements

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References

- Apprill AM, RR Bidigare and RD Gates. 2007. Visibly healthy corals exhibit variable pigment concentrations and symbiont phenotypes. *Coral Reefs* 26 (2): 387-397.
- Ben-Haim Y and E Rosenberg. 2002. A novel *Vibrio* sp. Pathogen of the coral *Pocillopora damicornis*. *Mar Biol* 141: 47-55.
- Borger JL 2005. Dark spot syndrome: a scleractinian coral disease or a general stress response? *Coral Reefs* 24: 139-144.
- Bruno JF, Petes LE, Harvell CD and Hettinger A. 2003. Nutrient enrichment can increase the severity of coral disease. *Ecol Lett* 6 (12): 1056-1061.
- Cervino JM, Hayes R, Goreau TJ and Smith GW. 2004. Zooxanthellae Regulation in Yellow Blotch/Band and Other Coral Diseases Contrasted with Temperature Related Bleaching: In situ Destruction vs Expulsion. *Symbiosis* 37: 63-85.
- Cróquer A, C Bastidas, D Lipscomp, R. Rodríguez-Martínez, E Jordán-Dahlgren and HM Guzman. 2006. First report of folliculinid ciliates affecting Caribbean scleractinian corals. *Coral Reefs* 25 (2): 187-191.
- Douglas AE. 2003. Coral bleaching- how and why? *Mar Pollut Bull* 46 (4): 385-392.
- Enriquez S, Mendez ER and Iglesias-Prieto R. 2005. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnol Oceanogr* 50 (4): 1025-1032.
- Harvell CD, K Kim, JM Burkholder, RR Colwell, PR Epstein, DJ Grimes, EE Hofmann, EK Lipp, ADME Oesterhaus, RM Overstreet, JW Porter, GW Smith and G R Vasta. 1999. Emerging Marine Diseases- Climate Links and Anthropogenic Factors. *Science* 285:1505-1510.
- Harvell CD, Mitchell ChE, Ward JR, Altizer S, Dobson AP, Ostfeld RS and Samuel MD. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* Vol. 296: 2158-2162.
- Highsmith RC. 1981. Coral bioerosion: damage relative to skeletal density. *Am Nat* 117: 193-198.
- Jordán-Dahlgren E, Maldonado MA and Rodríguez-Martínez RE. 2005. Diseases and partial mortality in the *Montastraea annularis* species complex in reefs with differing environmental conditions (NW Caribbean and Gulf of Mexico). *Dis Aquat Org* 63: 3-12.
- Kelmanson IV and Mikhail VM. 2003. Molecular basis and evolutionary origins of color diversity in great star coral *Montastraea cavernosa* (Scleractinia: Faviida). *Mol Biol Evol* 20(7): 1125-1133.
- KG Kuta and LL Richardson. 2002. Ecological aspects of black band disease of corals: relationships between disease incidence and environmental factors. *Coral Reefs* 21 (4): 393-398.
- Lang JC and Chornesky EA. 1990. Competition between scleractinian reef corals: a review of mechanisms and effects. In: Dubinsky Z (ed) *Ecosystems of the world 25: Coral Reefs*. Elsevier Science Publishers, Amsterdam: 209-252.
- Lesser MP, Mazel Ch.H. Gorbunov MY and Falkowski PG. 2004. Discovery of symbiotic nitrogen-fixing cyanobacteria in corals. *Science* 13 (305) 5686: 997-1000.
- Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19: 392-399.
- Lukas K.J. 1974. Two species of chlorophyte genus *Ostreobium* from skeletons of Atlantica and Caribbean reef corals. *J Phycol* 10 (3): 331-335.
- Patterson KL, Porter JW, Ritchie KB, Polson SW, Mueller E, Peters EC, Santavy DL and Smith GW. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. *PNAS* 99(13): 8725-8730-
- Peters EC. 1984. A survey of cellular reactions to environmental stress and disease in Caribbean scleractinian corals. *Helgol Meeresunters* 37: 113-134.
- Poryvkina L, S Babichenko, S Kaitala, H Kuosa and A Shalapjonok. 1993. Spectral fluorescence signatures in the characterization of phytoplankton community composition. *J Plankton Res* 16 (10): 1315-1327.
- Richardson LL. 1998. Coral diseases: what is really known? *Trends Ecol Evol* 13 (11): 438-443.
- Rodríguez-Román A, Hernández-Pech X., Thomé P.E., Enriquez S. and Iglesias-Prieto. 2006. Photosynthesis and light utilization in the Caribbean coral *Montastraea faveolata* recovering from a bleaching event. *Limnol Oceanogr* 51(6): 2702-2710.
- Rützler K, DL Santavy and A Antonius. 1983. The Black Band Disease of Atlantic Reef Corals. *Mar Ecol* 4(4): 301-319.
- Sutherland KP, Porter JW and Torres C. 2004. Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. *Mar Ecol Prog Ser* 266: 273-302.
- Work TM and Aeby GS. 2006. Systematically describing gross lesions in corals. *Dis Aquat Organ* 70 (1-2): 155-160.

Tak Fung

Modeling reefs at a local scale: the elements of design



Tak attended Imperial College London and completed an undergraduate degree in Mathematics with Management. Afterwards, he joined the four year integrated MRes/PhD CoMPLEX (Centre for Mathematics and Physics in the Life Sciences and Experimental Biology) programme on Modeling Biological Complexity, at University College London. For the PhD component of this programme, he worked with the MDSWG (Modeling and Decision Support Working Group) of the CRTR Program. Recently, Tak has completed his PhD and has started work on ecosystem modeling at Queen's University Belfast, to aid in the ecosystem approach to fisheries management in Ireland.



Modeling reefs at a local scale: the elements of design

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Introduction

Coral reefs are being degraded worldwide, with declines in hard coral cover in both the Caribbean (Gardner et al. 2003) and the Indo-Pacific (Bruno and Selig 2007), which may or may not be accompanied by increases in algae (Done 1992; Hughes 1994; Bruno et al. 2009). However, knowledge of the ecological processes underlying resilience of a reef to degradation is deficient (Bellwood et al. 2004). This has led to ongoing debates as to which stressors, affecting different processes, are the most important factors in reef degradation (e.g., Lapointe 1999; Hughes et al. 1999; Burkepille and Hay 2006; Littler et al. 2006). Addressing this deficiency would allow better management of processes critical to reef resilience.

In order to carry out manipulative experiments at a large enough scale to further our understanding of the processes underlying reef degradation, considerable resources and logistics would be required. Also, such experiments would be unethical if they involved deliberately degrading a reef. In this light, models can be used as a powerful method to carry out experiments *in silico* to increase theoretical knowledge of the stressors driving reef degradation and recovery, and the ecological processes by which this occurs. A key question is what type of model will be useful in this endeavour.

Designing models for a purpose

Coral reefs are complex, multi-scale social-ecological systems (Bradbury et al. 2005; Bradbury and Seymour 2009). Due to this immense complexity, it is necessary to simplify the systems in any modeling exercise. Thus, there arises the need to choose what to model and how to model what is chosen. These crucial stages in the design process are guided by the intended purpose of the modeling exercise.

The brief of the Modeling and Decision Support Working Group (MDSWG), which is part of the CRTR Program, is to use modeling to achieve a holistic, scientific understanding of reef-human interactions, with the aim of promoting the sustainable use and management of coral reefs (Bradbury et al. 2005). To do this, the MDSWG strategy is to use a cluster of models operating at different scales and with each model focusing on the ecology or the socioeconomics, or interactions between these two domains; these models can subsequently be linked to each other to create a multi-scale social-ecological model (Bradbury et al. 2005).

As part of the MDSWG strategy, a model has been developed that operates at a local scale, of approximately tens of metres to kilometres, and which is predominantly ecological. The purpose of this local model is to capture and to further understand the basic processes underlying coral reef degradation and recovery at a local scale, and also to act as a building block for the construction of a larger, regional scale model. These model aims are broad, and require careful consideration of what to model and how.

A process-oriented approach

To construct the local model, it was necessary to represent explicitly ecological processes that are thought to be important in reef degradation, together with the associated organisms. Furthermore, since the emphasis of the modeling was on processes, it was essential that the non-steady state dynamics of coral reefs were modelled. This is in contrast to network models that assume a steady state, such as ECOPATH models (Christensen et al. 2005).

As a result of a critical review of the literature, the organisms chosen to be modelled were: hard corals, turf algae, macroalgae, herbivorous fish, piscivorous fish and herbivorous sea urchins. Turf algae consist predominantly of filamentous algae, whereas macroalgae have a greater thallus size and structural complexity (Steneck and Dethier 1994). The reason for considering these two types of algae as separate groups is because there is evidence that they can interact in fundamentally different ways with hard corals (e.g., Lirman 2001; Jompa and McCook 2002; Nugues and Bak 2006). For each modelled group, key processes pertaining to recruitment, growth, mortality and trophic interactions were modelled explicitly, using differential equations to represent dynamic processes. In particular, hard corals and algae both grow over and compete for space in the local model. This is an advance on, for example, ECOSIM models that do not model coral-algal competition explicitly (Christensen et al. 2005). Also, exogenous recruitment for corals, fish and urchins were assumed to be constant – regional larval dynamics were not modelled because of the local scale used.

The effects of three key anthropogenic stressors – fishing, eutrophication (sensu Szmant 2002) and sedimentation – in the model were determined by first reviewing the literature and deciding which ecological processes are affected by each stressor. Since ecological processes in the model are represented by parameters, each stressor is then modelled as changing the parameter or parameters that represent the ecological processes affected.

Stepwise-refinement

To facilitate understanding of model results, a stepwise-refinement approach was used, which is novel in coral reef modeling. This involves beginning with a very simple model and adding complexity step-by-step until there is sufficient complexity available for the purpose of the model (Bradbury et al. 2005). The advantage of this approach is that by comparing results between successive model versions, the effects of added complexity can be more easily understood. In addition, the approach produces a model of sufficient complexity, in the sense that it is not so simple that it does not capture key features of the modelled system, or so complex that results obtained from it are incomprehensible (Fulton et al. 2003).

Following this approach, a simple differential equations model of a coral reef benthos with hard corals and turf algae competing for space was first constructed. In this benthic model, the fish and urchin community was assumed to act through a constant grazing pressure applied to the turf algal component of the benthos. Complexity was added to this model by including macroalgae in two different ways. A limitation of a benthic model, which is shared with other models that do not model fish and urchin dynamics explicitly (e.g., the model of McCook et al. 2001), is that there is no feedback from the benthos to the fish and urchins. Next, a differential equations model of a fish and urchin community was constructed, which includes herbivorous fish and sea urchins competing for a constant algal resource and piscivorous fish preying upon the herbivorous fish. Complexity was added to this model by splitting the piscivorous fish group up into two size classes, to reflect different life-history characteristics (Scales et al. 2007). A limitation of a fish and urchin model is that since benthic dynamics were assumed to be constant, there is no feedback from the fish and urchins to the benthos. The final level of complexity was added by joining a benthic model with a fish and urchin model to create different versions of an integrated model, which have dynamic interactions between the two components.

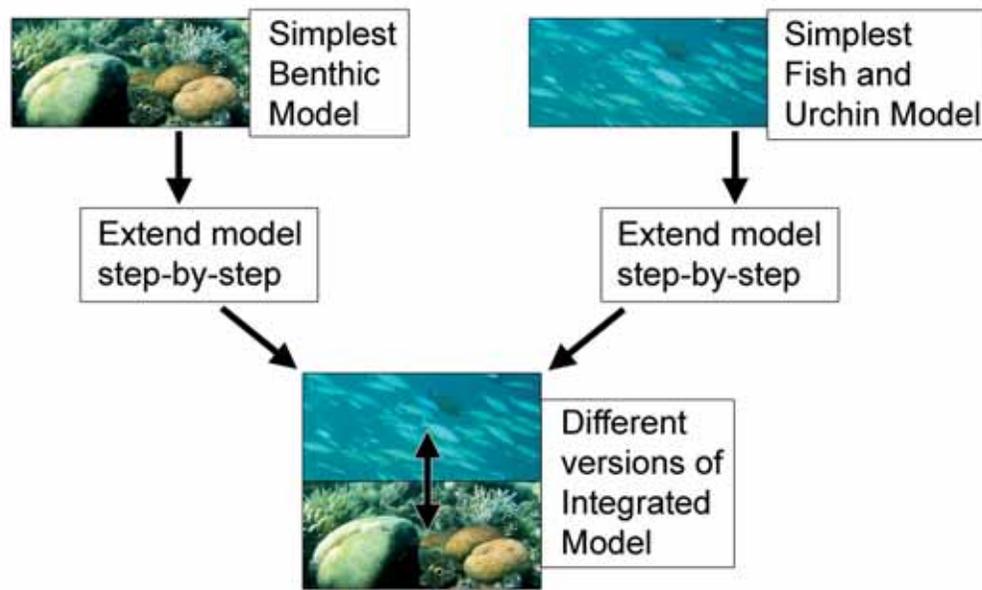


Figure 1. Schematic diagram of the stepwise-refinement modeling approach used. Starting from the simplest benthic model and the simplest fish and urchin model, complexity was added to each model step-by-step. Different versions of the integrated model were then constructed by combining different versions of the benthic model with different versions of the fish and urchin model. The double-headed arrow represents dynamic interactions between the benthos and the fish and urchins.

Analysing the local model

A variety of techniques were used to analyse the local model at each step of the stepwise-refinement process, for the purpose of gaining a better understanding of the processes driving reef degradation and recovery.

First, equilibrium properties were derived for the model at each step using analytic mathematical techniques, to give insights into the long-term behaviour of model systems; such a mathematical analysis is virtually non-existent for other coral reef models (e.g., McClanahan 1995; McCook et al. 2001; Tsehaye and Nagelkerke 2008). Second, at each step, the model parameters and the effects of the three anthropogenic stressors modelled were quantified using “typical” data from reefs worldwide. Afterwards, sensitivity analyses were applied to deduce which parameters, and therefore processes represented by these parameters, generally had the greatest effect in changing benthic covers and fish and urchin biomasses. Results from the sensitivity analyses also allowed an assessment of the potential for interactions between parameters, and this allowed an assessment of the potential for synergy between the three stressors modelled. Third, the most complex version of the local model was parameterised specifically for Banco Chinchorro in the Mexican Caribbean and Bolinao reef system in the Lingayen Gulf/South China Sea. Monte Carlo simulations can be performed using these site-specific models to generate frequency distributions of benthic covers and fish and urchin biomasses under different scenarios (see Figure 2 for example results for Banco Chinchorro).

1. Understanding local-scale ecological processes

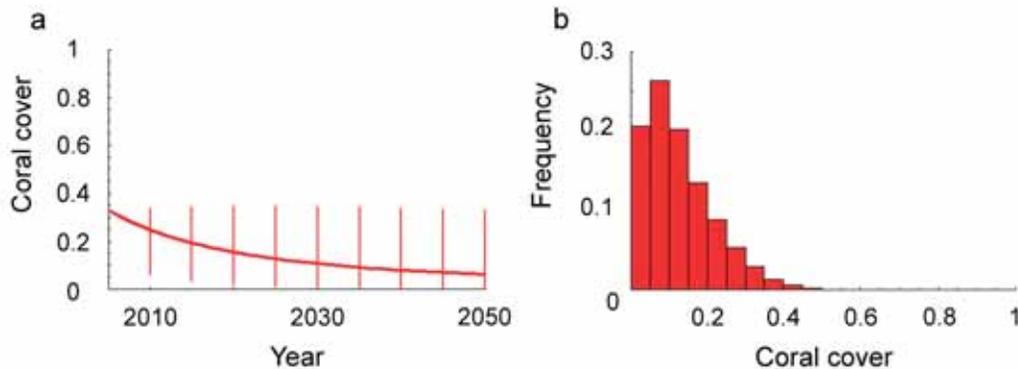


Figure 2. Example results from a Monte Carlo simulation using the most complex version of the local model, parameterised for Banco Chinchorro. 25,000 parameter sets were sampled randomly from the empirically-derived parameter ranges and for each set, dynamics were run for 45 yrs, starting from 2005. The scenario is “business-as-usual”, which involves no increase in exogenous coral or fish recruitment which could have arisen from an improvement in (non-modelled) upstream reefs. Only results for hard coral cover are shown. (a) Time trajectory for hard coral cover, from 2005-2050. The solid curve is the mean for all (25,000) runs and the vertical lines show the range of the middle 95% of values for all runs at every 5 yrs. The initial coral cover was taken from survey data. (b) Histogram showing the distribution of hard coral covers at 2025. Bins of size 0.05 were used to group the coral cover values.

These analyses demonstrate how the local model can be used to better understand the processes driving reef degradation and recovery at a local scale. In addition, the local model can be used as a building block for a regional scale model with regional larval dynamics (Melbourne-Thomas et al. 2007). Thus, the local model can be used to achieve its intended purpose, and this is a result of careful consideration of the elements of model design.

References

- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827-833.
- Bradbury RH, Seymour RM (2009) Coral reef science and the new commons. *Coral Reefs* 28: 831-837
- Bradbury R, Perez P, Aliño P, Arias-González E, Campbell P, Durnota B, Johnson C, Seymour R (2005) A designing strategy for modeling coral reefs. *Proceedings of HEMA/CABM/SMAGET Conference*
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 8:1-8
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478-1484
- Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87:3128-3139
- Christensen V, Walters CJ, Pauly D (2005) *Ecopath with Ecosim: a user's guide*
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121-132
- Fulton EA, Smith ADM, Johnson CR (2003) Effect of complexity on marine ecosystem models. *Mar Ecol Prog Ser* 253:1-16
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958-960
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551
- Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S (1999) Algal blooms on coral reefs: what are the causes? *Limnol Oceanogr* 44:1583-1586
- Jompa J, McCook LJ (2002) Effects of competition and herbivory on interactions between a hard coral and a brown alga. *J Exp Mar Biol Ecol* 271:25-39
- Lapointe BE (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). *Limnol Oceanogr* 44:1586-1592
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392-399
- Littler MM, Littler DS, Brooks BL (2006) Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. *Harmful Algae* 5:565-585
- McClanahan TR (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol Model* 80:1-19
- McCook LJ, Wolanski E, Spagnol S (2001) Modeling and visualizing interactions between natural disturbances and eutrophication as causes of coral reef degradation. In: Wolanski E (ed) *Physics biology links in the Great Barrier Reef*. CRC Press, Boca Raton, pp113-126
- Melbourne-Thomas J, Johnson CR, Fung T, Seymour RM (2007) Decision support tools for managing coral reef systems at local to regional scales. *Proceedings of Environmental Research Event 2007: Global Problems – Local Solutions*, Cairns, pp169-177
- Nugues MM, Bak RPM (2006) Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Mar Ecol Prog Ser* 315:75-86
- Scales H, Balmford A, Manica A (2007) Impacts of the live reef fish trade on populations of coral reef fish off northern Borneo. *Proc R Soc Lond B Biol Sci* 274:989-994
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476-498
- Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries* 25:743-766
- Tsehaye Y, Nagelkerke LAJ (2008) Exploring optimal fishing scenarios for the multispecies artisanal fisheries of Eritrea using a trophic model. *Ecol Model* 212:319-333



CRTR e-News,
February 2009

Effective reef governance: Southeast Asia

CRTR PhD student Heidi Schuttenberg is taking part in research to examine the different approaches to coral reef management in Indonesia, Philippines, Thailand and Malaysia. This information is being used to develop a systematic classification of management strategies commonly used in the region, which will become a useful planning tool and facilitate learning between sites. Field officers from each of the study countries, including Heidi, are collecting data from 50 organisations involved in coral reef management. Participation in the study is part of Heidi's doctoral research at James Cook University, Australia with additional technical support provided by CSIRO. The project is funded by the CRTR Program, the Marine and Tropical Sciences Research Facility and a postgraduate fellowship awarded by the International Society for Reef Studies and The Ocean Conservancy.

To communicate with its network, the CRTR Program produces a regular electronic newsletter for stakeholders, highlighting progress and achievements. Scholars' activities were frequently reported in CRTR e-News. Scholars were also encouraged to submit articles. Examples of articles are included throughout this anthology.





CRTR e-News,
February 2009

Sensing the complexity of habitat

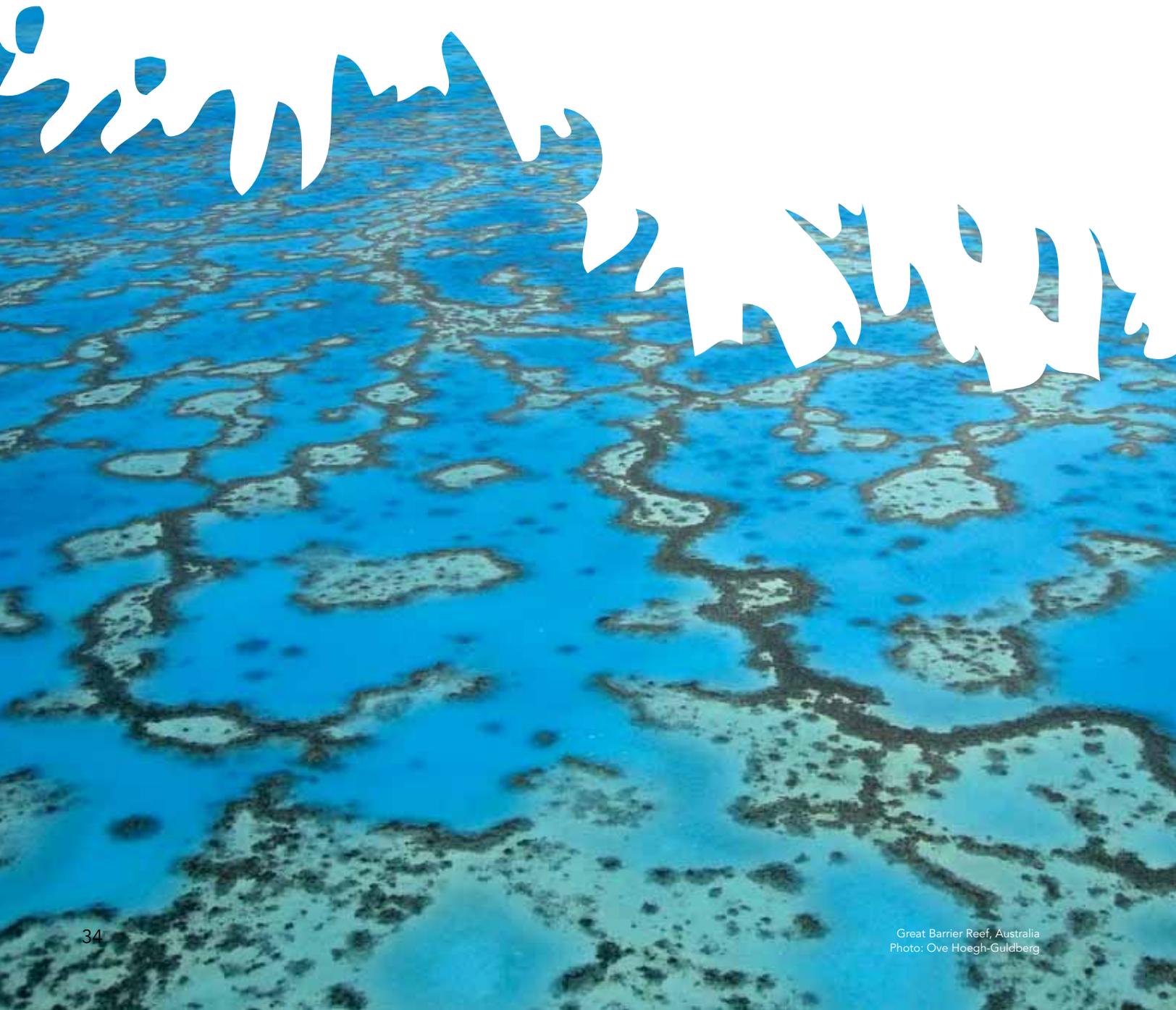
CRTR scholars in the Remote Sensing Working Group have forged such a good working relationship that they embarked on their own study of habitat associations of reef fish.

In May 2008, the team spent three weeks quantifying the fish and benthic communities of reef and lagoon habitats in Palau. David Idip, a Palauan coordinating mapping and GIS datasets for the Palau Government, had devised a habitat classification scheme for use in mapping the country's reefs. David had negotiated a break from his regular work to participate in the field component of the study. Victor Ticzon (University of the Philippines) carried out a detailed study of the microhabitat characteristics of each habitat type and this was complemented by Badi Samaniego (UP) and Sonia Bejarano (University of Exeter) who carried out species-level surveys of reef fish, including juveniles.

The study aimed to better-describe the differences in habitat association between juvenile and adult fish species. Surprisingly, the study also seemed to have generated interest from the local dugong population who visited frequently, much to the chagrin of those members of the working group that were absent.

Much of the study was carried out in the Ngederrak marine reserve with generous permission from Koror State. The data also provide a baseline against which future changes in the fish communities can be compared. The data will be repatriated to our partners at the Palau International Coral Reef Centre, who provided impeccable support as usual.

Reef dynamics and management actions at regional scales **2**



Isabel Porto & Ainhoa Leon Zubillga

Regional scale of genetic connectivity among *Acropora palmata* and *Montastraea faveolata* populations

Isabel was born in Bogota, Colombia, and completed her Bachelors in Science in 2006 and started a Masters degree at Universidad de los Andes in Colombia under the guidance of Dr. Camilo Salazar and Dr. Tonya Shearer at Georgia Institute of Technology investigating the biological connectivity of the Caribbean coral species, *Montastraea faveolata*. Currently, she works for Dr. Howard Lasker at the State University of New York at Buffalo, supporting his research on the Caribbean octocoral species *Pseudopterogorgia elisabethae* population dynamics.

Ainhoa recently completed her PhD at Simon Bolivar University. She completed her Bachelor degree at the Universidad Central de Venezuela, and then continued with her studies to complete her Masters in 2004 at Simon Bolivar University with honors. Over the past six years, Ainhoa has been studying different topics related to coral reef conservation, and more recently the population genetics and larval biology of *Acropora palmata*, an important and endangered Caribbean reef building coral species. Ainhoa has published several papers in peer-reviewed journals.



Connectivity also implies people working together beyond borders to achieve a common goal: protecting reef resources. Isabel Porto (left), Ainhoa Leon Zubillga (right), "Compa" (top) and Norlan Lamb (bottom) in the Glover Reef Research Station. Photo: Nathan Kwiatek

Regional scale of genetic connectivity among *Acropora palmata* and *Montastraea faveolata* populations

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Many benthic sessile coral reef dwellers have a planktonic larval stage that is very important for dispersal. Physical and biological variables influence the larvae dispersal, including site isolation, coastal complexity, flow variability (up and downwelling, gyres, tides, counter currents, etc.), water column stratification, adult fecundity, larval mobility, parental investment, larval release, period of development, motility, migration through the water column, larvae competency period and larval mortality (e.g. Sponaugle et al. 2002; Szmant and Meadows 2005).

There has been controversy between larval retention versus long distance dispersal as the main result for a variety of life history strategies for marine organisms. Earliest models that predict larval dispersion based on ocean currents thought that they are the major factor that affect larval transportation in an extensive way (Roberts 1997). Because ocean currents are strong the idea of self-recruitment seemed improbable.

These models, based only on simple passive dispersal mediated by ocean currents underestimate larvae retention (Cowen et al. 2002). Some studies in coral reef fish larvae had shown that larval behavior plays a stronger role (Leis 1991). Sponaugle et al. (2002) concluded that self-recruitment depends on the larval behavioral competency and pelagic larval duration. Other studies continue adding evidence to self-recruitment rather than extensive dispersal (Swearer et al. 1999).

To understand larval transport, scale (temporal and spatial) is very important because it changes accordingly to the species and affects larval dispersion in several ways (Cowen 2002). Cowen et al. (2002) found that the 100's km critical management unit scale is not appropriate, 10's km is better, because it describes effective dispersal distance. Lugo-Fernández et al. (2001) observed that the majority of the larvae disperse a maximum of 40 km, but they ignored the competency period, which will result in a large dispersal distance. Nevertheless, there are several studies showing potential of larvae to disperse long distances (Jones et al 2009; references therein).

Knowledge of biological connectivity, understood as the exchange of individuals among geographically separated subpopulations (Palumbi 2003; Cowen et al. 2007) among marine populations has important ecological and management implications (Cowen et al. 2000; 2006; Bode et al. 2006; van Oppen and Gates 2006; Levin 2006). It is necessary to determine the potential sources of reef recruits (self-seeding or depending on outsource population) in order to propose Marine Protected Areas (MPA) or assess the efficiency or success of MPAs currently in place (Roberts 1997; Palumbi 2003; Cowen et al. 2006).

Measuring biological connectivity among coral populations via larval dispersal is difficult to estimate using direct methods due to small larval size and difficulty collecting coral larvae from plankton (Sammarco et al. 1991). Generally, the estimation of larval dispersal distances is indirect (Levin et al. 1993) and is based on larval characteristics (e.g. pre-competency duration, survival rate and larval behavior) and environmental conditions (availability of suitable substrate and current patterns) (i.e. Harrison and Wallace 1990; Leis 1991). The use of population genetics is commonly employed as an alternative to indirectly estimate larval dispersal (Palumbi 2001).

During the past few years, descriptions of the patterns of genetic connectivity among Caribbean marine organisms (Mitton et al. 1989; Shulman and Bemingham 1995; Jones et al. 2005; Rocha et al. 2002; Bradbury et al. 2008; Hepburn et al. 2008) and scleractinian corals have received special attention (Jones et al. 2009). Some studies have found restricted gene flow (Baums et al. 2005); others have reported a lack of genetic structure (Severance and Karl 2006) and/or a moderate gene flow (Vollmer and Palumbi 2007; Zubillaga et al 2008). These results indicate that patterns of genetic connectivity among coral populations across the Caribbean are complex and involve a myriad of biological, physical and oceanographic processes that may operate at different temporal and spatial scales.

2. Reef dynamics and management actions at regional scales

Montastraea faveolata and *Acropora palmata* are among the main reef-builder species in the Caribbean (Goreau 1959) that have experienced dramatic reductions in population sizes during the last decades due to habitat loss, overfishing, pollution, tourism (Kramer and Kramer 2000, Jackson 2001) prevalence of diseases (Gladfelter 1982; Harvell et al. 1999; Aronson and Precht 2001; Garzon-Ferreira et al. 2001; Cróquer et al. 2003), and bleaching (Carilli and Norris 2008). Furthermore *Acropora palmata* was proposed as a threatened species (NOAA 2006) because of the rapid decline of live coral cover (<80%) during the 1980s and 1990s (Gladfelter 1982; Bythell and Sheppard 1993; Bruckner et al. 2002).

M. faveolata and *A. palmata* life history characteristics suggest long distance dispersal rather than local retention. Both species are hermaphroditic broadcast spawning corals (Szmant 1991). The complete development of *M. faveolata* embryos into competent planulae takes a minimum of 3 to 5 days after fertilization (Szmant et al. 1997; Szmant and Meadows 2005). *M. faveolata* eggs and larvae are positively buoyant until 56-78 hours after spawning (Szmant and Meadows 2005) and *A. palmata* larvae until 63 hours after fertilization. During this time eggs or larvae are transported as passive particles by ocean currents until the planulae develop vertical swimming behavior that allows them to move through the water column (Szmant and Meadows 2005, Zubillaga and Szmant unpublished data). *M. faveolata* competency period is c.a 4 days and *A. palmata* is c.a. 10 days but larvae can remain in the water column up to 30 and 20 days (Szmant and Miller 2005, Szmant unpublished data). All these biological characteristics enhance long distance dispersal rather than self-recruitment; given the appropriate hydrographic conditions.

Our study focused on the study of the biologic connectivity of *Acropora palmata* and *Montastraea faveolata* along the Mesoamerican Barrier Reef System (MBRS) and the southwestern Caribbean using variable microsatellite loci. Identifying sites for suitable recovery where recovery has already started and studying the connectivity between these areas is a priority. The novelty of this work relies on a larger sampling size per population (Figure 1) and the characterization of connectivity among reef populations at a regional scale (e.g. Mesoamerican Barrier Reef System (MBRS), Panama, Venezuela and Puerto Rico) in comparison to previous studies of these two species in the Caribbean (Baums et al. 2005; Severance and Karl 2006).

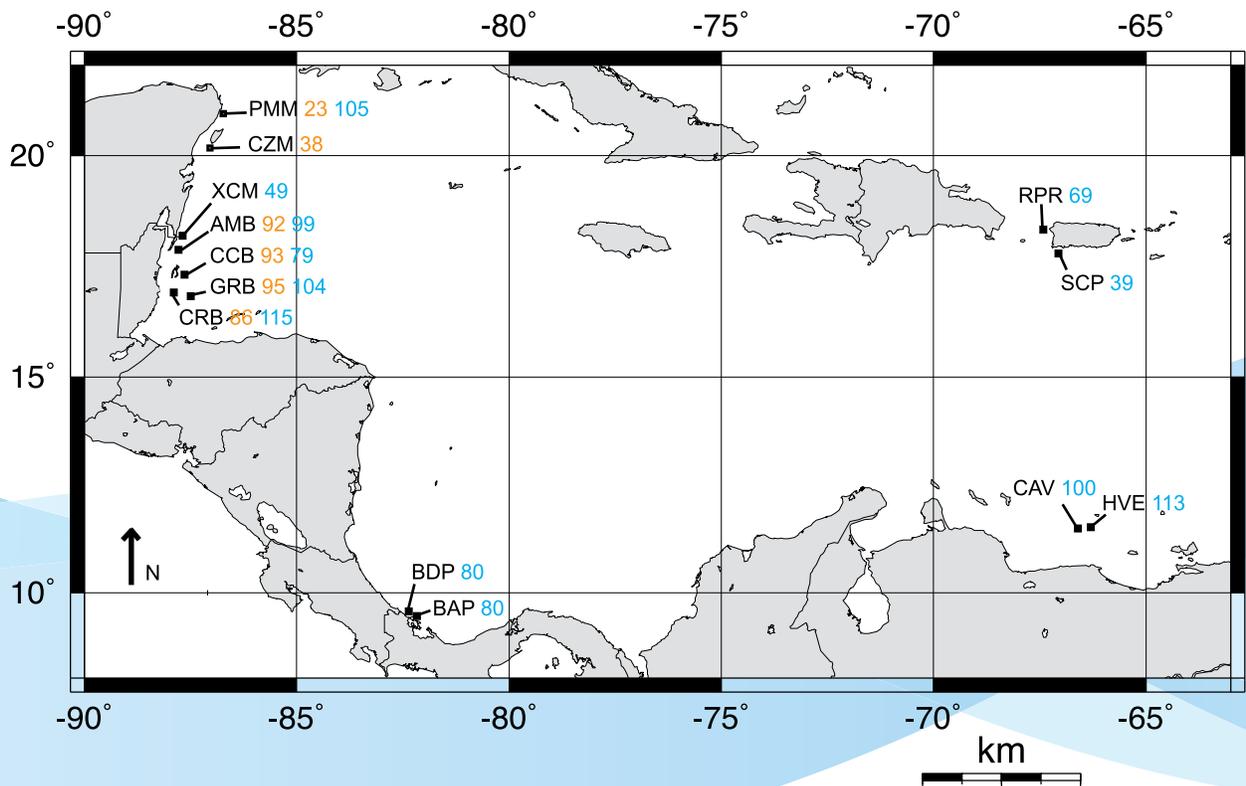


Figure 1. Number of samples collected per population of *Montastraea faveolata* (orange) and *Acropora palmata* (blue). México populations include Puerto Morelos (PMM), Cozumel (CZM), and Xcalak (XCM); Belize population include Ambergris (AMB), Calabash Cay (CCB), Columbus Reef (CRB) and Glovers Reef (GLB); Panamá populations include Bocas del Drago (BDP) and Bastimento (BAP); Venezuela population include Cayo de Agua (CAV) and Herradura (HVE); Puerto Rico include Rincón (RPR) and San Cristobal (SCP). Map was created at <http://www.aquarius.geomar.de/omc/>

Sample size has been shown to be important for gene flow estimations, particularly for genetic diversity which is extremely important for species conservation (Kalinowski 2004; Shearer et al. 2009). Small sample sizes could underestimate the actual number of alleles within a population with important consequences for the calculation of population genetic parameters which are based on allele frequencies. Likewise, the probability of finding private alleles (unique to a population) decreases with sampling size which may lead to an underestimation of the genetic diversity (Kalinowski 2004). For *A. palmata* 30 colonies are needed in order to observe more than 70% of the total allelic richness in a population, and 35 colonies for *M. faveolata* (Shearer et al. 2009). Genetic variability is one of the three aspects of biodiversity that the World Conservation Union (IUCN) has recommended for species conservation (McNeely et al. 1990); is an important factor for individual survival as it is directly correlated with fitness through the reduction of inbreeding.

Considering local and regional biological connectivity among reef populations has important management implications. The MBRS could have a central role in the potential recovery of *A. palmata* and *M. faveolata* as it comprises extensive reef areas, refuges and different habitats that might have either healthy populations of these species or suitable sites for recovery. In addition to this, other areas of the Caribbean could represent sources of larvae for regional recovery.

The MBRS, is the largest barrier reef in the Caribbean, extending over 1000 km. It includes reefs of México (Yucatán peninsula), Belize, Guatemala and Honduras (Kramer and Kramer 2002). The MBRS is a biodiversity hotspot and as such, it is recognized as a priority ecoregion by the World Wildlife Foundation (WWF). Protection of the MBRS is vital for the conservation of the world's biodiversity (Kramer and Kramer 2002) and the well-being of regional economies (e.g. fishing, tourism, etc.). Caribbean reefs, including the MBRS, have been in decline due to natural and anthropogenic impacts (Hughes 1994; Hughes and Tanner 2000; Gardner et al. 2003; Bellwood et al. 2004)

Extensive research on the spatial and temporal patterns of biodiversity, habitat diversity, ecological processes and ocean current patterns has been conducted in the MBRS (Kramer and Kramer 2002, McField and Kramer 2007 and references therein). Connectivity studies in the MBRS are limited and are based on coral reef fish (Hepburn et al. 2008), spatial patterns of fresh-water dispersal (Andréfouet et al. 2002), ocean circulation and terrestrial runoffs (Chérubin et al. 2008). To date, there are no studies focused on coral species connectivity patterns of the MBRS and this study will fill this gap.

Acknowledgments

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References

- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38
- Baums IB Miller MW, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Mol Ecol* 14:1377–1390
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833.
- Bode M, Bode L, Armsworth PR (2006) Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Mar Ecol Prog Ser* 308:17–25
- Bradbury IR, Laurel B, Snelgrove PVR, Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: the influence of geographic, taxonomic category, and life history. *Proc R Soc B* 275:1803–1809
- Bruckner AW (2002) Proceedings of the Caribbean Acropora workshop: potential application of the US Endangered Species Act as a conservation strategy. NOAA Technical Memorandum NMFS-OPR-24
- Bythell JC, Sheppard CR (1993) Mass mortality of Caribbean shallow corals. *Mar Poll Bull* 26(6):296–297
- Carilli J, Norris RD (2008) Threshold Decline in Mesoamerican Coral Growth and Resiliency. *Nature Preceedings* hdl:10101/npre.2008.2115.1
- Cowen RK (2002) Oceanographic influences on larval dispersal and retention and their consequences for population connectivity. *Coral Reef Fishes*. Academic Press. London, New York. pp. 149–170
- Cowen RK, Paris CB, Olson DB, Fortuna JL (2002) The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research Supplement*, pp. 1–10

2. Reef dynamics and management actions at regional scales

- Cowen RK, Lwiza KM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287: 857–859
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527
- Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population Connectivity in Marine Systems An Overview. *Oceanography* 20:14–21
- Cróquer A, Pauls SM, Zubillaga AL (2003) White plague disease outbreak in a coral reef at Los Roques National Park, Venezuela. *Revista de Biología Tropical*. 51:39–45
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Garzon-Ferreira J, Gil-Agudelo DL, Barrios LM, Zea S (2001) Stony coral diseases observed in southwestern Caribbean reefs. *Hydrobiologia* 460:65–69
- Gladfelter WB (1982) White-band disease in *Acropora palmata*—implications for the structure and growth of shallow reefs. *Bull Mar Sci* 32:639–643
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Ecosystems of the world*, Elsevier Amsterdam, pp 133–205
- Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus A, Overstreet RM, Porter JW, Smith GW, Vasta GR (1999) Review: Marine ecology - Emerging marine diseases - Climate links and anthropogenic factors. *Science* 285: 1505–1510
- Hepburn RI, Sale PF, Dixon B, Heath DD (2008) Genetic structure of juvenile cohorts of bicolor damselfish (*Stegastes partitus*) along the Mesoamerican barrier reef: chaos through time. *Coral Reefs* 28:277–288
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81: 2250–2263
- Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Curr Biol* 15:1314–1318
- Jones GP, Almany GR, Russ GR, Sale PF (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307–325
- Kalinowski ST (2004) Counting alleles with rarefaction: private alleles and hierarchical sampling designs. *Conservation Genetics* 5:539–543
- Kramer PA, Kramer PR (ed. M. McField) (2002) *Ecoregional Conservation Planning for the Mesoamerican Caribbean Reef*. Washington, DC: World Wildlife Fund. 140 pp. Available at www.healthyreefs.org or www.wwfca.org
- Leis J M (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. pp. 183–230. In PF Sale (ed.). *The Ecology of Fishes on Coral Reefs*. University of Hawaii. Honolulu
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology* 46:282–297
- Levin PS (1993) Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. *Oecologia* 94:176–185
- Lugo-Fernández A, Deslarzes JP, Price JM, Boland GS, Morin MV (2001) Inferring probable dispersal of Flower Garden Banks Coral Larvae (Gulf of Mexico) using observed and simulated drifter trajectories. *Continental Shelf Research* 21:47–67
- McField M and Kramer P (2007) *Healthy Reefs for Healthy People. A Guide to Indicators of Reef Health and Social Well-being in the Mesoamerican Reef Region*; with contributions by M. Gorrez and M. McPherson. 208pp. www.healthyreefs.org
- Mitton JB, Berg CJ, Orr KS (1989) Population Structure, Larval Dispersal, and Gene Flow in the Queen Conch, *Strombus gigas*, of the Caribbean. *Biol Bull* 177:356–362
- Palumbi SR (2001) The ecology of marine protected areas. Pages 509–530 in M. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine ecology: the new synthesis*. Sinauer, Sunderland, Massachusetts, USA.
- Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecol Appl* 13: S146–S158
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278: 278:1454–1457
- Rocha LA, Bass AL, Robertson DR, Bowen BW (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Mol Ecol*. 11:243–252
- Sammarco PW, Andrews JC, Risk MJ (1991) Coral reef geomorphology as a function of seasonal prevailing currents and larval dispersal. *Paleogeography, Paleoclimatology, Palaeoecology* 88: 1–12
- Severance EG, Karl SA (2006) Contrasting population genetic structures of sympatric, mass-spawning Caribbean corals. *Mar Biol* 150:57–68
- Shearer T, Porto I, Zubillaga AL (2009) Restoration of coral populations in light of genetic diversity. *Coral Reefs* 28:727–733.
- Shulman MJ, Bermingham E (1995) Early-life histories, ocean currents, and the population-genetics of Caribbean reef fishes. *Evolution*. 49:897–910
- Szmant AM, Weil E, Miller MW, Colón DE (1997) Hybridization within the species complex of scleractinian coral *Montastraea annularis*. *Marine Biology* 129: 561–572
- Szmant AM, Miller MW (2005) Settlement preferences and post-settlement mortality of laboratory cultured and settled larvae of the Caribbean Hermatypic corals *Montastraea faveolata* and *Acropora palmata* in the Florida Keys, USA. *Proc.10th Int Coral Reef Symp* 43–49
- Szmant AM, Meadows M (2005) Developmental changes in coral larval buoyancy and swimming behavior: Implications for dispersal and connectivity. *Proc 10th Int Coral Reef Symp* pp 431–437
- Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda JS, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bull Mar Sci* 70: 341–375
- Shulman MJ, Bermingham E (1995) Early-life histories, ocean currents, and the population-genetics of Caribbean reef fishes. *Evolution*. 49:897–910.
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef Fish. *Nature* 402:799–802
- van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Mol Ecol* 15: 3863–3883
- Vollmer AV, Palumbi SR (2007) Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. *Journal of Heredity* 98:40–50
- Zubillaga AL, Márquez LM, Cróquer A, Bastidas C (2008) Ecological and genetic data indicate recovery of endangered coral *Acropora palmata* in Los Roques, Southern Caribbean. *Coral Reefs* 27:63–72



Spotlight on:

Scholars at the International Coral Reef Symposium

CRTR scholars made a very significant contribution to the CRTR Program's participation in the 2008 International Coral Reef Symposium (ICRS) in Florida, USA. More than 30 scholars representing different CRTR Centres of Excellence and Working Groups attended the ICRS which is the largest and most influential conference for coral reef science, held every four years.

The CRTR was a major sponsor of the event, and was well represented by senior researchers and scholars from across the Working Groups and Centres of Excellence. More than 100 presentations and poster presentations were made on CRTR research findings including three of the five keynote speakers being CRTR representatives. All of the participating CRTR scholars made an oral or a poster presentation at the conference.

As part of its ICRS sponsorship, the CRTR Program hosted a trade stand with the theme "Coral Reefs. For Life." Scholars manned the stand with enthusiasm, helping to promote the Program, and distribute its information and products.

"ICRS offered the scholars a major and unique opportunity to learn from and to share our work with our peers and with management audiences," said Deborah Cleland, an Australian scholar from the Modelling and Decision Support Working Group.

The event, held six months after the CRTR Future Leaders Forum, consolidated the Program's Future Leaders Network, set up its goals and priorities, and established a way for the network to move forward.



Spotlight on:

Patrick Cabaitan

With several years experience in restoring degraded reefs, Patrick Cabaitan is now a Research Associate with the Restoration & Remediation Working Group. He is examining the best techniques for coral transplantation focusing on degraded bommies at two sites in the Bolinao reef complex.

"The bommies are unique habitats that need assistance in recovery because coral recruitment is low compared to reef slopes, coral breeding populations are depleted, and habitats of fish and other biota are degraded," says Patrick.

"We are trying to work out which species of coral is most suitable for transplantation in the area. A key objective is to compare the survival and growth of single species versus mixed species in transplant plots."

Corals are monitored at intervals for survival and growth in the various environmental conditions that prevail around the trial site bommies including temperature, salinity, irradiance, water turbulence, sedimentation rate and nutrient levels.

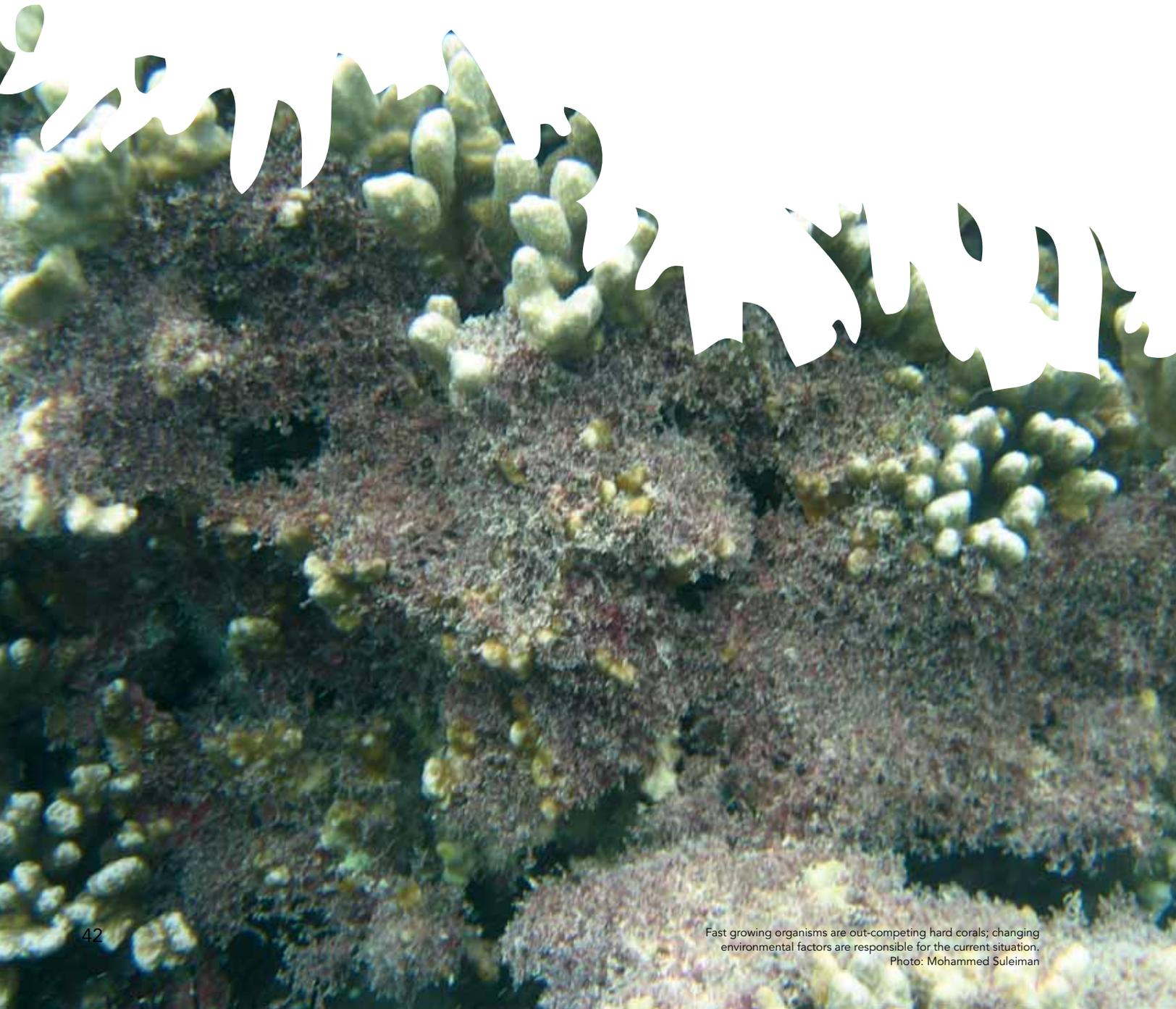
So far, *Porites cylindrica* has proven to be a good candidate for transplantation with higher survival and growth rates than other species investigated. The presence of *Drupella spp.* (coral eating snails) is a key factor influencing the survival of the transplants.

Mohammed Suleiman Mohammed

Preliminary investigation of coral reef diseases in Tanzania, East Africa



Mohammed was born on Pemba Island in Zanzibar. He went to the University of Dar es Salaam for undergraduate studies where he took marine biology and microbiology. He completed his Masters degree on marine biology at the same university, studying at the Institute of Marine Sciences. His activities included benthic chamber and nutrient flux experiments, coral reef monitoring in Tanzania and demarcation of MPAs. His PhD is in the distribution and dynamics of coral diseases and their relation to coral health and local environmental factors in Tanzania.



Preliminary investigation of coral reef diseases in Tanzania, East Africa

Mohammed Suleiman Mohammed

Institute of Marine Sciences, University of Dar es Salaam

Infectious diseases in corals appear as lesions or bands of tissue loss, and can be caused by bacteria, archaea, viruses, protozoa, or fungi. On their own, or in combination with other stressors (such as high temperature, increased sedimentation, elevated nutrient load, bleaching and mechanical damage), they can reduce coral cover, lower rates of reproduction and growth, and degrade reef structure and diversity.

The immensely important corals around the Tanzania coast appear to have relatively low disease occurrence. But this could be partly because disease has not been recognized and where disease has been detected there is no baseline data to indicate if it is increasing or spreading.

Coastal development and tourism are proceeding rapidly in East Africa without any comprehensive planning, and as result seawater quality keeps on deteriorating. These with increasing sea water temperature are among the factors that are considered to drive disease outbreaks. This research determines the distribution and dynamics of coral diseases and the relationship to local environmental factors in which some are directly associated with coastal development.

Methodology

Surveys are being undertaken on 12 reefs off the coast of Tanzania mainland and the islands. The survey sites represent regions close to human influence (such as pollution and increased turbidity) and regions that should be relatively unaffected.

Six 20 x 2 m belt transects at each site (Zanzibar, Pemba, Dar es Salaam and Bagamoyo) allow detailed assessment and monitoring of the incidence and type of disease on every coral species occurring within the transects. Quick surveys on other sites (Mtwara, Tanga and Songosongo) were done to assess the number, distribution and current status of coral reef diseases on the reefs. One hour dives in a zig-zag pattern, starting at a depth of approximately 15 m and moving upwards to the shallow area, were conducted.

A separate experiment is being done in which transplanted healthy and diseased corals are exposed to a forced environment of high nutrient and sediment load for three months. The disease response of corals will be compared with that of natural nutrient load.

Figure 1. Location of the study sites



Preliminary results of the surveys

Preliminary results of survey and monitoring show that the most important threats contributing to coral reef degradation in the country is bleaching and predation by crown of thorn starfish (COTS). There was widespread localized paling/partial bleaching of corals during the peak of the high sea surface temperature season in March/April 2009. From 2004 to-date there is an increased frequency of COTS outbreaks affecting some of the best reef areas in the country e.g Misali Island in Pemba (Zanzibar) and Mnazi Bay in Mtwara, South of Tanzania mainland (personal observation, 2009). The study also shows compromised health and/or competition with other reef organisms as a threat, incidences of sponges, soft corals and fleshy algae overgrowing hard corals are increasing. Occurrence of infectious diseases on the study sites is very low but some are increasing in their occurrence, e.g white syndrome on Misali Island and on Kizimkazi south of Zanzibar Island. There are few hard coral colonies showing black band disease, ulcerative white spots, yellow band disease, skeleton eroding band disease and skeletal anomalies. Other reef organisms have also shown disease symptoms, for example, crustose coralline algae suffer white syndrome, sponges show cyanobacterial growth and black band like disease and tissue necrosis in a band pattern while soft corals shows necrotic tissues.



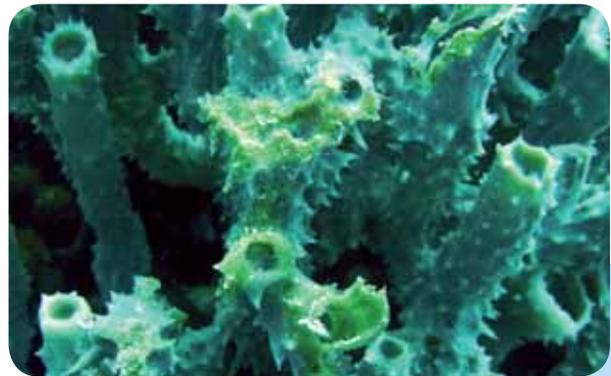
Algae overgrowing *Porites* branching and *Echinopora* in Dar es Salaam reefs



Black band disease (BBD) on *Pachyseris* in Misali Island, Pemba



Crown of thorn (COT) infestation north of Zanzibar island



Sponge disease on reef off Stone Town, Zanzibar



Bleaching on *Porites* massive during peak of warm season, March 2009, Bagamoyo, Tanzania



White Syndrome (WS) on *Merulina*, Chumbe Island, Zanzibar

Benefits from this research

The custodians of the East African reefs have a wonderful opportunity to secure their relatively disease-free status. To do this they must have a reliable measure of the incidence and profile of those diseases that are present, and of the environmental parameters that can be expected to have an impact. Testing the response of currently present coral diseases to severe environmental stressors will inform reef managers of where the greatest risks are to be found, the likely impact and the rate at which diseases can be expected to respond.

Armed with this information, reef managers should be better able to target risk management strategies and prepare for anticipated changes in environmental conditions. At the same time, this baseline information will enable scientists to assess the efficacy of any remedial action taken.



Spotlight on:

Dexter dela Cruz

Masters student and underwater gardener Dexter dela Cruz is working with the Restoration & Remediation Working Group to compare success rates of nursery reared versus directly transplanted coral fragments in the Bolinao reef complex.

Inspired in childhood by a cartoon show about a marine biologist and her pet killer whale, Dexter is cultivating (literally) his interest in the field with the CRTR Program. Now a marine biologist himself, Dexter's study involves assessing the growth and survivor rates of two common corals in the Bolinao reef system (*Echinopora lamellosa* and *Merulina scabricula*) following different rearing methods in an effort to ascertain the most efficient transplant techniques.

The first experiment compares the growth and survival of wild nubbins that are maintained in a field nursery versus those that are transplanted directly to experimental bommies. The second experiment compares nursery-reared coral nubbins with similar-sized fragments collected in the wild.

"We have had a few challenges in the project – storm damage to trial sites, and infestations by snails and Crown-of-Thorns starfish," says Dexter, "but that's life for coral reefs in the Philippines!"

"Our coral gardening project will make restoration work more viable, and ultimately help the reefs to meet the challenges they face."



Spotlight on:
Victor Ticzon

Although he almost drowned four times as a child, Victor Ticzon is now very much at home in the water but also enjoys looking to the skies for the information he seeks on how to protect fish habitat in the Philippines. Using habitat as a proxy, Victor's PhD project is examining ways to use remote sensing technology to estimate juvenile fish abundance. Such knowledge, he says, will be invaluable for management purposes.

"If we know where juvenile reef fishes are most likely to aggregate, we can prioritise the selection of these areas for protection. In a setting where coastal population continues to grow, and funds for coastal resource management are relatively scarce, identifying areas for immediate protection is vital. In my research, I try to incorporate information derived from remote sensing and hydrodynamic models to predict the best sites where reef fish would be likely to aggregate. The goal is to establish Marine Protected Areas in these localities to ensure maximum population replenishment on the stressed reefs of the Philippines."

Field work involves visiting fish in their homes which is great for someone who loves the water, and who is basically nosy. Victor examines rugosity, the number of refuge areas, and the size of openings where fish are found sheltering. He relates these physical reef features to the juvenile reef fish community in the area. This observation is done in an attempt to differentiate the habitats in terms of their physical structure, and to understand how these physical differences in the reef influence reef fish abundance and number of species.

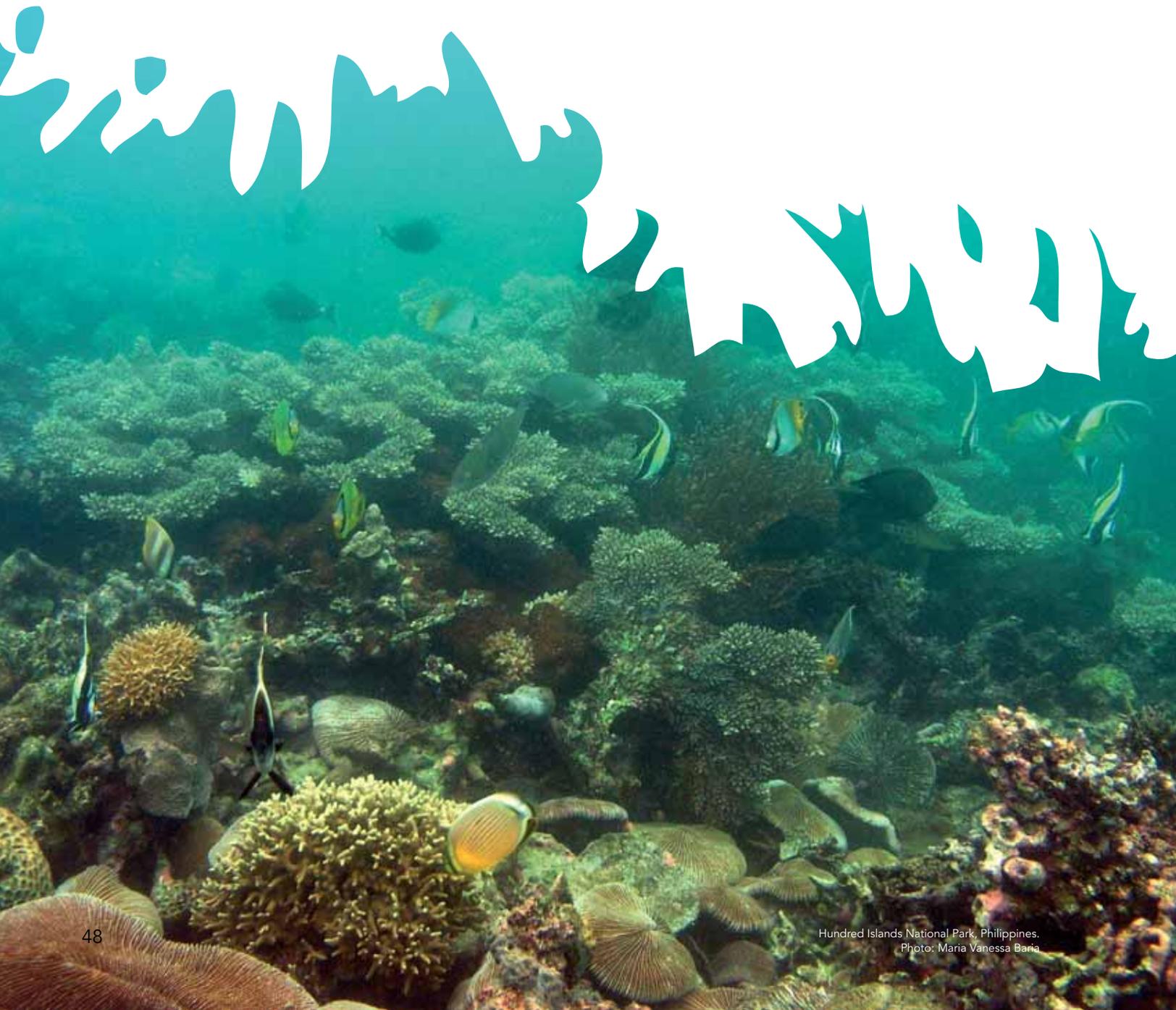
The collected in situ data, and the spatial information derived from Acoustic Ground Discrimination Systems (AGDS), high resolution satellite image analysis and hydrodynamic models, are used as decision parameters to identify areas for protection. The good news is remote sensing does seem to deliver accurate results in this application, therefore it is likely that it can be a useful tool for identification and management of fish habitat.

Eileen Peñaflo

Sea-surface temperature and thermal stress in the Coral Triangle over the past two decades



Eileen is a PhD student at the Marine Science Institute, University of the Philippines in Diliman. She is currently working on her dissertation that investigates the surface warming and thermal stress patterns in the Coral Triangle, which is one of the most important areas in marine biodiversity research. Her study is supported by the CRTR Program – Remote Sensing Working Group. Prior to this, she obtained a Masters degree in Remote Sensing and GIS in late 2003. Since then she has worked on various projects involving the use of satellite-derived data for coastal and ocean-related studies.



Sea-surface temperature and thermal stress in the Coral Triangle over the past two decades

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Abstract

Increasing ocean temperature has become one of the major concerns in recent times with reports of various related ecological impacts becoming commonplace. One of the more notable is the increased frequency of mass coral bleaching worldwide. This study focuses on the Coral Triangle region and utilizes the National Oceanic and Atmospheric Administration-Coral Reef Watch (NOAA-CRW) satellite-derived sea surface temperature (SST) and Degree Heating Weeks (DHW) products to investigate changes in the thermal regime of the Coral Triangle waters between 1985 and 2006. Results show an upward trend in SST during this period with an average rate of 0.2°C/decade. However, warming within this region is not uniform and the waters of the northern and eastern parts of the Coral Triangle are warming fastest. Areas in the eastern part have experienced more thermal stress events and these stress events appear to be more likely during a La Niña.

Introduction

The Coral Triangle (CT) is the center of the highest coastal marine biodiversity in the world (Allen and Werner 2002). This region, located in the heart of the Indo-Pacific, includes the countries of the Philippines, Indonesia, and Papua New Guinea (Fig. 1) and is home to more than 500 species of corals (Green and Mous 2004). Studies have also shown that the waters around Indonesia and the Philippines possess the highest reef fish endemism (Mora et al. 2003) and that the Philippines is also considered the global center of marine fish biodiversity (Carpenter and Springer 2005). As a bio-region, the CT, known also as the 'East Indies Triangle' (Briggs 2005, 2007) and the 'Indo-Malay-Philippines Archipelago' (Carpenter and Springer 2005), has become one of the most important target areas in marine biodiversity research.

Reports have shown, however, that species diversity and abundance in many parts of this region have been greatly threatened by both man-made and natural stresses (Burke et al. 2002; Wilkinson 2004). Specifically, studies have highlighted the alarming decline in coral cover in this region (Bruno and Selig 2007; Carpenter et al. 2008). The decline has been attributed to numerous contributing factors (Edinger et al. 1998; Fox et al. 2003) including the effect of increasing sea surface temperature (SST) over recent years (Carpenter et al. 2008).

The effect of SST increase has a wide range of effects on the marine ecosystem. Studies have shown that warm temperature anomalies have led to a reduction in primary production and a decrease in fish catch (Barber and Chavez 1986; McGowan et al. 1998). Another visible effect related to elevated SST is the resultant mass coral bleaching and related mortality (Hoegh-Guldberg 1999; Wilkinson 2004), which led to a decline in reef fish population in some areas (Pratchett et al. 2006), and may trigger coral disease outbreaks (Bruno et al. 2007). A pronounced increase in SST and coral bleaching such as that predicted for the coming decades (IPCC 2007; Hoegh-Guldberg et al. 2007) could therefore lead to a significant depletion of the CT's already stressed marine resources.

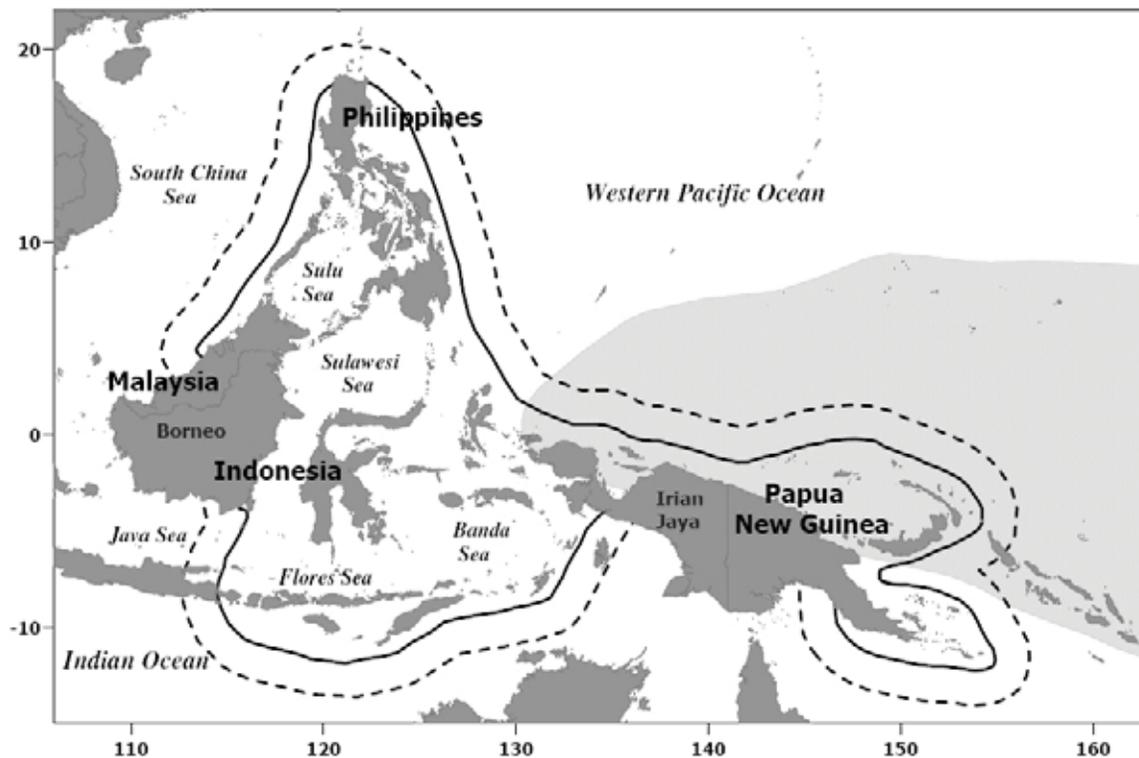


Figure 1. Map of the Coral Triangle region. Solid line depicts border after Green and Mous (2004) and J.E.N. Veron (pers. comm.). The broken line represents the 200-km buffer zone extension used in this study. The gray polygon near Papua New Guinea represents the western end of the western Pacific warm pool (after Kleypas et al. 2008)

The CT as a whole is known to experience a pronounced increase in SST during phases of ENSO (El Niño Southern Oscillation), which is a fluctuation between unusually warm and cold conditions in the tropical Pacific that typically recur with a period of 2-7 years (McPhaden et al. 2006). A good example of this was during the 1997-98 ENSO when intense warming led to the widespread occurrences of coral bleaching in this region (Wilkinson 1998; Oliver et al. 2009). Bleaching in corals can be triggered when the thermal condition is as little as 1°C higher than the mean summer maximum (Berkelmans and Willis 1999; Jokiel and Brown 2004).

In order to monitor the presence of large-scale thermal stress, the National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch (CRW) developed a suite of satellite products based on the NOAA 0.5o (approx. 50 km) resolution Advanced Very High Resolution Radiometer (AVHRR) twice-weekly SST product. This CRW suite of satellite products has been successfully used to predict and monitor bleaching events all over the world (Liu et al. 2003; Skirving et al. 2006b; Strong et al. 2006).

Beyond this near real-time warning of bleaching occurrence, it is important to investigate how the SST and thermal stress has changed through time and space in one of the most ecologically important regions in the world. To date, no study has been published that provides details of the long-term changes in spatial and temporal SST and thermal stress levels for the CT. This paper will use a hindcast version of the NOAA CRW satellite product suite to examine the changes in SST and bleaching-level thermal stress within the Coral Triangle for the period 1985 to 2006.

Materials and methods

This study utilized the gap-filled, 0.5° resolution, biweekly SST product developed by the NOAA's CRW over the period 1985-2006. This product is based on the AVHRR Pathfinder SST data (<http://pathfinder.nodc.noaa.gov>) and was derived by CRW mimicking the methodology of the CRW near real-time product (Eakin et al. 2009).

The study area was extended beyond the CT boundary (Green and Mous 2004; verified by J.E.N Veron, pers. comm. with WJS) by including a 200 km buffer zone to ensure that the analyses would not suffer from edge effects. Only data from this "buffered CT" (Fig. 1) were included in the study.

The SST data were then used to determine annual averages and ranges for the entire region. The annual average maximum and minimum for the entire region were calculated based on monthly SST averages. The trends in SST within the Coral Triangle were also calculated on a pixel by pixel basis by fitting a linear regression to the 22 years of biweekly SST data. Moreover, a spatial clustering of the entire SST data was also performed on the monthly means of each pixel, grouping pixels with similar SST signatures. The analysis made use of a web-based software, designed for geospatial clustering, called "Deluxe Integrated System for Clustering Operations" (DISCO) (<http://fangorn.colby.edu/disco-devel>). The clustering is based on *k*-means method, a popular clustering algorithm known for its speed and simplicity (Arthur and Vassilvitskii 2007). Several iterations of randomly-seeded runs were performed to determine the consistency of pixel classification. As *k*-means requires the number of clusters as input, DISCO also provides means to estimate the optimal number of clusters in a given dataset. A paper that describes the background of this online tool is downloadable at the URL cited above. The development of DISCO and its applications have been highlighted in Buddemeier et al. (2008).

An analysis using 0.5° resolution HotSpot and Degree Heating Weeks (DHW) was then conducted to determine the thermal stress levels and frequency of bleaching-level stress within the study area. The HotSpot anomaly, which is derived by subtracting a pixel's SST by its maximum monthly mean SST climatology, is an index that indicates the current intensity of thermal stress for a given location. The SST climatology is constant in time but differs in each of the pixels (Liu et al. 2003). DHW, on the other hand, computes the cumulative thermal stress by accumulating HotSpot values greater than or equal to one. This is performed over a running 12-week period. Both are anomaly products derived from satellite sea surface temperatures. It is assumed that the surface anomaly products are approximately representative of conditions experienced by corals at depth. This is a reasonable assumption since the absolute temperatures at depth are likely to trend in the same direction as those on the surface during a coral bleaching event due to a lack of wind-driven mixing (Skirving et al. 2006a). A full description of these products is presented in Skirving et al. (2006b) and Strong et al. (2006).

In this analysis, a pixel-by-pixel calculation of the thermal stress frequency and annual thermal stress levels of reef pixels (1985-2006) were determined. The former highlighted areas within the study area with high occurrences of thermal stress events while the latter was used to compare the interannual changes in thermal stress level in reef locations. Data from the World Resources Institute's Reefs at Risk (<http://www.wri.org>) were utilized to determine the reef locations within the study area. A mask was then created to select pixels in the satellite products with reef sites, deemed "reef-pixels". All reef-pixels were then divided into clusters, as previously defined. The thermal stress level was calculated by determining the maximum DHW of that pixel within the duration of a stress event. A stress event is defined in this study to begin when DHW first has a value greater than 0 and ends just before HotSpot goes below the value of 1. The event year is defined as the year when the stress event started. For example, if a stress event in a certain reef-pixel started in 1997 and ended in 1998 then the DHW value will be attributed to 1997. For some reef-pixels with multiple stress events in a year, only the event with the highest DHW value was considered. The per-pixel thermal stress frequency, on the other hand, was calculated by counting all the number of events reaching $DHW > 0$ and $DHW \geq 4$. Occurrences of multiple stress events within a year were therefore considered in this part of the analysis.

The ecological impact of the thermal stress at particular DHW values is well established (Skirving et al. 2006b; Strong et al. 2006). DHW values greater than zero indicate the existence of thermal stress (regardless of severity) while DHW values of 4 and greater indicate the existence of sufficient thermal stress to produce significant levels of coral bleaching.

Results and discussion

The annual averages show that the entire region as a whole has experienced a slight increase in SST (maximum, average, and minimum) over the period 1985-2006 (Fig. 2). This trend seems to have stabilized since 2000. There are two noteworthy years. During 1991 the region experienced a drastic decrease in SST as a result of the Mt. Pinatubo eruption in the Philippines. The effects of this cooling are evident for 2-3 years after the eruption. Conversely, the region experienced dramatic warming in 1998. This warming resulted in widespread bleaching in many parts of this region (Wilkinson 1998; ReefBase [<http://www.reefbase.org>]). Interestingly, temperatures during 1997 were remarkably low considering the dramatic warming in 1998. This seesaw in SST was due to the occurrence of a very strong El Niño in 1997 and a very strong La Niña in 1998. The contrasting differences in SST during these years is due to the temperature and geographic extent of the western Pacific warm pool (WPWP, SST > 28°C) that oscillates during ENSO events (Kawahata and Gupta 2004). This warm pool of surface water, which is normally located in the western equatorial Pacific, spreads eastward as the trade winds in the western and central equatorial Pacific weaken during an El Niño and shifts to the west of average location during a La Niña as trade winds intensify (McPhaden 1999; Kawahata and Gupta 2004). Normally, these easterly trade winds create a warm surface water pool in the western Pacific while upwelling cold water occurs on the eastern side (McPhaden et al. 2006). The weakening, or relaxation, of the trade winds during an El Niño leads to an ocean relaxation process, as well, resulting in a shallower thermocline and cooler than normal temperature in the west Pacific and a deeper thermocline and warmer than normal temperature in the east Pacific (Enfield 2001). Consequently, in the CT region, an El Niño has a relative cooling effect while a La Niña is accompanied by warming.

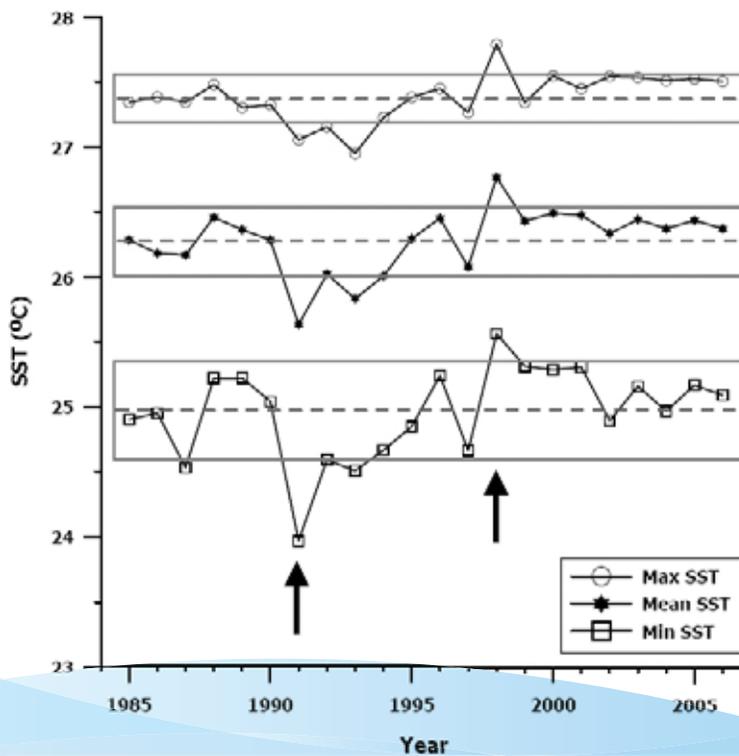


Figure 2. Average sea surface temperatures (annual maximum, mean, and minimum) for the entire study area for the period 1985-2006. Arrows indicate Mt. Pinatubo eruption (1991) and strong El Niño/La Niña events (1998). Boxes indicate one standard deviation around 1985-2006 mean (in broken, horizontal line)

2. Reef dynamics and management actions at regional scales

The trends in SST within the Coral Triangle show that on average, the region's SST increased at a rate of $0.2^{\circ}\text{C}/\text{decade}$ over the period 1985-2006 (Fig. 3). This value is comparable with the trends in many other tropical seas (Hoegh-Guldberg 1999). The SST trends varied spatially across the region with higher warming rates around the Philippines and north of Irian Jaya and Papua New Guinea, as compared to the southern most CT areas (below 5° south) where rates were much lower. Investigating the SST trends in an area can be valuable in explaining the occurrences of mass bleaching events because of the strong correlation between SST and bleaching events (Hoegh-Guldberg 1999). Studies have also shown that a rapid increase in SST has been a major factor in many large-scale coral bleaching occurrences in recent decades (Berkelmans et al. 2004; Lough et al. 2006).

Clustering analysis allows further examination of the SST scenarios within the region, and indicated 12 distinct sub-regions (clusters). Annual mean SST's were calculated for each of the clusters to determine the temporal changes in SST of these areas (Fig. 4). The majority of the clusters had greater number of warmer-than-average years in the latter 11 years, which explained the SST trends shown in Figure 3. The pronounced increase in SST in 1998 was also evident in many of the clusters. Northern clusters showed a consistent positive slope but with less frequent annual fluctuations. Corals located in these areas are more likely to be susceptible to future bleaching unless they develop mechanisms to cope with expected rapid increases in SST. The caveat to this statement is that corals in these areas could also have more time to reestablish due to the infrequency of stress events. The southern clusters, on the other hand, had smaller positive trends in SST but exhibited frequent pronounced fluctuations. The fluctuations may indicate that these areas frequently undergo temperature changes and it is possible that marine organisms in these areas (e.g., corals) have adapted to cope with more variable temperatures (more eurythermal). It has also been pointed out that high variability in temperature may help corals to better acclimate or adapt to an increase in temperature (McClanahan et al. 2007).

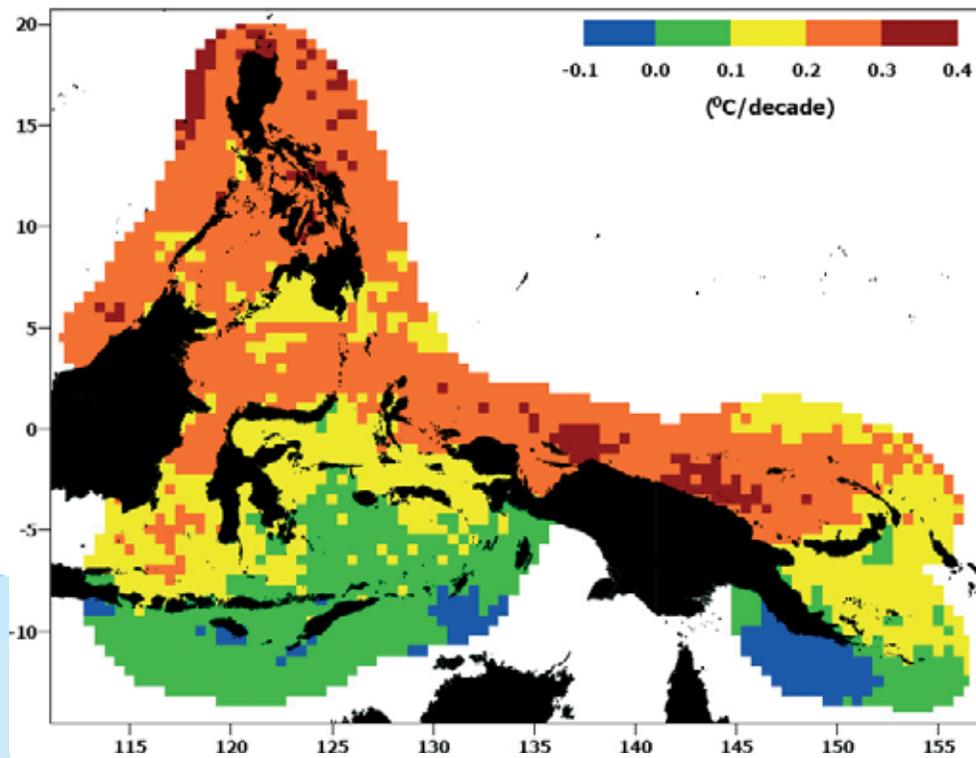


Figure 3. Trends in sea surface temperature within each $0.5^{\circ} \times 0.5^{\circ}$ pixel for the period 1985-2006 calculated from biweekly data.

2. Reef dynamics and management actions at regional scales

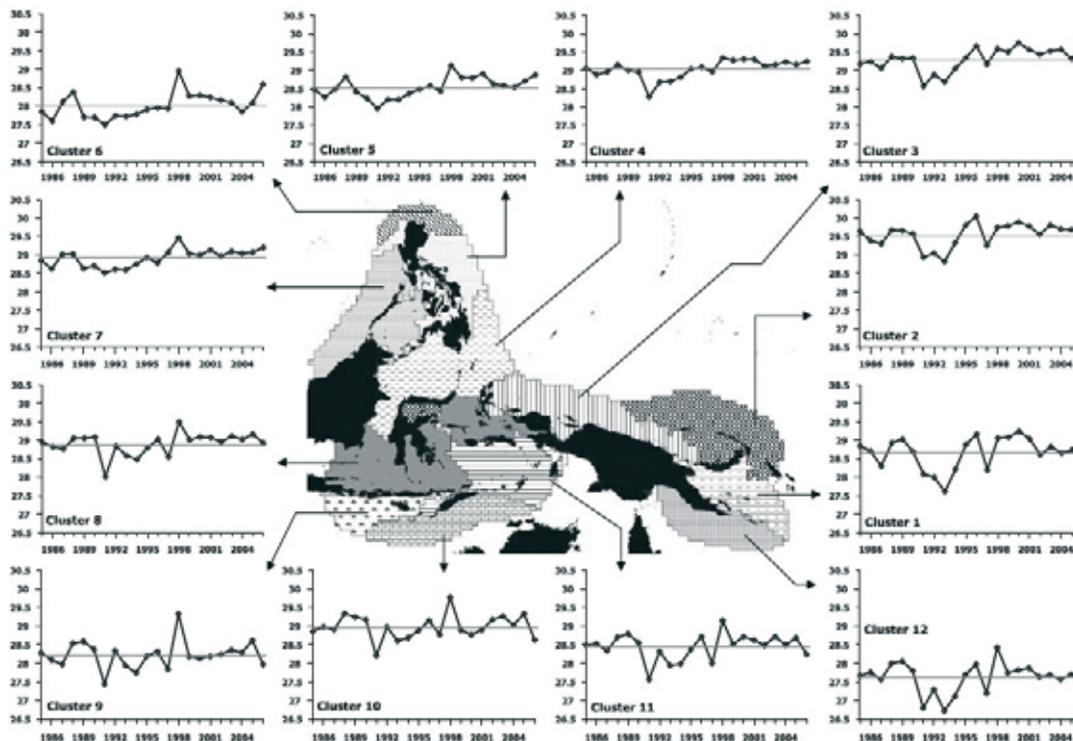


Figure 4. The Coral Triangle divided into 12 clusters. Graphs show the annual mean SST for each cluster with horizontal line indicating the mean of the biweekly SST for all years.

SST trends, however, are not the whole story as the length of time that corals are exposed to thermal stress is as important as the temperature reached. While the relatively slow SST increase in the southern sub-region could be interpreted to mean that coral reefs in this part of the CT have been subjected to less long-term thermal stress levels than in other areas of the region, this may not necessarily be the case. The DHW product provides the metric to investigate trends in thermal stress.

An analysis of the thermal stress event frequency in this region (Fig. 5) revealed more thermal stress ($DHW > 0$) events and more occurrences of bleaching-level thermal stress ($DHW \geq 4$) during 1996-2006 than during 1985-1995. Results also indicated the emergence of multiple stress events within a single year ($DHW > 0$) during the latter 11 years. The multiple stress events were most prominent in areas nearest to the WPWP.

The WPWP is of particular interest as this part of the Pacific has been shown to have warmed less over the past six decades in comparison to other tropical seas (Kleypas et al. 2008). This suggests a higher sensitivity of the corals in this region to small temperature fluctuations, yet these reefs seem to have a lower proportion of bleaching reports relative to other reefs in the world (Kleypas et al. 2008). Reefs in southeastern Papua New Guinea have experienced a relatively high frequency of thermal stress events (Fig. 5) but also showed a lower rate of increase in SST and experienced more extreme temperature fluctuations that oscillated about a relatively stable mean (Figs. 3 and 4, respectively). In contrast, the inner seas of Indonesia had few to no occurrences of significant thermal stress ($DHW \geq 4$) even during the latter 11 years. The low frequency of thermal stress events in these areas may possibly have been due to the complex hydrodynamic processes in these areas (Gordon 2005; Qu et al. 2005). The complex geometry and connectivity through straits and passages coupled with other factors such as surface heat flux, tidal mixing, and monsoonal winds drive the complex distribution of SST in this region (Qu et al. 2005).

2. Reef dynamics and management actions at regional scales

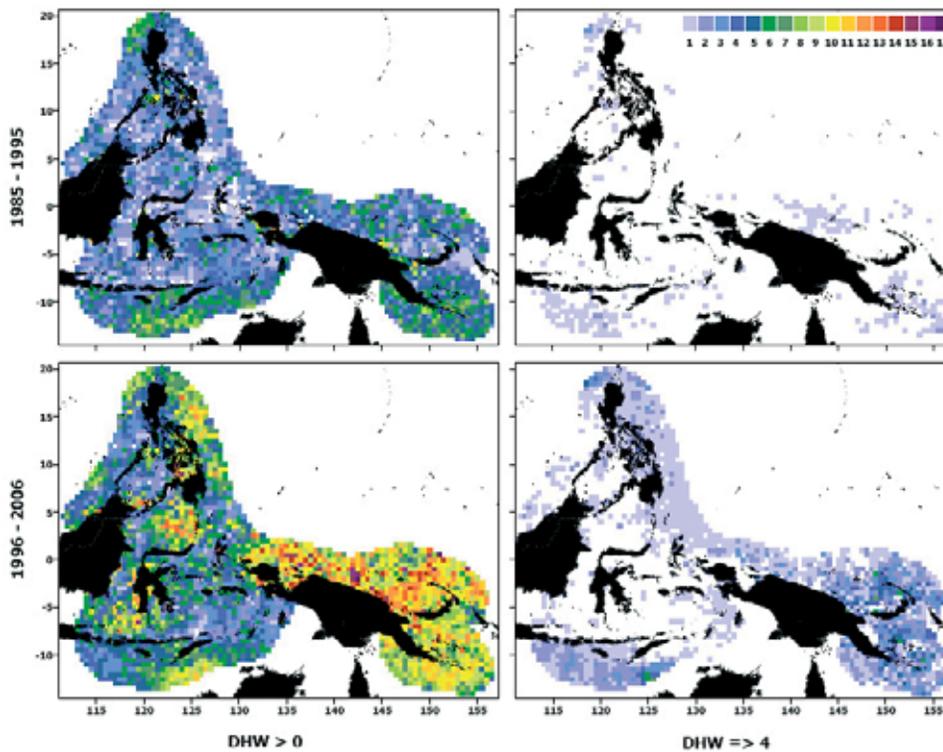


Figure 5. Maps of the return frequency of thermal stress events reaching two thresholds, $DHW > 0$ (left) and $DHW \geq 4$ (right). Upper images show the frequency of stress event occurrences from 1985-1995 while lower images depict years from 1996-2006. Some pixels show multiple event occurrences within a year, indicated by values greater than 11.

To investigate changes in thermal stress level for the CT, a temporal analysis of DHW data was performed for pixels known to contain coral reefs. The annual thermal stress levels are shown in Figure 6, which shows that 1998 was the most anomalous year with 77% of the reef pixels having $DHW > 0$ and 25%. Higher levels of thermal stress were observed in 1996-2006 as compared to 1985-1995. The dramatic increase in the levels of thermal stress during the 1996-2006 period may have been linked to the Pacific Decadal Oscillation (PDO) reversal in the late 1990s (Strong et al. 2006). The PDO refers to the interdecadal (~2-3 decades) oscillation of Pacific Ocean temperatures between warm and cold phases (Strong et al. 2006; Mantua and Hare 2002).

Further analysis was performed on the data from the five years with the highest percentages of reef pixels with $DHW \geq 4$: 1996, 1998, 1999, 2000, and 2005 (Fig. 7). These years are concurrent with the La Niña events with the exception of 2005, which is an ENSO-neutral year. 2005 is currently the warmest year on record based on global temperature averages (Shein 2006). In this analysis, only pixels with $DHW \geq 4$ were included since this level of thermal stress has been observed to indicate significant bleaching in corals (Skirving et al. 2006b; Strong et al. 2006). The year 1998, when a very strong La Niña occurred, again stands out with the highest number of clusters showing bleaching-level stress. This further supports the occurrence of widespread bleaching in many parts of the CT in 1998. Noticeably, clusters 5 and 6 in the northernmost Philippines are the most impacted during the very strong La Niña. Cluster 1, at the southeastern extent of the CT, is the only cluster that had no reef pixels with bleaching-level thermal stress in 1998. The observed SST in that year (Fig. 4) was not high enough or sustained for long enough to cause bleaching-level thermal stress. Clusters 2 and 3 also have lower proportions of reef pixels with this level of thermal stress in 1998 but all three clusters (1, 2, and 3) showed higher percentages of stress in the other four years. Figure 7 also shows that reef pixels in clusters 1, 2, 3, 10, and 12 have more frequent occurrences of bleaching-level thermal stress ($DHW \geq 4$) in the selected five years, while the middle latitude clusters, 4 and 7, are among the least frequent. Cluster 8 seemed to be the least affected overall with very low proportions of this level of stress.

2. Reef dynamics and management actions at regional scales

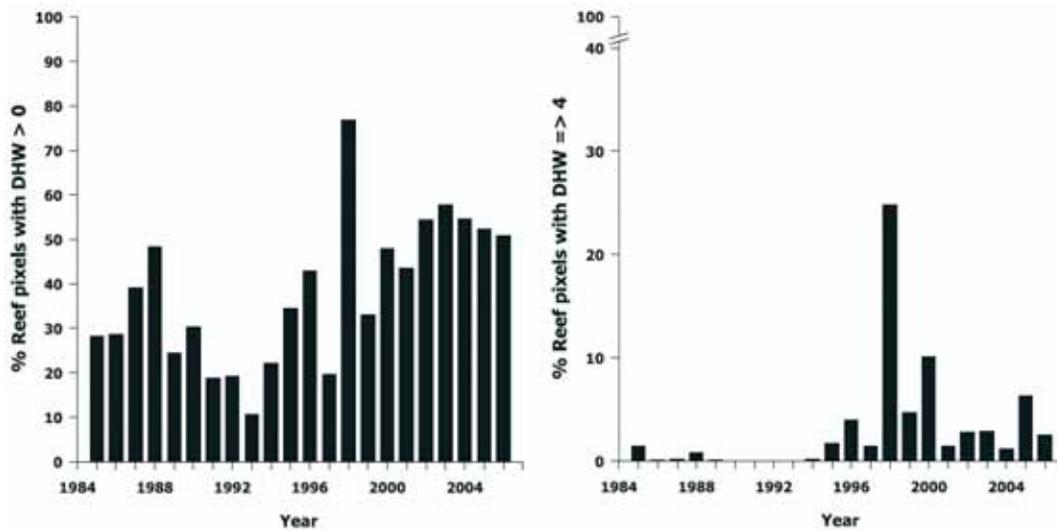
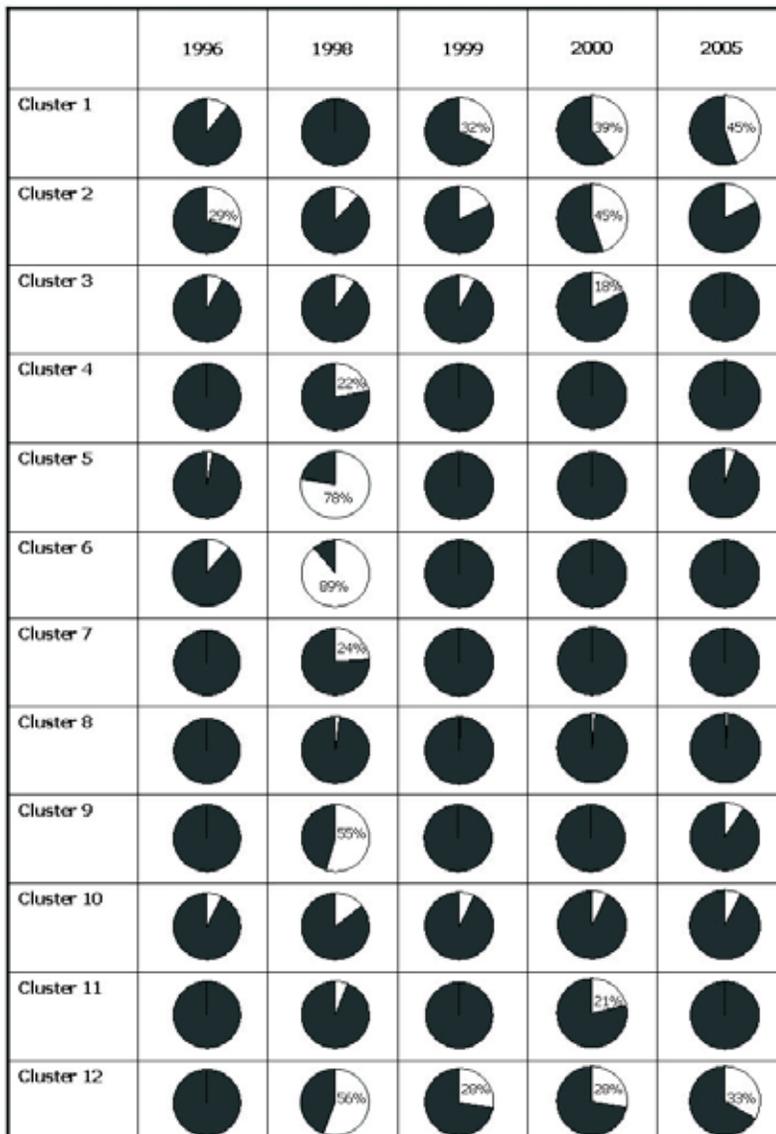


Figure 6. Annual percentages of all known reef-containing pixels in the entire Coral Triangle reaching thermal stress thresholds of $DHW > 0$ (left) and $DHW \geq 4$ (right).



56 Figure 7. Percentages of reef pixels (white portion in each pie chart) for each cluster with $DHW \geq 4$ during selected years.

Overall, this study shows that more warming and more thermal stress events were observed from 1996 onwards as compared to the earlier half of the record. This is likely to be a consequence of climate change, i.e., PDO phase shift superimposed on the warming trend. However, further investigation is needed to check that this increase is not an artifact of the relatively short satellite SST record. Results also show the variability of SST in both time and space for various parts of the Coral Triangle. There are areas that are warming up faster but are experiencing less frequent annual SST fluctuations. These areas are also affected by significant levels of thermal stress as in the case of the northern Coral Triangle (particularly clusters 5 and 6). Corals in these areas are likely to be susceptible to future bleaching occurrences if they cannot cope with the rapid increase in SST.

There are also areas that afford natural protection from warming events as in the case of the inner seas of Indonesia. Some areas in the southern portion of the region (clusters 1, 10, and 12) have highly fluctuating SSTs accompanied with frequent thermal stress events, and yet exhibit no significant increase in long-term SST. In these areas, corals may be more adapted to warm SST anomalies and more likely to see slower warming in coming decades. Also, more thermal stress occurrences were observed in the easternmost parts of the region (clusters 2 and 3), which may have provided opportunity for the development of corals that are more resistant to thermal stress events. The effect of the faster warming rates on corals located in these areas needs further investigation.

The analyses of SSTs and thermal stress in the Coral Triangle portray a significantly varied story. The northern areas are experiencing greater increases in SST through time compared to the southern areas. The eastern parts of the region, on the other hand, show significant increases in thermal stress events compared to the western parts. Lastly, significant bleaching events are more likely to occur in the Coral Triangle during a La Niña, and not during El Niño, with the northern areas more likely affected during a very strong event.

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References

- Allen GR, Werner TB (2002) Coral reef fish assessment in the 'coral triangle' of southeastern Asia. *Environ Biol Fish* 65:209–214
- Arthur D, Vassilvitskii S (2007) K-means++: The advantages of careful seeding. *Proceedings of the 18th annual ACM-SIAM Symposium on Discrete Algorithms*, pp1027-1035
- Barber RT, Chavez FP (1986) Ocean variability in relation to living resources during the 1982-83 El Niño. *Nature* 319:279-285
- Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs* 18:219-228
- Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs* 23:74-83
- Briggs JC (2005) Coral reefs: Conserving the evolutionary sources. *Biol Conserv* 126: 297–305
- Briggs JC (2007) Marine longitudinal biodiversity: causes and conservation. *Divers Distrib* 13:544–555
- Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol* 5:e124 [doi:10.1371/journal.pbio.0050124]
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE* 2:e711 [doi:10.1371/journal.pone.0000711]
- Buddemeier RW, Smith SV, Swaney DP, Crossland CJ, Maxwell BA (2008) Coastal typology: An integrative "neutral" technique for coastal zone characterization and analysis. *Estuar Coast Shelf Sci* 77:197-205
- Burke L, Selig E, Spalding M (2002) *Reefs at risk in Southeast Asia*. World Resources Institute, Washington D.C.
- Carpenter KE, Springer VG (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environ Biol Fish* 72:467–480
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzmán HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560-563
- Eakin CM, Lough JM, Heron SF (2009) Climate variability and change: Monitoring data and evidence for increased coral bleaching stress. In: van Oppen M, Lough JM (eds) *Coral bleaching: Patterns, processes, causes and consequences*. Springer, Heidelberg, pp 41-67

2. Reef dynamics and management actions at regional scales

- Edinger EN, Jompa J, Limmon GV, Widjtmoko W, Risk MJ (1998) Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. *Mar Pollut Bull* 36: 617-630
- Enfield DB (2001) Evolution and historical perspective of the 1997-1998 El Niño-Southern Oscillation event. *Bull Mar Sci* 69:7-25
- Fox HE, Pet JS, Dahuri R, Caldwell RL (2003) Recovery in rubble fields: long-term impacts of blast fishing. *Mar Pollut Bull* 46: 1024-1031
- Gordon AL (2005) Oceanography of the Indonesian seas and their throughflow. *Oceanography* 18:14-27
- Green A, Mous PJ (2004) Delineating the Coral Triangle, its ecoregions and functional seascapes. Report on an expert workshop held in Southeast Asia Center for Marine Protected Areas, Bali, Indonesia, April 30-May 2, 2003, The Nature Conservancy
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50: 839-866
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell DR, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioles ME (2007) The carbon crisis: coral reefs under rapid climate change and ocean acidification. *Science* 318:1737-1742
- IPCC (2007) Summary for Policymakers. In: *Climate change 2007: Synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change*. IPCC, Switzerland
- <http://www.ipcc.ch/ipccreports/ar4-syr.htm>
- Jokiel PL, Brown EK (2004) Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Global Change Biol* 10:1627-1641 [doi: 10.1111/j.1365-2486.2004.00836.x]
- Kawahata H, Gupta LP (2004) Settling particles flux in response to El Niño/Southern Oscillation (ENSO) in the equatorial Pacific. In: Shiyomi M, Kawahata H, Koizumi H, Tsuda A, Awaya Y (eds) *Global environmental change in the ocean and on land*. Terrapub, Tokyo, pp 95-108
- Kleypas JA, Danabasoglu G, Lough JM (2008) Potential role of the ocean thermostat in determining regional differences in coral bleaching events. *Geophys Res Lett* 35: L03613 [doi:10.1029/2007GL032257]
- Liu G, Strong AE, Skirving W (2003) Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *EOS Trans Am Geophys Union* 84:137-144
- Lough J, Berkemans R, van Oppen M, Wooldridge S, Steinberg C (2006) The Great Barrier Reef and climate change. *Bull Aust Meteor Oceanogr Soc* 19: 53-58
- Mantua NJ, Hare SR (2002) The Pacific Decadal Oscillation. *J Oceanogr* 58:35-44
- McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Mar Ecol Prog Ser* 337: 1-13
- McGowan JA, DR Cayan, Dorman LM (1998) Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210-217
- McPhaden MJ (1999) Genesis and evolution of the 1997-98 El Niño. *Science* 283:950-954.
- McPhaden MJ, Zebiak SE, Glantz MH (2006) ENSO as an integrating concept in Earth science. *Science* 314:1740-1745
- Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA (2003) Patterns and processes in reef fish diversity. *Nature* 421: 933-936
- Oliver JK, Berkemans R, Eakin CM (2009) Coral bleaching in space and time. In: van Oppen M, Lough JM (eds) *Coral bleaching: Patterns, processes, causes and consequences*. Springer, Heidelberg, pp 21-39
- Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. *J Fish Biol* 69:1269-1280 [doi:10.1111/j.1095-8649.2006.01161]
- Qu T, Du Y, Strachan J, Meyers G, Slingo J (2005) Sea surface temperature and its variability in the Indonesian region. *Oceanography* 18:50-61
- Shein, KA (Ed.) 2006 State of the climate in 2005. *Bull Am Meteorol Soc* 87:S1-S102
- Skirving W, Heron M, Heron S (2006 a) The hydrodynamics of a bleaching event: Implications for management and monitoring. In: Phinney JT, Hoegh-Guldberg, O, Kleypas J, Skirving W, Strong A (eds). *Coral reefs and climate change: Science and management, coastal and estuarine studies 61*, American Geophysical Union, Washington, D.C., pp 145-161
- Skirving W, Strong AE, Liu G, Arzayus F, Liu C, Sapper J (2006 b) Extreme events and perturbations of coastal ecosystems: Sea surface temperature change and coral bleaching. In: Richardson LL, LeDrew EF (eds). *Remote sensing of aquatic coastal ecosystem processes: Science and management applications*. Springer, Netherlands, pp 11-25
- Strong AE, Arzayus F, Skirving W, Heron SF (2006) Identifying coral bleaching remotely via Coral Reef Watch – Improved integration and implications for changing climate. In: Phinney JT, Hoegh-Guldberg, O, Kleypas J, Skirving W, Strong A (eds). *Coral reefs and climate change: Science and management, coastal and estuarine studies 61*, American Geophysical Union, Washington, D.C., pp 163-180
- Wilkinson C (ed) (1998) *Status of coral reefs of the world: 2000*. Australian Institute of Marine Science, Townsville, Queensland, Australia
- Wilkinson C (ed) (2004) *Status of the coral reefs of the world: 2004*. Australian Institute of Marine Science, Townsville, Queensland, Australia

Status of coral reef research in the Bolinao-Anda reef complex, northwestern Philippines



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Status of coral reef research in the Bolinao-Anda reef complex, northwestern Philippines

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Abstract

The Bolinao-Anda reef complex (BARC) supports one of the most important fishing grounds in the Philippines, the Lingayen Gulf. This ~200 km² reef complex in northwestern Philippines is home to the Bolinao Marine Laboratory of the Marine Science Institute of the University Philippines, designated as the GEF Coral Reef Targeted Research's (GEF CRTR) Southeast Asia Center of Excellence. Although the BARC area was among the first coral reef areas to be assessed in the Asian region (1977) it still continues to unlock secrets of the seas through collaborative and interdisciplinary research of both local and international scientists. Unfortunately, it has also been subjected to numerous natural and anthropogenic disturbances (blast fishing, coral bleaching, increased freshwater input, fishkills, overfishing, predator infestation, poison fishing, trawl fishing, etc.) and has shown signs of habitat degradation since. This compilation aims to provide an updated status of coral reef research conducted by student scholars and post-docs of the GEF CRTR in the BARC area and synthesize these findings to come up with recommendations for future studies that will contribute to the recovery efforts in the area.

I. The Bolinao-Anda reef complex (1980s to 2004)

Covering more than 200km², Bolinao-Anda reef complex (BARC) sustains one of the most important fishing grounds in the Philippines, the Lingayen Gulf. Located in the province of Pangasinan, its reef flats harbor the largest seagrass area in the country. It has seen some of the first significant scientific research and discoveries on marine science in the Philippines and still continues to unlock secrets of the seas through collaborative and interdisciplinary research of both local and international scientists. Complex biological and ecological processes link the various marine communities to each other, maintaining the high biodiversity of animals and plants present in these communities.

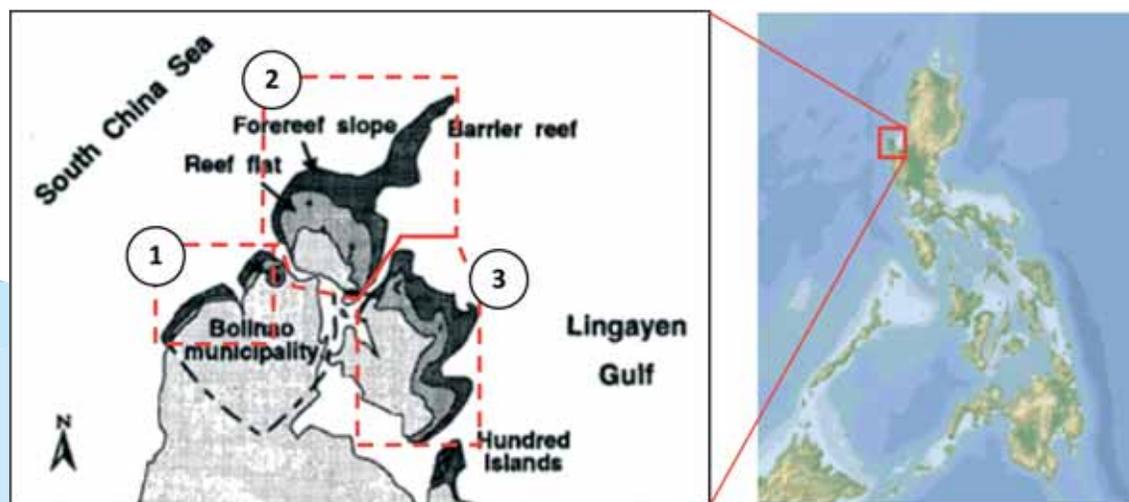


Figure 1. Map of Bolinao-Anda reef complex (from McManus et al. 1992) and its location in the Philippines. (1) reefs facing the South China Sea and fringing the mainland; (2) reefs fringing Santiago Island; and (3) reefs fringing the island town of Anda.

2. Reef dynamics and management actions at regional scales

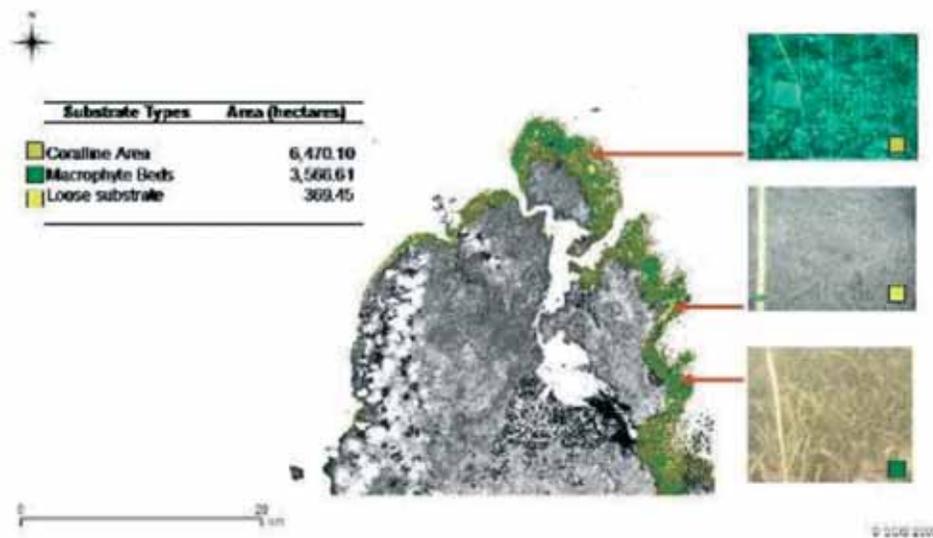


Figure 2. Dominant benthic habitat types of BARC and their estimated area.

The BARC provide subsistence fisheries and other benefits such as ecotourism (Cruz-Trinidad et al. 2009). Two towns share most of the reefs of the BARC – Bolinao and Anda. The recently concluded Sagip Lingayen Gulf Project (“Save Lingayen Gulf”) estimates a total of at least 6,700 artisanal fishers from both towns. Fishers from the adjacent city of Alaminos also frequent the BARC.

The Bolinao-Anda Reef Complex can be divided into three reef systems separated by vast sand channels: (1) the narrow and steep slopes along the mainland facing the South China Sea with reefs abruptly dropping to more than 30 meters; (2) the fringing reefs of Santiago Island with an extensive seagrass-dominated reef flat and a talus extending 14 miles into the middle of the Lingayen Gulf; and (3) the sandy reef flats and shallow slopes fringing the Anda municipality (Figures 1 and 2). The first two systems are highly exposed to strong wave action brought by the Northeast monsoon from November to March while the latter is more sheltered (Quan 2002). In the late 1980s to early 1990s, most monitoring projects surveyed sites around Santiago Island only. From 2000 onwards, with the rapid increase in the number of established Marine Protected Areas (MPAs) in the reef complex, monitoring programs focused on MPAs along the South China Sea side of mainland Bolinao and the reefs around Anda.

Total population in Bolinao has been increasing linearly in the last 15 years (Figure 3). The population of barangays in Santiago Island, the main fishing villages, is increasing faster than the population of the town. Almost 150 fishers are added every year to the total number of fishers in Bolinao (Uychiaoco et al. 2003).

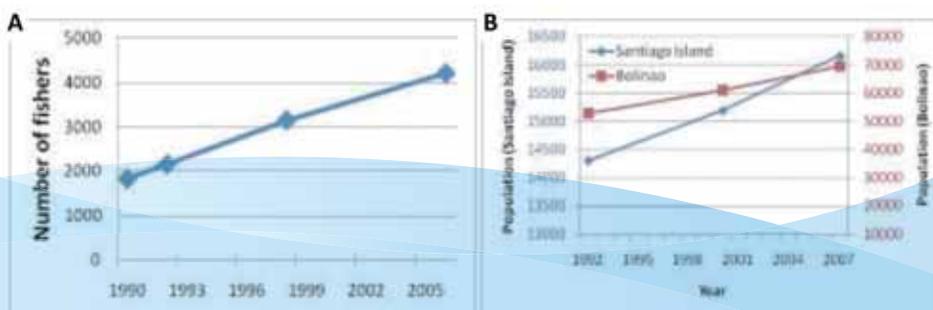


Figure 3. (A) Trends in number of fishers in Bolinao and (B) total population in Bolinao and Santiago Is. from 1992 to 2007

The BARC provides significant production for the municipal fisheries of these towns. From 1983 to 1985, reef fish comprised 17% to 33% of the total landed catch of municipal fishers in Pangasinan (BFAR 1985). Siganid fishery, from fries to adults, form a considerable industry even before the 1970s (Calvelo and Ginon 1974) and even up to the present. The Bolinao sea urchin (*Tripneustes gratilla*) fishery collapsed in 1992 but re-seeding and re-stocking efforts have been initiated and is showing significant successes (Juinio-Meñez et al. 2008). Aquarium fishing, seaweed harvesting and farming, and shell gathering are still practiced in Bolinao’s reefs.

2. Reef dynamics and management actions at regional scales

The BARC has been in various states of degradation and overfishing since the first systematic surveys were conducted in the 1980s. It has been subjected to a wide range of stresses and monitored for three decades. Major reef disturbances in the early 1990s were attributed mostly to excessive extraction and habitat-destructive fishing (del Norte et al. 1989; McManus et al. 1997). Ten years later, these pressures were exacerbated by the increased occurrence of bleaching (Arceo et al. 2001), crown-of-thorns infestation, sedimentation (Wesseling et al. 2001), and pollution from mariculture.

The latter half of the 1990s marked the start or end of major events that significantly driven the Bolinao-Anda reef complex's present state (Figure 4). The strict banning on the use of dynamites and cyanide in fishing started in 1997 (Uychiaoco et al. 2003), although efforts at reducing their use have already began in the early 1990s (McManus et al. 1992). Mariculture structures along Guiguivanen channel rapidly increased since 1997 (Verceles et al. 2000). Uncontrolled development led to overstocking and excessive feeding which eventually resulted in massive fish kills in February 2002 (Yap et al. 2004).

Mass coral bleaching occurred along the Bolinao reefs in 1998 which reduced live coral cover from 45% to 17% in three sites surveyed a month before and after this natural disturbance (Arceo et al. 2001). A minor bleaching event also happened in 2007 followed by severe crown-of-thorns infestations within the year. In response to the threats, the first marine protected area (MPA) around Santiago Island was established only in 2004 in front of Brgy. Victory and another one in front of Brgy. Lucero in 2005 (Geronimo et al. 2008).

It is under these conditions and intense historical background of disturbances that most GEF-CRTR students from the Philippines worked on to generate new knowledge on coral reef dynamics and apply these in diversifying management options for the Bolinao-Anda reef complex.

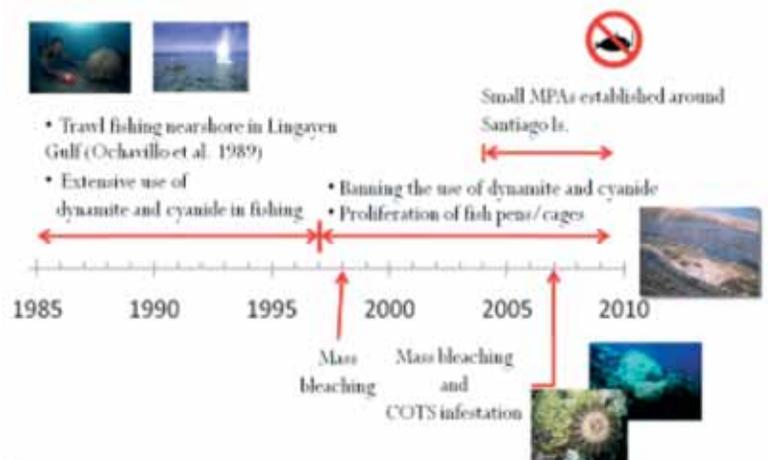


Figure 4. Timeline of disturbances and major events that have affected the Santiago Island reefs.

II. New knowledge and discoveries on the Bolinao-Anda reef complex (2005 to 2009)

From 2005 to 2009, the GEF/WB Coral Reef Targetted Research has generated new information on state indicators and processes driving the Bolinao-Anda Reef Complex (BARC). Some of these information have been directly applied to coastal resource management and improving the state of the BARC while others advanced our knowledge on reef processes in this part of the world (Figure 5). Most of the methods can be generally applied to other reefs in the Philippines.

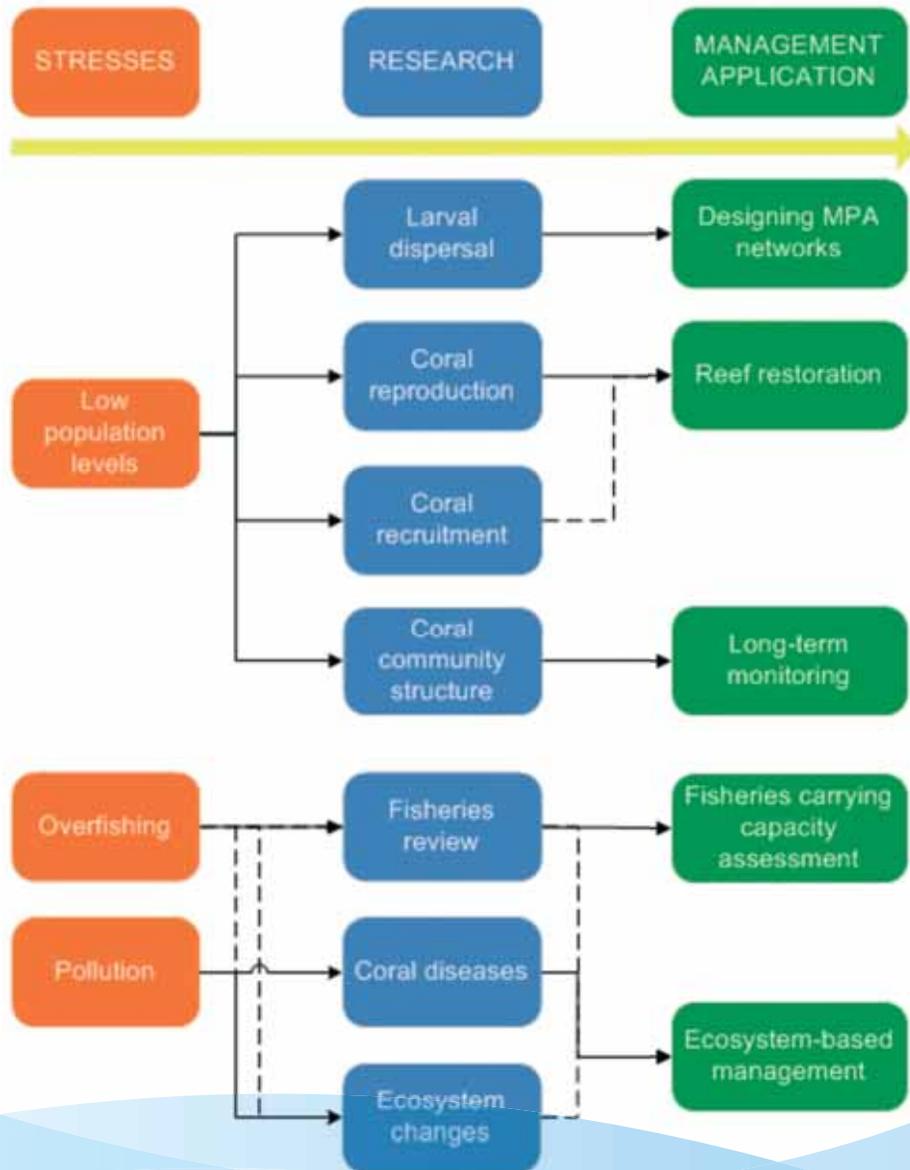


Figure 5. Researches conducted by the CRTR students in the Bolinao-Anda Reef Complex from 2005-2009 vis-a-vis major reef stresses and management applications

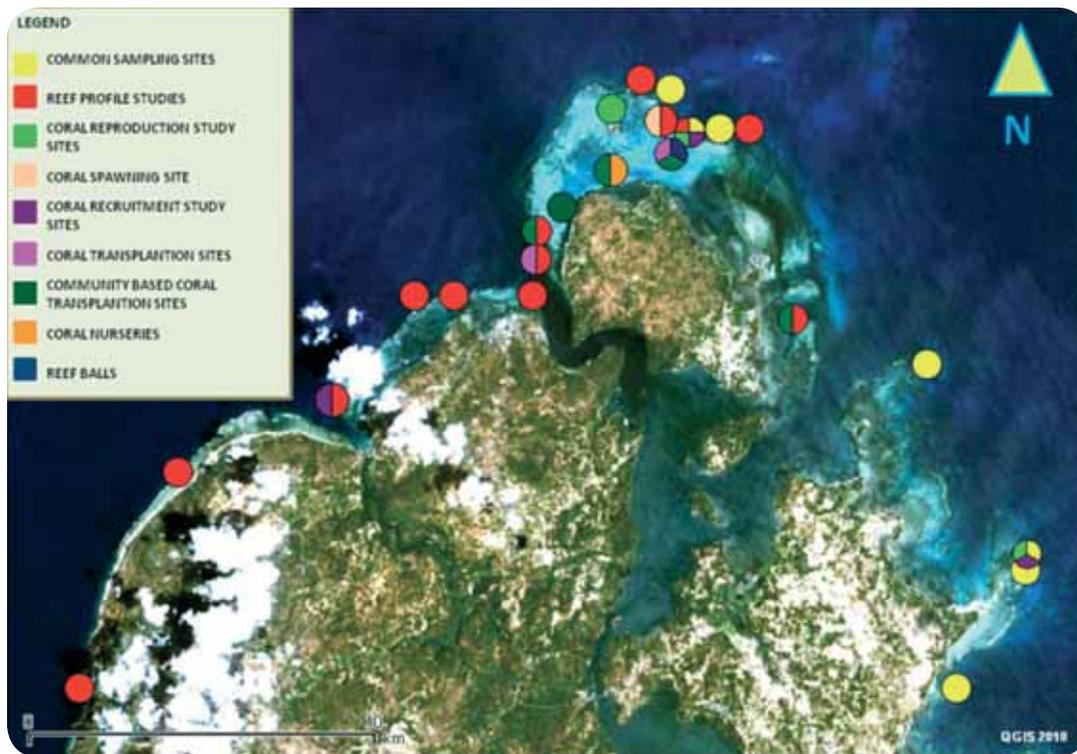


Figure 6. General location of the different GEF-CRTR study sites in the BARC (Landsat 7, March 2009).

Benthic and fish changes (1997 to 2008)

While the BARC experienced high fishing pressure, natural disturbances further stressed the reefs. The prolonged warm sea surface temperature in 1998 resulted in massive coral bleaching on the BARC. This represents probably the most catastrophic change that the reef complex has experienced over the last thirty years. A minor bleaching in 2004 and crown-of-thorns infestation in 2007-2008 kept coral cover at low levels. Surveys conducted along the northern reef slopes of Santiago Island from 1997 to 2008 indicate a decrease in mean live coral cover from 33% to 15% ($F(3,27)=5.0$, $p<0.01$; $n=10$) one year after the mass bleaching event while algal cover doubled ($F(3,27)=13.0$, $p<0.01$) (Figure 7) (Geronimo 2009). Multivariate analyses reveal a progression of benthic composition from massive and soft-coral dominated in 1998 to bare rock substrates with silt and algae in 1999 to algae and the blue coral (*Heliopora coerulea*) in 2008 (see Box 1). However, despite the large declines in coral cover, total fish abundance did not change between 1997 to 2008 but total fish biomass increased significantly by four times between 1999 and 2008 ($F(3,27)=10.2$, $p<0.01$). Principal components analysis revealed a shift from specialist fish species to more generalist species comprised of detritus feeders, benthic invertebrate feeders, and general herbivores and omnivores.

Ctenochaetus striatus contributed the most to the increase in total fish biomass between 1999 and 2008.

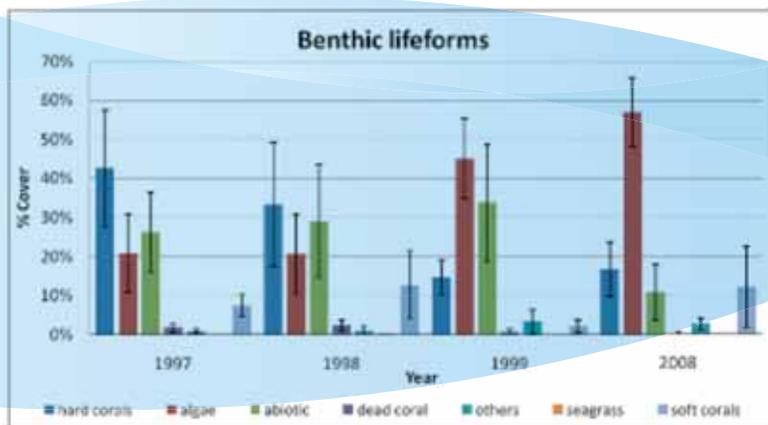


Figure 7. Change in percent cover of benthic lifeform categories along the northern Santiago Island reef slope from 1997-1999 and 2008. Whiskers represent 95% confidence interval.

Fisheries

The capture fishery around the BARC is multi-gear and multi-species in nature. Major gears used are gillnets, hook and line, spearfishing, and gleaning (McManus et al. 1992). Many mobile invertebrates (e.g., sea urchins and sea cucumbers along the reef flat) and fish species are heavily exploited by subsistence fishers and gleaners along the reef flat and slopes (FRMP 2002).

Individual fishers' daily fish catch data collected through the Sagip Lingayen Gulf Project (2004 to 2007) were collated together with data from fish buyers' logbooks compiled by Uychiaoco (unpublished data) from various projects and fisheries monitoring activities in Bolinao from 1987 to 2001. A cursory look at the available fishery dataset for Bolinao from 1987 to 2007 shows that mean catch rates, pooled across gears and landing areas, generally increased in the mid-1990s (Figure 8a). Catch rates increased by 1 to 2 kg•fisher⁻¹•trip⁻¹ between the periods 1987-1993 and 1996-2007. Catches of fishers, however, are primarily comprised of pelagic and soft-bottom demersal fishes than reef fishes (Figure 8b).

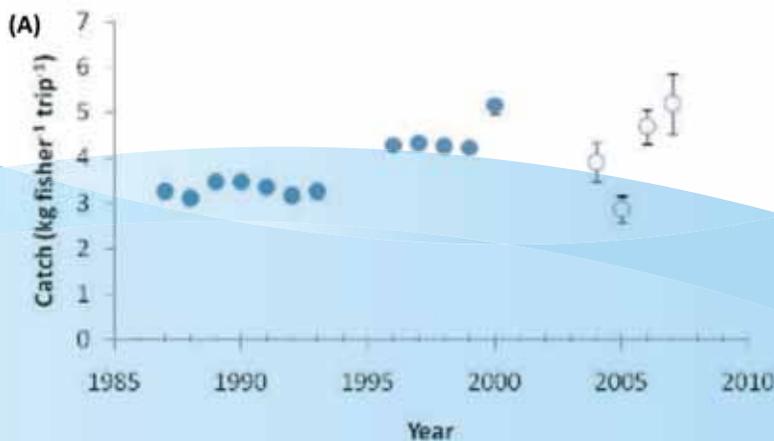
Accounting for landing sites and gears used in the data from buyers' log books show predominantly stable or increasing trends in catch rates particularly up to the late 1990s. For Barangay Binabalian, the main fishers fishing near the Malilnep channel, catch rates of spearfishers were relatively stable at 3.5 kg•fisher⁻¹•trip⁻¹ while gillnet fishers, pooling all gillnet variations, recorded increased catch rates from 1987 to 2000. Buyers' records show changes in primary gillnet variations used by Brgy. Binabalian fishers from the mid-1990s to late 1990s with current dominance of bottom-set gillnets. Hook and lines in Brgy. Lucero showed increasing trends in catch rates reaching up to 15 kg•fisher⁻¹•trip⁻¹ in 1997. Brgy. Pilar, which had the most complete temporal data set from 1988 to 2000 for one gear type, recorded increasing catch rates for bottom-set gillnets at an average linear rate of 14% per year from 1988 to 2007.

Box 1. Blue and green: colors of Bolinao reef

Green and blue appear to be the dominant colors in Bolinao reefs in recent years. After the 1998 mass coral bleaching, algae began to increase in cover around most of the reefs giving them an eerie greenish color especially during days with high turbidity along the shallows. An extensive coral community survey of Bolinao reefs from 2006-2007 also reveal dominance of blue coral (*Heliopora coerulea*) around the area. Along the northern reef slopes of Santiago Island, coral cover became dominated by *H. coerulea* (i.e., 66% of live coral cover) between 1999 and 2008.

Heliopora coerulea is known to be highly tolerant to bleaching and low salinities. They appear to have been spared from *Acanthaster planci* infestations as well. Its niche extends beyond the normal environmental range of most scleractinian corals. Unlike other reefs, the presence of *H. coerulea* could mean that the "slippery slope to slime" might be less steep than normal for the reefs around Bolinao.

– Mark Vergara (SEA CoE) and Rollan Geronimo (MDSWG)



2. Reef dynamics and management actions at regional scales

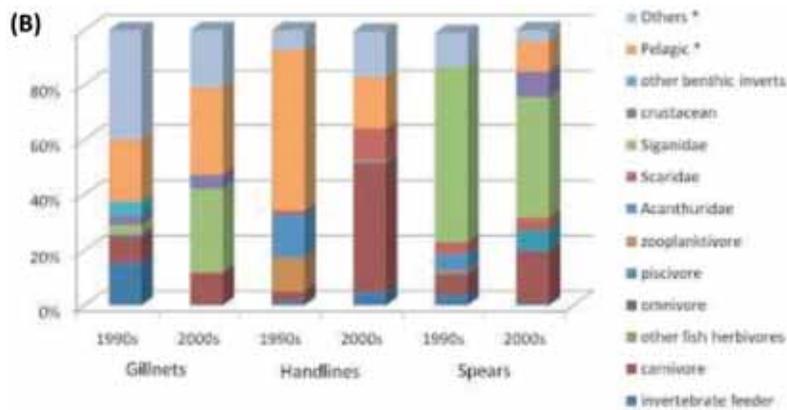


Figure 8. (A) Fish catch per fisher per trip trends using pooled gear and landing site data from 1987 to 2007 and (B) Catch composition changes in the top three dominant fishing gears along the northern Santiago Island reef slope from 1996-1998 and 2005-2007.

Ecosystem comparison (pre-1998 and post-1998)

Trophic models of the Santiago Island reef slope for the mid-1990s (1995-1997) versus the mid-2000s (2006-2008) using Ecopath with Ecosim (Christensen et al. 2005) expose subtle ecosystem changes (Geronimo et al. 2009). Primary, secondary, and detritus production are all higher in the mid-2000s but system indicators point to degenerated ecosystem functionality. Algal biomass and production rate at present is greater than the overall grazing rates and consumption of detritus thus resulting in lower recycling properties of the ecosystem compared to the mid-1990s. Ecosystem indices of the modeled food webs such as Finn's cycling index and mean path length also denotes a decline in overall ecosystem stability. Given the present state of the Santiago Island reef slope, future perturbations will result to a longer recovery time for the ecosystem than it was in the mid-1990s or shift entirely to an alternative stable state.

Ecosystem simulations discriminated the drivers of change (i.e., continued fishing, increased algal production and coral mortalities) for the Santiago Island reefs from the 1990s to 2000s. The change in reef fish and invertebrate functional groups from the mid-1990s to mid-2000s can be explained by the synergistic effects of reduced fishing and increased algal productivity, driven by increased nutrient inputs to the reef. Reconstruction of forcing factors also highlighted the dominant role of declining water quality or increasing algal productivity on the observed changes in the Santiago Island reef slope over the last decade. Thus, management of coral reef resources around Santiago Island requires more than just fishery interventions. Improving water quality or reducing anthropogenic nutrient inputs into the reefs and adjacent waters should also be targeted in order to reverse the current state of the reefs and provide a stimulus for moving towards a more favourable alternative stable state (i.e., coral-dominated reefs).

Coral community structure in Bolinao

Bolinao reefs have been surveyed as early as 1978 and were found to have high coral cover, even reaching more than 50% in some areas (UPMSC 1980). It is among the priority marine conservation areas in the country (Ong et al. 2002) and reef fishes account for 55% of fisheries catch and provide employment to 31% of the population (McManus et al. 1992). However, Bolinao has long been considered to be overfished (del Norte et al. 1989, McManus et al. 1992, McManus 1997a, Hilomen et al. 2000, UNEP 2004; Nanola et al. 2003). It has also been under a lot of stress from destructive fishing practices (Meñez et al. 1991, McManus et al. 1992, McManus 1997, Nañola 2002, UNEP 2004), mariculture activities (Verceles et al. 2000, McGlone et al. 2008), coral bleaching (Yap et al. 1992, Arceo et al. 2001) and crown-of-thorns-starfish infestation (pers. obs.). Despite these, basic information on reef locations, coral species composition, lifeform composition and other simple reef descriptors have not been studied in detail three decades after it was first surveyed and found to have among the highest coral cover in the country.

2. Reef dynamics and management actions at regional scales

The coral community structure of the Bolinao Reef System was studied (Vergara 2009) by conducting a total of 93 phototransects (Vergara and Licuanan 2007) in 44 sites. Results showed that reefs on the western side of the Bolinao mainland are deep steep slopes (up to 24m) while those found on the eastern side and around Santiago Island are gently sloping and shallow (3-15m). The average hard coral cover of Bolinao Reefs is 22% while algal assemblage occupied 62% of its reef. Cluster analysis in Primer© revealed six distinct groupings. Most of the sites (86%) aggregated due to the dominance of *Heliopora coerulea*. In contrast, the other five groups were composed of only 1-2 sites and were due to dominance of single species/species groups.

Heliopora cover averaged 8% and was present in all but one site and comprised up to 98% of the corals encountered in one of the sites (Arnedo). Overall, *Heliopora* contributed 39% of all corals encountered in Bolinao. Although only a single species of *Heliopora* is recognized, *H. coerulea* has varied lifeforms (columnar, plate-like, arborescent, encrusting and a combination of forms (Figure 9).



Figure 9. The many growth forms of *Heliopora coerulea* in Bolinao reefs; columnar (top left panel), laminar (top right panel), encrusting to columnar (lower right panel), arborescent (bottom left panel). The forms found at the top panels are more common than the forms found at the lower panels.

The abundance of *Heliopora* in some sites in Bolinao has previously been associated by Licuanan and Gomez (1988) to freshwater tolerance. High concentrations of *H. coerulea* were observed in the reefs east of Malilnep Channel, Arnedo and Balingasay. A study by Siringan et al. 2009 confirmed submarine groundwater discharge (SGD) activity in the Malilnep area while the Balingasay sites were near fronting the mouth of Balingasay River. SGD activity at the Arnedo sites have yet to be confirmed but personal communication with Dr. FP Siringan suggests the possibility of SGD activity in the area due to the presence of a fault. A study by Villanueva (2009) revealed that *Heliopora* juveniles survived experimental exposure to salinity of down to 22 ppt. In addition to surviving warm water episodes (Zann and Bolton 1985) and its ability to resist *Drupella* and COTS predation (Villanueva 2009, pers. obs.), its high tolerance to low salinity may afford Bolinao reefs some resistance to future stresses such as coral bleaching, predator infestation, and increased rainfall.

Larval dispersal and connectivity

Life history traits of larvae (i.e., mortality, pelagic larval duration, competency period, habitat preference), and hydrodynamic conditions emerge as important factors that strongly influence recruitment and population subsidies in the marine ecosystem (Ellien et al., 2004; Cowen et al., 2006). The post-processing settlement tool called MarLaST or the Marine Larvae Settlement Tool (Ticzon et al., unpublished), integrate the critical life history traits of larvae, with oceanographic regimes, and spatial configuration of preferred habitats, to arrive at a much improved larval settlement patterns in BARC. In addition, the post processing tool was also used to elucidate source-sink potential of selected Marine Protected Areas in BARC.

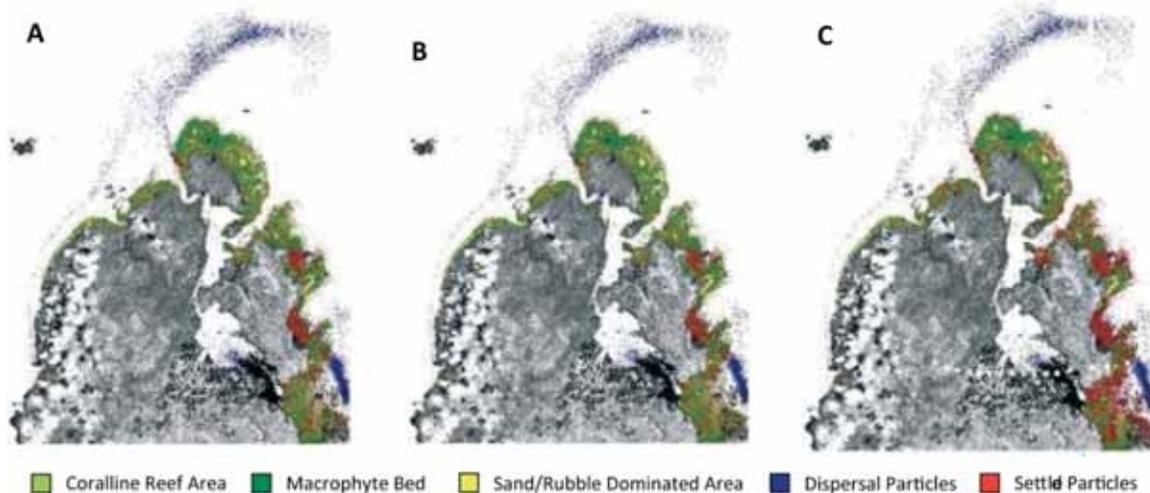


Figure 10. Generated model scenarios with: (A) no mortality, no settlement condition; (B) with mortality, no settlement condition; and, (C) with mortality and settlement condition. Estimate of particles settled on the different reef habitats is shown in the summary table. Marked with light blue arrows are entrainment areas shown only in Model C (MarLaST).

Model scenarios generated for passive larvae with relatively short pelagic larval duration showed; (a) high larval settlement in BARC, and (b) different entrainment patterns operating in the established MPAs of the reef complex. Larval settlement was high in the vicinity of Lucero, Cabungan-Marcos-Cory, Caniogan-Panacalan, Balingasay-Arnado, Trinchera, Dewey, Carot, and Cangaluyan (Figure 10). Different source-sink potentials of these MPAs were also elucidated using MarLaST. Predicted juvenile settled was highest in Panacalan and lowest in Magsaysay and Carot. Other MPA's noted to have high settlement potential were Caniogan and Balingasay. The model also showed both larval import and self recruitment operating in the reef complex (Figure 11). These connectivity patterns contribute to the resilience of reef populations (Jones et al., 2009), and could be the primary factor preventing the total collapse of fishery in BARC.

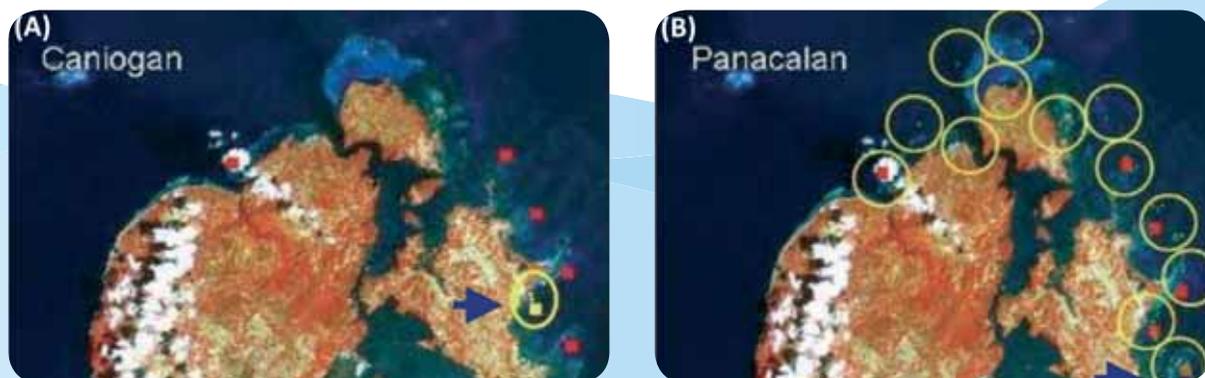


Figure 11. Larval entrainment patterns in selected MPAs in BARC showing high self entrainment (A; in Caniogan MPA), and high larval sink potential (B; in Panacalan MPA). Marked with blue arrows are the evaluated MPAs.

III. Management interventions

Because of the dwindling coral reef resources of BARC brought about by localized anthropogenic stresses occurring in a backdrop of global scale changes (e.g., sea surface temperature elevation), steps are deemed necessary to help curb, or at the very least slow down, reef degradation. An information campaign to enhance awareness of locals, initially targeting primary school students, around the BARC on environmental conservation focusing on coral reefs has been initiated by GEF-CRTR. The local governments around the BARC have played a significant role in the preventive management of reef degradation through effectively enforced laws banning blast fishing and trawling near the reefs in the early 1990s. They also set up Marine Protected Areas (MPAs) off the shores of several coastal villages whose management was given to the local people's organizations, with the help of village officials. Although comprising only 3% of the total area of the BARC, these MPAs were a welcome move to, at the very least, carry out active conservation. Furthermore, after several fish kill events, the local governments imposed reduction in the number of mariculture pens and floating cages in the area. It is noteworthy that the recent intensification of fish farming in the area promoted eutrophication and degradation of water quality which, aside from causing fish kills (San Diego-McGlone et al. 2008), damages the coral reef receiving the fish farm effluent (Villanueva et al. 2006).

In areas where reef recovery is either too slow or absent, active reef restoration is needed to help kick start natural recovery processes. More than a decade after the 1998 bleaching event, it was observed that several bommies of *Porites cylindrica* in the lagoonal area north of Santiago Island remained without live coral cover (Box 2). With this in mind, several experiments are being carried out at the BARC to study:

- reef complex-wide coral reproduction and recruitment patterns
- efficacy and cost-effectiveness of restoration interventions
- applicability of the methods given the local environmental and socio-economic conditions
- consequent collateral damage to donor reefs when carrying out restoration activities
- potential sustainability of the effort at larger spatial and longer temporal scales

Coral reproduction and recruitment

Spawning for many coral species in the BARC occurred in the months of March to June (Vicentuan et al. 2008). Data from several years of monitoring using actual field observations (Vicentuan et al. 2008), periodic histological analyses of coral tissues (Vicentuan 2009, Lampayan et al. 2009), and hatchery observations (Villanueva et al. 2008) showed that different species produced sexual propagules at annual, semi-annual and monthly frequencies. Recruitment, on the other hand, showed a peak around the time of the annual spawning (Feb-May), congruent with the peak of multi-species spawning of broadcasters at the study sites. The results indicate that larvae are either sourced from other reef areas (e.g., Balingasay, Malilnep and Cory Sand Bar) or from the adult population of the same reef area (e.g., Caniogan) (Baria 2009). This finding was corroborated by larval dispersal simulations for the BARC (Ticzon et al. 2009).

Box 2. Bringing the bommies back to life.

The lagoonal area north of Binabalian Labas on Santiago Island in Bolinao is dotted with dead bommies of the branching coral *Porites cylindrica*. These once thriving mounds were badly affected by the 1998 bleaching event and have not, since then, regained their live coral cover. Preliminary surveys of these bommies showed that there were only few and small coral colonies, including *P. cylindrica*, growing on them, indicating that the larval supply necessary for natural recovery was very limited.

In an effort to kick start recovery and test some aspects of direct transplantation, 3-4 cm fragments of *P. cylindrica* were collected from a nearby donor reef and attached to the bare reef substrate using an epoxy adhesive. The experiment yielded a high survival rate of transplants after 3 years and inspired an attempt to teach a stripped down version of the method to local stakeholders – fisherfolk and volunteer MPA managers. Without using adhesives and scuba gear, volunteers were able to transplant over 1,800 fragments of *P. cylindrica* in 144 m² of degraded reef in 2008. Survival of transplants after over a year of transplantation is around 60%, an appreciably good proportion considering the low technology that was employed.

A flyer of the community-based coral restoration activity is available at www.gefcoral.org

- Rommi M. Dizon (SEA CoE)

Reef restoration

At various degraded areas of the BARC, a number of coral reef restoration techniques were tested to assess the relative success of each effort. One of the most common methods explored was the direct transplantation of coral fragments. Various adhesives (Dizon et al. 2008) and substrates (Guest et al. 2009, Vicentuan 2009, Cabaitan et al. in prep.) for coral transplantation were tested. The feasibility of employing the two-step technique of rearing coral fragments at in situ nursery prior to transplantation was also assessed (Shaish et al. 2008, dela Cruz et al. 2009, dela Cruz 2010). The addition of nursery phase had its advantages over direct transplantation, namely: (1) it afforded transplant materials of bigger sizes and (2) it allowed the production of more propagules (i.e., thousands versus hundreds). However, the higher robustness of the nursery-reared fragments than freshly sourced fragments has yet to be proven experimentally when these are transplanted back to the natural reef. Studies on the effects of fragmentation donor and transplant corals were also undertaken. Although there were no observed negative effects on the growth and survival of both donor and transplant colonies on the species tested (i.e., *Acropora muricata* and *Hydnophora rigida*), a negative effect on the reproductive status of the former was detected. This finding reveals that fragmentation may affect coral colonies negatively although this does not hold true for all coral species. Stocking of the cultured gastropod herbivore, *Trochus niloticus* on artificial substrates (reef balls) at the heavily fished reef in Malilnep channel did not enhance algal grazing or assist recruitment of corals (Villanueva et al. 2009). Furthermore, the reef balls experienced coral recruitment at rates similar to those of natural reef substrates in the short-term (i.e., over 2 yr), though the initial recruit composition varied between the two substrates (Bollozos et al. 2009). An attempt to stabilize the unconsolidated reef substrate to allow natural coral recruits to grow into reproductive colonies was also carried out. However, the natural fiber mesh (coconut fiber net) that was used to stabilize the substrate disintegrated sooner than expected thus the few monitoring data obtained could not show anything conclusive.

Sustainable sources of restoration materials

As large-scale restoration of live coral cover is not feasible using the traditional sources of coral material (i.e., fragments broken from donor colonies), alternative sources are needed and should be able to sustainably supply the material. One source would be 'corals of opportunity', naturally broken coral fragments lying on the reef floor and are at risk of sediment burial. These fragments are gleaned from source reefs, cut into desired sizes and are either directly transplanted on the reef or kept in coral nurseries until they reach a size when they can be fragmented further to yield coral branches for transplantation. Similar sustainable sources of transplant material are coral transplants that have grown sufficiently after direct transplantation. These are further broken to produce more fragments for transplantation. A third sustainable source of transplant material that has been explored is the use of sexually produced coral propagules. Adult coral colonies are brought to the laboratory and made to spawn. The gametes are collected, fertilized and the resulting larvae are made to settle and grow on wall plugs with concrete heads. After several months of nursery rearing, the juvenile corals are then transplanted on the degraded reef where they could grow into reproductive colonies (Baria et al. 2009). The advantage of using sexually produced corals is that more propagules of different genotypes are made available. Some of these genotypes might be better at tolerating certain environmental conditions than others, thus, avoiding local species extinctions and potentially enhancing reef resilience. A facility for coral larval spawning and rearing is currently being set up at the Bolinao Marine Laboratory to help explore this alternative sustainable source more intensively.

Long-term permanent monitoring sites

Despite the hundreds of transects that have already been surveyed in the Bolinao-Anda Reef Complex since 1978 (McManus and Chua 1990, McManus et al. 1992, FRMP 2002, Deocadez et al. 2003), there has been no long-term monitoring program to properly assess the extent of changes at different spatio-temporal scales in the reefs.

A total of 12 stations, comprised of 60 random transects and 36 permanent quadrats spread in the BARC area have been established as part of the Common Sampling protocol conducted in all GEF/WB CRTR Centers of Excellence. A phototranssect method was developed to facilitate fast, simple, and cost-efficient monitoring of large areas (Box 3). The establishment of permanent monitoring sites in the Bolinao-Anda Reef Complex is fairly recent and only a total of three samplings have been collected so far since 2008. While data analysis is still ongoing, partial results from the Malilnep site in Bolinao show a 5.6% decrease

in coral cover from 18.7% in 2008 (Vergara 2009). This decrease may have been a response to several stresses that the reefs have experienced such as COTS predation, mild bleaching, strong typhoons and destructive fishing practices.

Box 3. Cheap, fast and simple alternative to monitor changes in coral communities

An effective monitoring program is essential to provide data for making effective management decisions. Since monitoring programs are expensive, selection of an appropriate monitoring method is therefore of vital importance. The phototranssect method (Vergara and Licuanan 2007) has been promoted as a cheap, fast and simple alternative method to monitor coral communities. The method involves taking photographs of the substrate at regular intervals along the transect using a digital camera attached to an aluminium distance bar. The high-resolution, scaled and color correct images also allows for improved taxonomic identification using point sampling (Osborne and Oxley 1997) and colony measurements. The method has been utilized in the country since 2005 and has been continuously improved. In addition, power analysis (Vergara 2009) revealed that a minimum of 4 random transects per site, 50 frames per transect and 10 sampling points per frame are needed to achieve 90% statistical power to detect a 10% absolute change in coral cover in the communities being monitored in Bolinao. Since the method is very simple, it has empowered non-technical stakeholders in conducting their own coral reef monitoring.

– Mark Vergara (SEA CoE)

Reducing fishing pressure (MPAs and alternative livelihoods)

With a density of 46 fishers per kilometer of coastline in Bolinao and Anda, the area is considered as heavily exploited compared to other towns in the country (White and Cruz-Trinidad 1998). Previous studies of the fishery of Bolinao clearly indicate that it is at various states of overfishing including Malthusian overfishing (Calud et al. 1989; McManus 1997). This is recently corroborated by simulations using a system dynamic model called Fisheries Information for Sustainable Harvests – BioEconomic model (FISH-BE; see Box 4).

Although marine protected areas are critical interventions for conservation, high extraction rate of resources from the BARC requires active fishing pressure regulation in conjunction with larger and effectively-enforced MPAs to abate the rapid degradation of resources. Previous coastal resource management and development projects within the BARC have often focused on expanding supplemental or alternative livelihood options. In addition, the rapid growth of mariculture provided a potential opportunity for reducing fishing pressure by absorbing fishers as caretakers of fish cages and pens. Unfortunately, socioeconomic household surveys and focused group discussions conducted around the BARC revealed limited entry of fishers into the mariculture sector (Cruz-Trinidad et al. 2009).

Box 4. Estimating fishery carrying capacities for Bolinao and Anda

Overfishing has remained as one of the top stressors affecting the Bolinao-Anda reef complex since the early 1970s. In 2005, the Sagip Lingayen Gulf Project estimated a total of 6,741 fishers from both municipalities. Recent surveys around the BARC indicate a mean total reef fish biomass of approximately 5mt/km² in fished areas. A question always asked by local government officials is “how much fishing can their municipal waters support without causing the fishery to collapse?”

A system-dynamic modelling tool called Fisheries Information for Sustainable Harvests – BioEconomic Model or FISH-BE (Licuanan et al. 2006) was applied to the towns surrounding the BARC to estimate municipal fishery carrying capacities. Simulations reveal that given the current state of the resource, relying on Marine Protected Areas alone for sustaining fish catches at current fishing pressure for the next 20 years would require closing 81% and 52% of municipal waters in Bolinao and Anda, respectively. At current catch rates, the municipal waters of Bolinao and Anda can only support ~800 (19%) and ~1,200 (47%) of the current fisher population in each town, respectively, to ensure that fishers meet minimum household daily living requirements in the next 20 years. This highlights the urgent need for active management of fishing pressure especially on the BARC and full implementation of other fishery management interventions.

– Rollan C. Geronimo (MDSWG)

IV. Research gaps and management recommendations

Although the Bolinao-Anda Reef Complex (BARC) is among the largest in the country, it is also among the most damaged and stressed. The Bolinao Marine Laboratory has provided critical scientific information to support decisions regarding management of the BARC. But more research are still needed to address fundamental questions as to how to conserve the BARC's remaining diversity and resources and restore the once thriving coral communities and associated fisheries back to life in the area. As an example, although the coral reefs of Bolinao have been surveyed as early as 1976 (UPMSC 1980) and the BML established there in 1983, the coral community structure of Bolinao reefs has only been studied very recently (Vergara 2009). Continuation of some important project-based initiatives (e.g., resource and ecological monitoring) has also been lacking.

Assisting the recovery of the BARC from recent successive natural disturbances require additional information and synthesis of these information to support management decisions. Some of the identified information needs are:

1. Studies on submarine groundwater discharge should be expanded for the whole BARC region.
2. Molecular analysis of the different morphologies of the monospecific coral *Heliopora coerulea* should be done to determine if they are indeed only a single species. Differences in the timing of release of larvae between two morphs have already been documented (Villanueva 2009).
3. A complementary study on the coral community structure of the Anda reefs is needed for directed management measures. While Bolinao reefs are dominated by the blue coral, *Heliopora coerulea*, Anda reefs do seem to be dominated by *Acropora* species.
4. The long-term monitoring of BARC should be institutionalized or have in-house funding so that continuity of monitoring beyond the project lifespan can be addressed and data collection not halted.
5. Long term study on coral recruitment is also recommended to assess inter-annual consistencies and variation.
6. Post-settlement studies are also necessary to further understand the processes that greatly influence juvenile and adult distribution of corals in the BARC area.
7. Studies to validate dispersal scenarios of BARC should also be conducted initially for corals, and other invertebrates with passive larvae.
8. Integrating results of long term coral recruitment monitoring with different model dispersal scenarios would elucidate recruitment patterns operating in the reef complex. This information is crucial in formulating management strategies, and setting-up priority areas for protection.
9. Continue evaluating coral restoration methods in terms of efficiency, cost and appropriate species.
10. Future work should also focus on determining how long different coral species should remain in the nurseries to reach an "escape size" in order to achieve full growth and survival potential after transplantation.
11. Continue studies to confirm the self-recruitment of BARC populations, especially commercial species such as *Siganus fuscus*.
12. A compilation CD of all studies done in the area should be prepared so that literature reviews can be made accessible and recommendations for future studies can be easily addressed.

References

- Ahmed, M, Umali, GM, Chong, CK, Rull, MF, Garcia, MC. 2007. Valuing recreational and conservation benefits of coral reefs - The case of Bolinao, Philippines. *Ocean and Coastal Management*. 50(1-2):103-118.
- Arceo, HO, Quibilan, MC, Aliño, PM, Lim, G, Licuanan, WY. 2001. Coral bleaching in Philippine reefs: coincident evidences with mesoscale thermal anomalies. *Bulletin of Marine Science* 69:579-593.
- Baria, MV. 2009. Coral recruitment and larval rearing for reef restoration. M.Sc. thesis, University of the Philippines – Marine Science Institute.
- Baria MV, Guest JR, Edwards AJ, Gomez ED, Heyward AJ. 2009. Survivorship of reared juveniles of the corals *Acropora millepora* and *A. hyacinthus* during nursery rearing and outplanting to degraded coral outcrops. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- BFAR. 1985. Fisheries statistics of the Philippines. Bureau of Fisheries and Aquatic Resources, Manila.
- Bollozos, IS, Villanueva, RD, Edwards, AJ. 2009. Recruitment of corals on artificial substrates and adjacent reef at Bolinao, northwestern Philippines. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- Calud, A, Rodriguez, G, Aruelo, R, Aguilar, G, Cinco, E, Armada, N, Silvestre, G. 1989. Preliminary results of a study on the municipal fisheries in Lingayen Gulf. In: Silvestre, G, Miclat, E, Chua, T-E (eds) Towards sustainable development of the coastal resources of Lingayen Gulf, Philippines ICLARM Conference Proceedings 17. Philippine Council for Aquatic and Marine Research and Development, Los Baños, Laguna, and International Center for Living Aquatic Resources Management, Makati, Metro Manila, Philippines, pp200.
- Calvelo, RR, Ginon, JS. 1974. Siganid fishery of Northwestern Pangasinan. *Philippine Journal of Fisheries* 12:114-130.
- Christensen, V, Walters, CJ, Pauly, D. 2005. *Ecopath with Ecosim: a user's guide*. Fisheries Centre, University of British Columbia, Vancouver.
- Cowen, RK, Paris, CB, Srinivisan, A. 2006. Scaling of connectivity in marine populations. *Science* 311:522-527.
- Cruz-Trinidad, A, Geronimo, RC, Aliño, PM. 2009. Development trajectories and impacts on coral reef use in Lingayen Gulf, Philippines. *Ocean and Coastal Management* 52:173-180
- dela Cruz, DW. 2010. Comparison of coral gardening and direct transplantation methods in restoring the corals of Bolinao, Pangasinan, northwestern Philippines. M.Sc. thesis, University of the Philippines – Marine Science Institute.
- dela Cruz, DW, Gomez, ED, Rinkevich, B, Yap, HT. 2009. Growth and attachment of directly transplanted nursery-grown corals in Bolinao, Pangasinan. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- del Norte, AGC, Nañola Jr, CL, McManus, JW, Reyes Jr, RB, Campos, WL, Cabansag, JBP. 1989. Overfishing on a Philippine reef: a glimpse into the future. In: Magoon, OT, Converse, H, Miller, D, Tobin, LT, Clark, D (eds) *Coastal Zone '89 Proceedings of the Sixth Symposium on Coastal and Ocean Management*. Association of American Engineers, New York.
- Dizon, RM, Edwards, AJ, Gomez, ED. 2008. Comparison of three types of adhesives in attaching coral transplants to clam shell substrates. *Aquatic Conservation: Marine & Freshwater Ecosystems* 18: 1140-1148.
- Ellien, C., Thiebaut, E., Dumas, F., Salomon, J. C., and P. Nival. 2004. A modeling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida : Polychaeta) in the Bay of Seine (English Channel). *Journal of Plankton Research* 26(2):117-132.
- Geronimo, RC. 2009. Trophic dynamics of the Santiago Island reef slope (Pangasinan, Philippines). M.Sc. thesis, University of the Philippines – Marine Science Institute.
- Geronimo, RC, Salmo III, S, Deocadez, MR, Castrence Jr., F, Pacifico, K, Junsan, C, Sagip Lingayen Gulf Project and Partners. 2008. Status of Coral Reefs in Lingayen Gulf. In: Mamaug, SS, Gonzales, ROM (eds) *Philippine coral reefs through time 2008: Initiating the state of the coasts reports*. Coral Reef Information Network of the Philippines (PhilReefs), MPA Support Network, Marine Environment & Resources Foundation, Inc. and the Marine Science Institute, Quezon City, Philippines, pp152.
- Guest, JR, Dizon, RM, Edwards, AJ, Franco, C, Gomez, ED. 2009. How quickly do fragments of coral 'self-attach' after transplantation? *Restoration Ecology* doi: 10.1111/j.1526-100X.2009.00562.x.
- Hijmans RJ, van Etten J (2009). Raster: Raster data handling for geographic data analysis and modeling. R package version 0.8.9-21/r464. <http://R-Forge.R-project.org/projects/raster/>
- Hilomen, VV, Nañola, CL, Dantis, AL. 2000. Status of Philippine reef fish communities. Paper presented in the Workshop on the Status of the Philippine Reefs, January 24, 2000, Marine Science Institute, University of the Philippines, Diliman, Quezon City.
- <http://glovis.usgs.gov/>
- Jones, GP, Almany, GR, Russ, GR, Sale, PF, Steneck, RS, Van Oppen, MJH, Willis, BL. 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307-325.
- Juinio-Meñez, MA, Bangi, HG, Malay, MC, Pastor, D. 2008. Enhancing the recovery of depleted *Tripterygion* stocks through grow-out culture and restocking. *Reviews in Fisheries Science* 16:35-43
- Lampayan, R, Vicentuan-Cabaitan, K, Guest, J, Gomez, E. 2009. Sexual reproduction of the reef-building coral *Porites cylindrica* Dana (Scleractinia: Poritidae) in northwestern Philippines. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- Licuanan, WY, Aliño, PM, Campos, WL, Castillo, GB, Juinio-Meñez, MA. 2006. A decision support model for determining sizes of Marine Protected Areas: biophysical considerations. *The Philippine Agricultural Scientist* 89(1):507-20.
- Licuanan, WY, Gomez, ED. 1988. Coral reefs of the Northwestern Philippines: A physiognomic-structural approach. *Proceedings of the Sixth International Coral Reef Symposium, Townsville*. 3:275-280.
- McManus, JW. 1997. Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. *Coral Reefs* 16:S121-S127.
- McManus, JW, Nañola Jr, CL, Reyes Jr, RB, Kesner, KN. 1992. Resource ecology of the Bolinao coral reef system. *ICLARM Stud Rev* 22.
- McManus, JW, Reyes, RB, Jr., Nañola Jr., CL. 1997. Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environmental Management* 21:69-78.
- Nañola, CL Jr. 2002. Bolinao. pp. 31-34. In: Aliño, PM, Miclat, EFB, Nañola Jr, CL, Roa-Quiaoit, HA, Campos, RT (Eds). 2002. *Atlas of Philippine Coral Reefs*. Philippine Coral Reef Information (PhilReefs). Goodwill Trading Co., Inc., Quezon City, Philippines. xvi + 264 pp.
- Ong, PS, Afuang, LE, Rosell-Ambal, RG (eds.). 2002. *Philippine Biodiversity Conservation Priorities: A Second Iteration of the National Biodiversity Strategy and Action Plan*. Department of Environment and Natural Resources-Protected Areas and Wildlife Bureau, Conservation International Philippines, Biodiversity Conservation Program-University of the Philippines Center for Integrative and Development Studies, and Foundation for the Philippine Environment, Quezon City, Philippines.

2. Reef dynamics and management actions at regional scales

- Osborne, K, Oxley, WG. 1997. Sampling benthic communities using video transects. In: English, S, Wilkinson, C, Baker, V (eds.). Survey manual for tropical marine science, 2nd ed., Australian Institute of Marine Science, Townsville.
- Quan, N. 2002. The influence of habitat complexity and monsoon on reef fish communities at Cape Bolinao, Lingayen Gulf. M.Sc. thesis, University of the Philippines – Marine Science Institute.
- San Diego-McGlone, ML, Azanza, RV, Villanoy, CL, Jacinto, GS. 2008. Eutrophic waters, algal bloom and fish kill in fish farming areas in Bolinao, Pangasinan, Philippines. *Marine Pollution Bulletin* 57: 295-301.
- Shaish, L, Levy, G, Gomez, ED, Rinkevich, B. 2008. Fixed and suspended coral nurseries in the Philippines: establishing the first step in the “gardening concept” of reef restoration. *Journal of Experimental Marine Biology and Ecology* 358: 86-97.
- Siringan, FP, Zamora, PB, Cardenas, MBR, Jacinto, GS, San Diego-McGlone, ML, Villanoy, CI, Cabrera, O, Senal, MI. 2009. Submarine groundwater discharge at the reef flat of Santiago Island, Bolinao, Philippines Paper presented at the 10th National Symposium in the Marine Science. 22-24 October 2009. Eden Nature Park, Davao City, Philippines.
- Ticzon, VS, David, LT, Borja, R, Pacheco, A, Mumby, P. 2009. Factoring habitat and mortality in juvenile settlement patterns. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- Ticzon, VS, David, LT, Pacheco, AC, Borja, RT, Mumby, PJ. 2009. Marine Larvae Settlement Tool (MarLaST): A Post-Processing Tool for Connectivity Studies. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- UNEP. 2004. Coral Reefs in the South China Sea. UNEP/GEF/SCS Technical Publication No. 2.
- UPMSC. 1980. Investigation of the coral resources of the Philippines (Phase II final report). University of the Philippines Marine Sciences Center, Quezon City, Philippines.
- Uychiaoco, AJ, Castrence Jr., FI, Aliño, PM. 2003. Bolinao, Pangasinan: A decade of Bolinao reef fish and fisheries: Part I. Fisheries. In: Coral Reef Information Network of the Philippines (PhilReefs) (ed) Philippine Coral Reefs through time: Workshop Proceedings Second of the Atlas of Philippine Coral Reefs Series Coral Reef Information Network (PhilReefs), University of the Philippines Marine Science Institute, Quezon City, Philippines and the Marine Parks Center, Tokyo, Japan.
- Verceles, LF, Talaue-McManus, L, Aliño, PM. 2000. Participatory monitoring and feedback system: an important entry towards sustainable aquaculture in Bolinao, Northern Philippines. *Science Diliman* 12:78-87
- Vergara, MWB. 2009. Coral community structure of the Bolinao Reef System, northwest Philippines. M.Sc. thesis, University of the Philippines – Marine Science Institute.
- Vergara, MWB, Licuanan, WY. 2007. Survey of Coral Communities Using Digital Photography. Paper presented at the 9th National Symposium in Marine Science. Oct 19-22, 2007. Iloilo City, Philippines.
- Vicentuan, KC. 2009. The effects of fragmentation and transplantation on reproduction in *Acropora muricata* and *Hydnophora rigida*. M.Sc. thesis, University of the Philippines – Marine Science Institute.
- Vicentuan, KC, Guest, JR, Baria, MV, Cabaitan, PC, Dizon, RM, Villanueva, RD, Aliño, PM, Edwards, AJ, Gomez, ED, Heyward, AJ. 2008. Multi-species spawning of corals in north-western Philippines. *Coral Reefs* 27: 83.
- Villanueva, RD. 2009. Notes on the biology and ecology of the blue coral, *Heliopora coerulea*, in Bolinao, northwestern Philippines. Paper presented at the 10th National Symposium in the Marine Science. 22-24 October 2009. Eden Nature Park, Davao City, Philippines.
- Villanueva, RD, Edwards, AJ, Bell, JD. 2009. Addition of macroinvertebrate grazer (*Trochus niloticus*) does not enhance coral recruitment on artificial substrate. Paper presented at the 10th National Symposium in Marine Science. Oct 22-24, 2009. Davao, Philippines.
- Villanueva, RD, Yap, HT, Montaño, MNE. 2008. Timing of planulation by pocilloporid corals in the northwestern Philippines. *Marine Ecology Progress Series* 370:111-119.
- Villanueva, RD, Yap, HT, Montaño, MNE. 2006. Intensive fish farming in the Philippines is detrimental to the reef-building coral *Pocillopora damicornis*. *Marine Ecology Progress Series* 316: 165-174.
- Wesseling, I, Uychiaoco, AJ, Aliño, PM, Vermaat, JE. 2001. Partial mortality in *Porites* corals: variation among Philippine reefs. *International Review of Hydrobiologists* 86:77-85.
- White, AT, Cruz-Trinidad, A. 1998. The Values of Philippine Coastal Resources: why protection and management are critical. Coastal Resource Management Project, Cebu City, Philippines
- Yap, HT, Aliño, PM, Gomez, ED. 1992. Trends in growth and mortality of three coral species (Anthozoa: Scleractinia), including effects of transplantation. *Marine Ecology Progress Series*. 83:91-101.
- Yap, LG, Azanza, RV, Talaue-McManus, L. 2004. The community composition and production of phytoplankton in fish pens of Cape Bolinao, Pangasinan: a field study. *Marine Pollution Bulletin* 49:819-832.
- Zann, LP, Bolton, L. 1985. The distribution, abundance and ecology of the blue coral *Heliopora coerulea* (Pallas) in the Pacific. *Coral Reefs* 4:125-134.



Deborah Cleland,
CRTR e-News
December 2009

Building community capacity

Three Modeling and Decision Support Working Group (MDSWG) students have recently been getting out into coastal communities in the Philippines to communicate their research to a broad range of stakeholders in a unique and refreshing way.

Last October, Georgina Gurney presented the results of her Honours thesis, which focused on modeling coral reef futures under alternative management and climatic scenarios for Bolinao, Pangasinan, to a group of local government representatives, aquaculture operators, fishers, and resort owners.

Also in Bolinao, Rollan Geronimo facilitated and ran a workshop on 'ReefGame', MDSWG's participatory modeling tool. ReefGame engages fishers in animated discussions and reflections about livelihood and employment options that would meet their daily needs and secure the long-term sustainability of reefs.

Deb Cleland then joined Rollan in Zambales, where they jointly ran a participatory workshop on ReefGame 2.0, which added new roles and dynamics, including resort owners, industry interests and aquaculture operators. Rollan and Deb will continue developing ReefGame for upcoming workshops in Batangas and Mindoro.

ReefGame was also recently showcased in the East Asian Seas Congress in November as part of a complementary project on ecosystem-based management tools funded by the David and Lucille Packard Foundation and entitled: "Finding a way out for depleted subsistence fisheries in the Philippines".



Kareen Vicentuan,
CRTR eNews
December 2009

Lessons in coral culture

Two CRTR students from the Philippines, Kareen Vicentuan and Dexter de la Cruz, attended a three week training course on coral culture earlier in the year in Akajima Marine Science Laboratory (AMSL), Okinawa, Japan.

AMSL, headed by Prof Makoto Omori, has been successful in culturing *Acropora tenuis* for reef restoration. The training gave the students experience on techniques developed at ASML for culturing sexually-propagated corals, looking at larval rearing in-situ and ex-situ. This training enabled the students to identify the differences in the culture techniques currently being used in the Bolinao Marine Laboratory (BML) and at ASML, which are useful in the refinement of larval rearing efforts.

Both students gained firsthand experience in collecting egg bundles from coral slicks and in-situ using bundle collectors, something that has not yet been tried at BML. Rearing corals is a great challenge but it is feasible as shown by both laboratories, providing hope for reef restoration.

Jess Melbourne-Thomas

A decision support tool for managing coral reefs
at regional scales



Jess has a background in ecology and has been involved with research relating to a range of marine systems, from temperate to tropical reefs, and from local to regional scales. She's a born and bred Tasmanian, with Bachelor of Science from the University of Tasmania, and Honours in Marine Ecology. She was a Rhodes Scholar at the University of Oxford from 2003 – 2005 and is currently in the third year of her PhD under the UTAS/CSIRO Quantitative Marine Science program. Jess's main research interests relate to ecosystem modeling, spatial ecology and approaches to understanding and predicting coupled biophysical-socioeconomic dynamics.



A decision support tool for managing coral reefs at regional scales

Jess Melbourne-Thomas

University of Tasmania, Australia

The problem: multiple threats and complex feedbacks

Coral reef ecosystem function is under severe threat from a broad range of stressors, and the call for improved approaches to managing these ecosystems has been resounding (e.g. Folke et al. 2004; Mumby and Steneck 2008; Sale 2008; Tupper et al. 2008). Threats to coral reefs act at local, regional and global scales, and debate continues about the relative importance of impacts, particularly in relation to coral-algal phase shifts (Szmant 2002; McManus and Polsenberg 2004; Heck and Valentine 2007). However, there is little doubt that cumulative, synergistic stressors and disturbances pose a significant threat to reef health (Thacker et al. 2001; McClanahan et al. 2002; Burkepile and Hay 2006).

Given the numerous threats to coral reef health, there is a pressing need for tools to help prioritise management actions and guide investment decisions. Such tools must of course be grounded in sound science. However coral reefs are complex systems with multiple components and processes acting at different scales in space and time and their dynamics are inherently difficult to understand and predict (Hatcher 1997; Hughes et al. 2005; Dizon and Yap 2006). Further to this, many authors have recognised that to achieve proper understanding of coral reef dynamics, and to facilitate effective management, we must recognise the interactions between biophysical and socioeconomic components of reef systems (Clua et al. 2005; Hughes et al. 2005; Pelletier et al. 2005; Mumby and Steneck 2008; Bradbury and Seymour 2009; Cinner et al. 2009). Since both ecological and socioeconomic systems are complex systems, interactions between the two are also necessarily complex, and are characterised by resilience, thresholds and feedbacks (Liu et al. 2007).

Tools to evaluate potential solutions

Models provide a useful means for dealing with complexity in ecological and socioeconomic systems and are becoming integral tools for informing decision-making in coral reef management. Two key challenges in developing models of complex coral reef systems are: (i) the multi-scale nature of processes that affect reef systems; and (ii) a lack of information about the interactions between biophysical and socioeconomic components. There is a dearth of multi-scale approaches amongst existing coral reef models (McCook et al. 2001; Langmead and Sheppard 2004; Mumby 2006; Mumby et al. 2006), and limited attempts to couple biophysical and socioeconomic dynamics for coral reef systems (Gray et al. 2006; Shafer 2007). In developing model systems that couple dynamics across spatial scales, or between biophysical and socioeconomic components, there is a risk of models becoming too complicated. Fulton (2003) emphasises that complicated models can be costly in terms of development and maintenance, and complexity introduced for the sake of completeness accomplishes nothing if the resulting model is actually of poor quality.

Desirable characteristics of models for decision support include: (i) robust, testable frameworks; (ii) understandable inputs and components; (iii) portability (so that models don't have to be reformulated for different geographical locations where species assemblages may be different); (iv) accessibility to end-users; and (v) bottom-up architecture so that complex behaviours are not pre-programmed but are emergent. Simulation models are particularly useful in decision support contexts because they facilitate scenario analysis. By envisioning alternative futures, scenario analysis can help decision makers identify management approaches that will be robust across a range of potential future outcomes. Scenario analysis can also be an effective way of engaging stakeholders who might otherwise be unresponsive to conventional methods for presentation of scientific information (Biggs et al. 2007).

Regional-scale modeling for decision support

As part of the modelling effort by the Modelling and Decision Support Working Group (MDSWG) of the CRTR Program we have developed a generic, biophysical model for coral reef systems which couples dynamics from local to regional scales (Figure 1). Interactions between benthic and consumer functional groups at local scales ($10^2 - 10^3$ m) are linked across regional scales ($10^5 - 10^6$ m) by larval dispersal. The approach is bottom-up; simple components are combined to create a portable framework which can be applied for reef systems anywhere in the world. Model components and outputs are understandable for non-experts, but the system is able to generate complex, emergent patterns. Moreover, there is the facility to incorporate larval connectivity data from sophisticated dispersal simulations (e.g. Paris et al. 2007). The model, CORSET (Coral Reef Scenario Evaluation Tool), is equally applicable as a research tool or as a decision support tool for coral reef management.

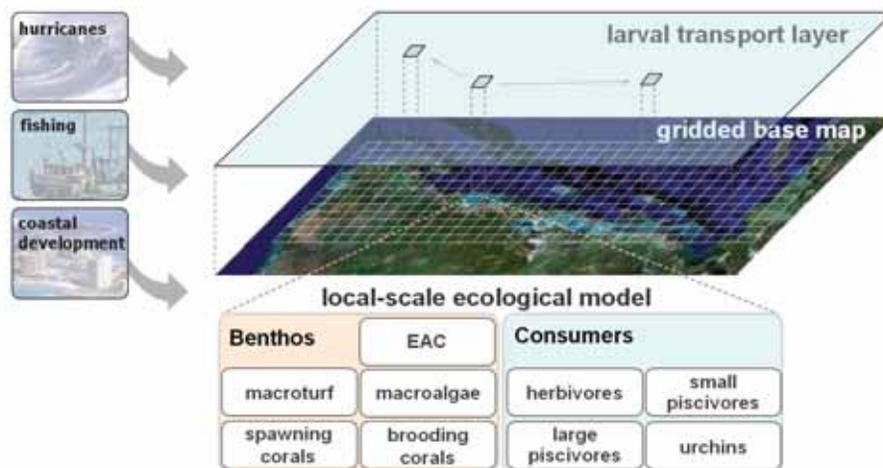


Figure 1. Components of the regional-scale model (CORSET). Nine mean-field equations describing local-scale interactions between functional groups (Fung 2009) are instantiated in each reef cell of a gridded base map for the region of interest. Reef cells are connected through larval transport. Fishing, pollution and disturbance are modelled as external forcings. EAC stands for epilithic algal communities.

CORSET has been instantiated for the Mesoamerican Reef (MAR) system and the Philippines region of the South China Sea. Calibration and validation of the MAR instantiation of CORSET indicate that: (i) the model is long-term stable; (ii) it can recreate a healthy reef state; and (iii) it responds to external forcings to reproduce trajectories that correspond with observed changes in reef state in the region (Melbourne-Thomas et al. in review-b). The model exhibits emergent dynamics, driven by regional-scale patterns of larval connectivity, that have implications for reef management in the region (Figure 2). Portability of the framework has been demonstrated by instantiating CORSET for the Philippines/South China Sea (PSCS) region (Melbourne-Thomas et al. in review-a). Both the MAR and PSCS versions of CORSET can be used to explore potential reef futures under a range of scenarios; a DVD demonstration product developed by the MDSWG provides a variety of examples of scenario projection for both regions.

2. Reef dynamics and management actions at regional scales

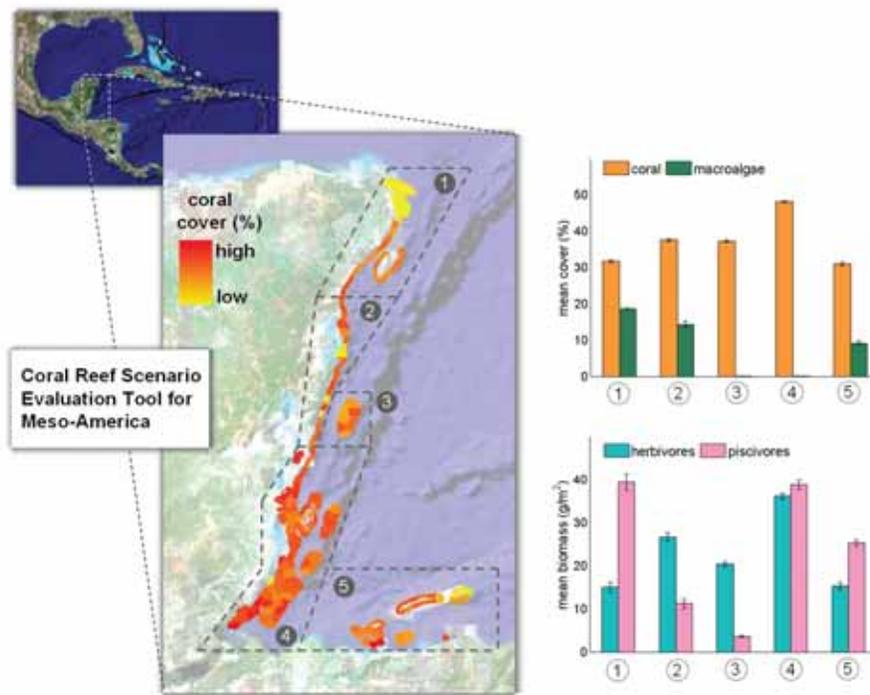


Figure 2. Spatial variation in modelled coral cover, macroalgal cover, herbivore biomass and piscivore biomass for the Mesoamerican Reef system under a 'healthy reef' scenario where there are no external forcings. Circled numbers identify the five model subregions. Variability in modelled community composition between subregions is pronounced and emerges as a result of variability in larval supply. Reefs that have inherently low larval supply are less able to recover from disturbance events.

A modified version of CORSET has been coupled to an agent-based socioeconomic model for the Mexican Caribbean region (Perez et al. 2009). This coupled system is currently being validated. The coupled model represents an important advance in overcoming the technicalities of coupling biophysical and socioeconomic dynamics and will enable the user to explore potential futures for a diverse range of indicators of coral reef state. Regional scale scenario analysis, integrated with existing approaches for vulnerability assessment, marine reserve design and reef state visualization (e.g. Hinkel 2005; Chuenpagdee et al. 2007; Watts et al. 2009), can make an important contribution in addressing challenge of effective management for complex coral reef systems.

Acknowledgements

Thank you to Prof. Craig Johnson (University of Tasmania) and Dr. Beth Fulton (CSIRO) for their contributions to the development of models presented in this article. This research has been supported by a joint UTAS-CSIRO scholarship in Quantitative Marine Science and a CSIRO fellowship in Marine Ecosystem Modelling. Contributions from members of the MDSWG have been invaluable.

References

- Biggs R, Raudsepp-Hearne C, Atkinson-Palombo C, Bohensky E, Boyd E, Cundill G, Fox H, Ingram S, Kok K, Spehar S, Tengo M, Timmer D, Zurek M (2007) Linking futures across scales: a dialog on multiscale scenarios. *Ecology and Society* 12:17
- Bradbury R, Seymour R (2009) Coral reef science and the new commons. *Coral Reefs* DOI: 10.1007/s00338-009-0540-6
- Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87:3128-3139
- Chuenpagdee R, Agbayani E, Atanacio R, Juntarashote K, Kay R, Pierce G, Pita C, Traesupap S, Wang J (2007) Coastal Transects Analysis Model, World Wide Web electronic publication. www.coastaltransects.org version (06/2007)
- Cinner JE, McClanahan TR, Daw TM, Graham NAJ, Maina J, Wilson SK, Hughes TP (2009) Linking social and ecological systems to sustain coral reef fisheries. *Current Biology* 19:206-212
- Clua E, Beliaeff B, Chauvet C, David G, Ferraris J, Kronen M, Kulbicki M, Labrosse P, Letourneur Y, Pelletier D, Thébaud O, Léopold M (2005) Towards multidisciplinary indicator dashboards for coral reef fisheries management. *Aquatic Living Resources* 18:199-213
- Dizon RT, Yap HT (2006) Understanding coral reefs as complex systems: degradation and prospects for recovery. *Scientia Marina* 70:219-226
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581
- Fulton EA, Smith ADM, Johnson CR (2003) Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series* 253:1-16
- Fung TC (2009) Local scale models of coral reef ecosystems for scenario testing and decision support. PhD Thesis in Modeling Biological Complexity, University College London, p346
- Gray R, Fulton E, Little R, Scott R (2006) Ecosystem model specification within an agent based framework. NWSJEMS Technical Report No. 16, CSIRO, Hobart, Tasmania
- Hatcher BG (1997) Coral reef ecosystems: how much greater is the whole than the sum of the parts? *Coral Reefs* 16:S77-S91
- Heck K, Valentine J (2007) The primacy of top-down effects in shallow benthic ecosystems. *Estuaries and Coasts* 30:371-381
- Hinkel J (2005) DIVA: an iterative method for building modular integrated models. *Advances in Geosciences* 4:45-50
- Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends In Ecology & Evolution* 20:380-386
- Langmead O, Sheppard C (2004) Coral reef community dynamics and disturbance: a simulation model. *Ecological Modeling* 175:271-290
- Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenco J, Ostrom E, Ouyang Z, Provencher W, Redman CL, Schneider SH, Taylor WW (2007) Complexity of coupled human and natural systems. *Science* 317:1513-1516
- McClanahan T, Polunin N, Done T (2002) Ecological states and the resilience of coral reefs. *Conservation Ecology* 6:18
- McCook LJ, Wolanski E, Spagnol S (2001) Modeling and visualizing interactions between natural disturbances and eutrophication as causes of coral reef degradation. In: Wolanski E (ed) *Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef*. CRC Press, Boca Raton, pp113-125
- McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60:263-279
- Melbourne-Thomas J, Johnson CR, Aliño PM, Geronimo RC, Villanoy CL, Gurney GG (In review-a) A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. *Environmental Modeling & Software*
- Melbourne-Thomas J, Johnson CR, Fung T, Seymour RM, Paris CB, Chérubin LM, Arias-González JE, Fulton EA (In review-b) Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system. *Ecological Applications*
- Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747-769
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends In Ecology & Evolution* 23:555-563
- Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, Blackwell PG (2006) Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. *Ecological Modeling* 196:131-148
- Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Marine Ecology Progress Series* 347:285-300
- Pelletier D, García-Charton J, A. , Ferraris J, David G, Thébaud O, Letourneur Y, Claudet J, Amand M, Kulbicki M, Galzin R (2005) Designing indicators for assessing the effects of marine protected areas on coral reef ecosystems: A multidisciplinary standpoint. *Aquatic Living Resources* 18:15-33
- Perez P, Dray A, Cleland D, Arias-González JE (2009) An agent-based model to address coastal management issues in the Yucatan Peninsula, Mexico. 18th World IMACS / MODSIM Congress, Cairns, Australia 13-17 July 2009
- Sale PF (2008) Management of coral reefs: where we have gone wrong and what we can do about it. *Marine Pollution Bulletin* 56:805-809
- Shafer JL (2007) Agent-based simulation of a recreational coral reef fishery: linking ecological and social dynamics. PhD Thesis, University of Hawaii, p209
- Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries* 25:743-766
- Thacker RW, Ginsburg DW, Paul VJ (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19:318-329
- Tschirhart J (2009) Integrated ecological-economic models. *Annual Review of Resource Economics* 1:381-409
- Tupper M, Oliver J, Kenchington R, McClanahan T, Muthiga N, Gill D, Burnham D, Campbell S, Andrew N, Mahon R, Walfoort D (2008) Lessons learned and best practices in the management of coral reefs. *The WorldFish Center, Penang, Malaysia* 7
- Watts ME, Ball IR, Stewart RS, Klein CJ, Wilson K, Steinback C, Lourival R, Kircher L, Possingham HP (2009) Marxan with Zones: software for optimal conservation based land- and sea-use zoning. *Environmental Modeling & Software* 24:1513-1521

Narinratana Kongjandtre

Insights from the genus *Favia* to overcome taxonomic uncertainties in coral



Narinratana (Nong), originally from Thailand, completed a Bachelors degree in Aquatic Science (2000) and a Masters degree in Biological Science (2004) at Burapha University. Her career began with coral taxonomy and ecology. She did her first coral reef research in taxonomy and spatial distribution of faviid population in the Gulf of Thailand. She believes good taxonomy is the basis for any ecological study. In July 2006, she started a PhD under the supervision of Prof. Ove Hoegh-Guldberg at the Centre for Marine Studies, the University of Queensland. She is interested in taxonomy and systematics of the corals (in particular the genus *Favia*).



Insights from the genus *Favia* to overcome taxonomic uncertainties in coral

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Abstract

Faviidae is one of the most prominent coral families on reefs. They have a wide depth and geographic range, and are tolerant of a wide array of environmental conditions. Despite the prominence of this group, their taxonomy needs considerable work. As a result of their wide depth, geographic and environmental tolerances, there is considerable variation between species and difficulty in identification, such as found in the genus *Favia*. A unique multi-disciplinary approach using ecological, morphological, molecular, genetic and reproductive characteristics is proposed. Thailand had been selected as a case study due to the variety of habitats available, but the results and principles involved will be highly transferable to other coral species.

Introduction

Coral reefs in one form or another have persisted on the Earth for hundreds of millions of years despite vast changes in the environment, maintaining a remarkable similarity in taxonomic composition and diversity over the past 500,000 years (Pandolfi, 1996). Our understanding of the composition of coral communities is based on species identification, which is the baseline for all biological disciplines where it provides the building blocks for biological research. Traditional taxonomy and, more recently, systematics are also central to our understanding of the biodiversity of ecosystems such as coral reefs. This role has become more important as coral reefs worldwide have begun to be influenced by the activities of humans such that, despite their persistence in geological time, coral reefs have begun an unprecedented decline in abundance and community composition over the last three decades (Hughes et al., 2003). Given potential losses to coral reefs due to disturbances and climate change, the need for knowing what is being lost (i.e. via effective taxonomy) cannot be underestimated.

While coral taxonomy and systematics have developed as closely related topics, it has been suggested that the primary objective of taxonomy is to define the morphological limits of species (thereby separating, naming, and describing species in a way that is meaningful to other taxonomists), whereas systematics has been seen to be more focused on the study of evolution and the genetic relationships between species (Veron 1995). Coral reefs provide an interesting case in terms of taxonomy and systematics in that they represent one of the most diverse and productive ecosystems on earth, with hundreds of coral species currently described (Veron 2000). Coral reefs have also been subject to extensive ecological analyses during the past 50 years, yet coral taxonomy and systematics still remain largely unresolved (Miller and Babcock 1997; Stobart 2000; Lam and Morton 2003; Wolstenholme et al. 2003; Stefani et al. 2008; Huang et al. 2009), which complicates many of the current projections of reefs into the future.

Taxonomic uncertainties in corals

The unresolved problems that plague the taxonomy of corals may be attributable to the disproportionate number of researchers working on ecology as opposed to taxonomy. Yet, it is equally likely that the wide species distributions and considerable habitat heterogeneity on coral reefs as well as the apparent phenotypic plasticity of corals are significant contributing factors. Phenotypic plasticity is influenced on the local scale by a number of environmental factors including terrestrial runoff and a gradient of salinity, sedimentation (Carlson and Budd 2002), wave action exposure (Stobart 2000), depth, light and energy regimes, and space availability (Wolstenholme et al. 2003; Todd 2008). On the larger scale, however, the geographic extent and location of coral reefs can further complicate taxonomy. Budd et al. (1994) suggest that the inter- and intra-specific morphological variation problems are intensified when comparisons are made between geographic locations, since species commonly described at one geographic location may not correspond morphologically with those to which the same name is applied at another location. Thus, coral species morphological variation appears to be due to an undefined combination of local physical environmental and geographic factors, reflecting particular genetic controls acting in particular environments in particular regions (Veron, 1995).

To further complicate the issue, the recent discovery of hybridization between species challenges the current understanding of coral taxonomy and systematics (Wallace and Willis 1994; Veron 1995; Miller and Babcock 1997; Wolstenholme 2004; Willis et al. 2006). Molecular assessments have confirmed introgressive events in corals, revealing that *Acropora prolifera* are F1 hybrids of *A. cervicornis* and *A. palmata* (Vollmer and Palumbi 2002). Moreover, cross-fertilization experiments reveal the potential for many hybrids among closely related species (Willis et al. 1997; van Oppen et al. 2002; Fukami et al. 2003; Wolstenholme 2004), which often are overlooked by, or complicate traditional morphological analyses. Willis et al. (2006) have concluded that hybridization may lead to the merging of species and ultimately to the extinction of pure parental species along with their morphological, behavioural and/or ecological distinctions. This process of genetic mixing may provide increased genetic diversity, new traits, and heterosis for the emerging species but may carry the cost of a net loss of species diversity. On the other hand, hybridization may also give rise to new species that are reproductively isolated from parental species through either polyploid or recombinational speciation, with both processes representing mechanisms for the rapid evolution of genetic novelty without the loss of parental species (Willis et al. 2006).

Despite the discussed uncertainties, coral species are traditionally described according to differences in the morphology of the colony and micro-morphological structure characters of the coral skeleton (Veron and Pichon 1976, 1979, 1982; Veron et al. 1977; Veron and Wallace 1984; Veron 1986, 2000). Whilst morphological characters are largely robust, the observed level of morphological variation has created formidable taxonomic as well as interpretive problems – with current methodologies failing at times to recognize the full extent of intra-specific variation (Budd and Stolarski 2009). These issues in coral taxonomy militate toward the development of more traditional methods that are combined with multi-character and multi-variate statistical approaches in order to fully understand species delineation in a number of coral species groups (Budd et al., 1994; Weil and Knowlton 1994; Stobart 2000; Lam and Morton 2003; Mate 2003; Wolstenholme et al. 2003; Budd and Pandolfi 2004; Carlson and Budd 2002; Fukami et al. 2004a; Benzoni et al. 2007). The development of a '3-D coordinate landmark' method using size and shape coordinates rather than linear distances as characters has provided increased resolution of potential differences among morphospecies (Carlson and Budd 2002; Fukami et al. 2004a). The use of three-dimensional observations using scanning electron microscopy of calicular surfaces have been effective at distinguishing Atlantic and Pacific Mussidae and Faviidae (Budd and Stolarski 2009).

Molecular techniques have caused major conceptual advances in the understanding of the taxonomy and systematics of reef-building corals. Underpinning these advances is the increased ease with which taxon boundaries can be explored using molecular techniques (Stobart 2000; Carlson and Budd 2002; Vollmer and Palumbi 2002, 2004; Wolstenholme, et al. 2003; Lam and Morton 2003; Mate 2003; Fukami et al. 2004b), which also overcomes some of the problems of phenotypic plasticity. However, results repeatedly show that morphological boundaries are not necessarily related to genetic boundaries and the existing "classical" taxonomies of corals are therefore in need of critical re-evaluation (Huang et al. 2009). While approaches based on morphometric analysis help to recognize the differences between species at an overt scale, molecular techniques have the potential to reveal differences between species and hence provided insight into the underlying evolutionary processes.

The genus *Favia* as a test case

After the Acroporidae, the Faviidae is the next most speciose family of corals, which also shares taxonomic difficulties and discrepancies between morphological and genetic characters (e.g. Fukami et al. 2004b, 2008; Mangubhai et al. 2007, Nunes et al. 2008; Huang et al. 2009). The genus *Favia* is particularly interesting in this respect, as recent work has suggested the existence of complex relationships between morphology, environments and molecular identities (Fig. 1). An example of this is *Favia fragum*, which is the only species reported to occur in the Caribbean. Carlon and Budd (2002) identified two different morphotypes of *F. fragum* with opposing depth distributions, which, although being morphologically similar, may represent cryptic species that are irresolvable using traditional morphological techniques. Huang et al. (2009) also recently showed the *Favia* to be polyphyletic with the species distributed across two different major genetic clades.

Veron (1995) states that the first need of coral taxonomy is to gain an understanding of how species differ from each other as well how they vary intra-specifically. Within the genus *Favia*, besides being widely distributed, most species have wide depth ranges on reefs, and are tolerant of a wide range of environmental conditions (Veron, 2000). Members of the *Favia* are often difficult to recognize underwater due to colour variation and that the soft tissue of living polyps obscures underlying skeleton structures. Based on the currently available methodologies, a comparison of morphometric, molecular and reproductive strategies should provide an enhanced understanding of species boundaries in reef-building corals. As such, this project integrates both traditional morphological assessments with newer state-of-the-art 3-D morphometric analyses, as well as reproductive hybridization trials, and both mitochondrial and nuclear DNA sequencing in order to understand and describe the biogeography and relationships among species of *Favia* on Thailand's coral reefs.

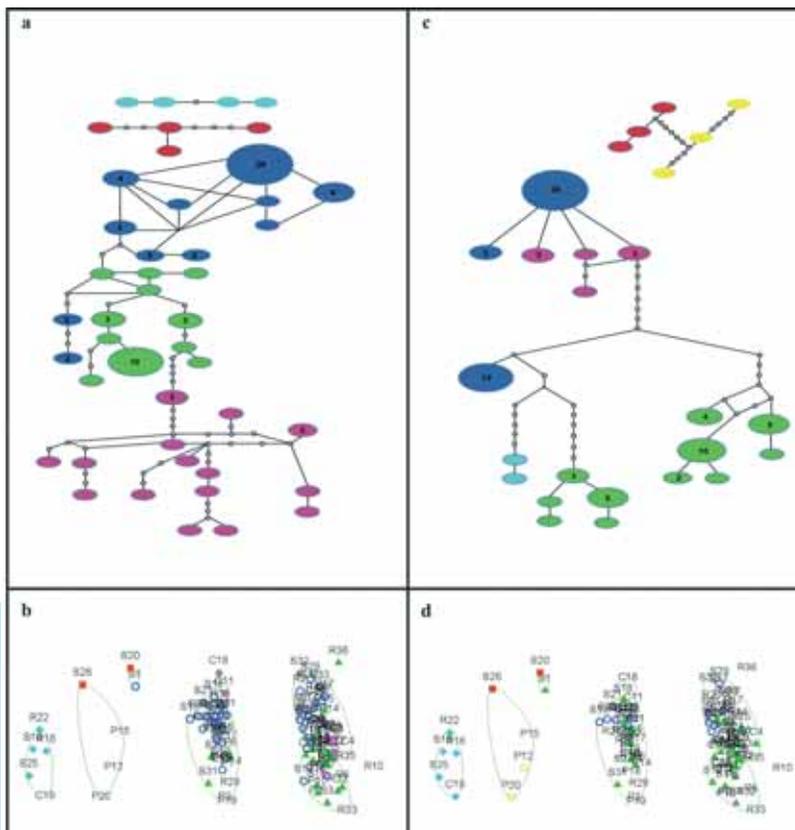


Figure 1. Comparison between phylogenetic trees derived from TCS network analysis of the nuclear and mitochondrial sequences from *Favia* samples from Thailand and plots of multidimensional scaling (MDS) analysis from 14 morphological traits. A. Phylogenetic tree derived from TCS network analysis of the nuclear (18S, ITS1, 5.8S, ITS2, 28S) sequences of the *Favia* species. Each circle on the tree represents *Favia* that share the same haplotypes label with number of colony (no label = 1 colony). B. Plots of scores on MDS, each point on the plot represents 1 colony; colour light blue represents *F. truncatus*; red represents *F. helianthoides*; pink represents *F. fava*, green represents *F. pallida* and dark blue represents *F. speciosa* species complex. C. Phylogenetic tree derived from TCS network analysis of the mitochondrial (COI-trnM intergenic spacer: IGR) sequences of the *Favia* species. Each circle on the tree represents *Favia* that share the same haplotypes label with number of colony (no label = 1 colony). D. Plots of scores on MDS, each point on the plot represents 1 colony; colour light blue represents *F. truncatus*; red represents *F. helianthoides*; pink represents *F. fava*, green represents *F. pallida*; dark blue represents *F. speciosa* species complex and yellow represents cf. *Favites*.

3. New tools for understanding and managing coral reef systems

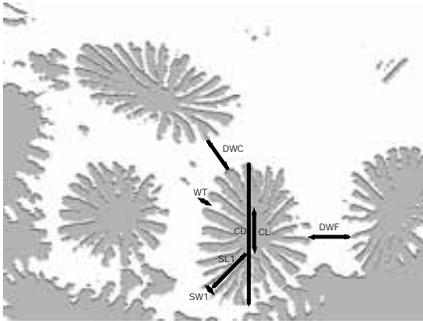
a) *Favia cf. helianthoides* morphological variation within colony



b) variation between colony



c) linear measurement method



d) 3 D coordinate landmark method

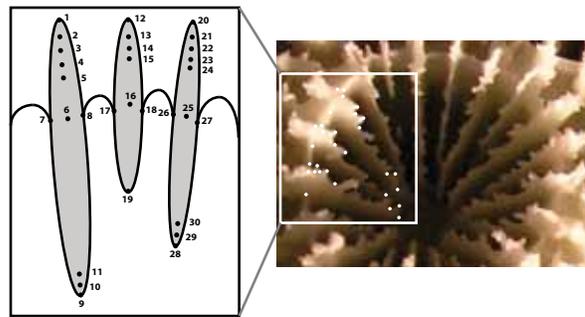


Figure 2 Variation within and between colony found in *Favia* and morphological techniques used in this study. a) Morphological variation within colony in *Favia cf. helianthoides* b) Variation between colony of *F. cf. helianthoides* c) Measurements made on individual corallites for morphometric analyses. CD, calice diameter; CL, columella diameter; SL1, length of primary septa; SW1, width of primary septa; WT, wall thickness; DWL, distance from wall to closest calice; DWF, distance from wall to farthest neighboring calice d) Photo of costosepta within a corallite and the location (inset) of three-dimensional Cartesian coordinates collected for 30 landmarks along costosepta. Photograph shows a side view of the inner edges (septa) of costosepta from the corallite center. This inset depicts a two-dimensional representation of the costosepta in a top view of the corallite surface. Landmark 1-11 and 20-30 are located on major, and 12-19 are located on minor septa. Shape coordinates were calculated by rotating and transforming each landmark relative to a plane defined by points 7 (0,0,0), 27 (1,0,0) and 16 (x, 0,z). These landmarks were selected to characterize the shape of the septa margin (the uppermost growing edge) and the development of costal extensions between calices. (Landmarks applied from Carlon & Budd, 2002).

Conclusion

Corals are the backbone for the richness and productivity associated with tropical coastal communities, and as we begin to get an understanding of the potential magnitude of change facing coral reefs, it is essential to know what exactly we have if we are to accurately assess what we are likely to lose. The multi-disciplinary approach of this study will therefore provide the first robust assessment of coral species within the genus *Favia*, which will not only provide a good baseline for the genus *Favia* for Thai waters, but the results and principles involved will be highly transferable to other coral species throughout the world.

References

- Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P (2007) Debating phylogenetic relationships of the scleractinian *Psammocora*: molecular and morphologies evidences. *Contrib Zool* 76:35-54
- Budd AF, Pandolfi JM (2004) Overlapping species boundaries and hybridization within the *Montastrea* "annularis" reef coral complex in the Pleistocene of the Bahama Islands. *Paleobiology* 30:396-425
- Budd AF, Stolarski J (2009) Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. *Acta Zool* 90:142-165
- Budd AF, Johnson KG, Potts DC (1994) Recognizing morphospecies in colonial reef corals: I. Landmark-based methods. *Paleobiology* 20:484-505
- Carlson DB, Budd AF (2002) Incipient speciation across a depth gradient in a Scleractinian coral? *Evolution* 56:2227-2242
- Fukami H, Omori M, Shimoike K, Hayashibara T, Hatta M (2003) Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Mar Biol* 142:679-684
- Fukami H, Budd AF, Levitan DR, Jara J, Kersanach R, Knowlton N (2004a) Geographical differences in species boundaries among members of the *Montastrea annularis* complex based on molecular and morphological markers. *Evolution* 58:324-337
- Fukami H, Chen CA, Budd AF, Paulay G, Sole-Cava A, ChenCLA, Iwao K, Knowlton N (2004b) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature* 427:832-835
- Fukami H, Chen CA, Budd AF, Collins A, Wallace C, Chuang YY, Chen C, Dai CF, Iwao K, Sheppard C, Knowlton N (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *Plos ONE* 3:e3222
- Huang D, Meier R, Todd PA, Chou LM (2009) More evidence for pervasive paraphyly in scleractinian corals: systematic study of Southeast Asia Faviidae (Cnidaria; Scleractinia) based on molecular and morphological data. *Mol Phylogenet Evol* 50:102-116
- Hughes TP, Baird AH, Bellwood DR Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts , and the resilience of coral reefs. *Science* 301(5635):929-933
- Lam K, Morton B (2003) Morphological and ITS1, 5.8S, and partial ITS2 ribosomal DNA sequence distinctions between two species *Platygyra* (Cnidaria: Scleractinia) from Hong Kong. *Mar Biot* 5:555-567
- Mangubhai S, Souter P, Grahn M (2007) Phenotypic variation in the coral *Platygyra daedalea* in Kenya: morphometry and genetics. *Mar Ecol Prog Ser* 345:105-115
- Mate JL (2003) Ecological, genetic, and morphological differences among three *Pavona* (Cnidaria: Anthozoa) species from the Pacific coast of Panama. *Mar Biol* 142:427-440
- Miller K, Babcock RC (1997) Conflicting morphological and reproductive species boundaries in the coral genus *Platygyra*. *Biol Bull* 192:98-110
- Nunes F, Fukami H, Vollmer SV, Norris RD, Knowlton N (2008) Re-evaluation of the systematics of the endemic corals of Brazil by molecular data. *Coral Reefs* 27:423-432
- Pandolfi JM (1996) Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: Constancy during global change. *Paleobiology* 22(2):152-176
- Stefani F, Benzoni F, Pichon M, Cancelliere C, Galli P (2008) A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). *Zool Scr* 37:71-91
- Stobart B (2000) A taxonomic reappraisal of *Montipora digitata* based on genetic and morphometric evidence. *Zool Stud* 39:179-190
- Todd PA (2008) Morphological plasticity in scleractinian corals. *Biol Rev* 83:315-337
- van Oppen MJH , Willis BL, Rheede T van, Miller DJ (2002) Spawning times, reproductive compatibilities and genetic structuring in the *Acropora aspera* group: evidence for natural hybridization and semi-permeable species boundaries in corals. *Mol Ecol* 11:1363-1376
- Veron JEN (1986) *Corals of Australia and the Indo-Pacific*. North Ryde, NSW: Angus & Robertson.
- Veron JEN (1995) *Corals in space and time: the biogeography and evolution of the Scleractinia*. UNSW Press, Sydney
- Veron JEN (2000) *Corals of the world*. Aust Inst Mar Sci, Townsville
- Veron JEN, Pichon M (1976) Scleractinia of eastern Australia. Part I. Families *Thamnasteriidae*, *Astrocoeniidae*, *Pocilloporidae*. *Aust Inst Mar Sci Monogr Ser* 1:1-86
- Veron JEN, Pichon M (1979) Scleractinia of eastern Australia Part III. Families *Agariciidae*, *Siderastreidae*, *Fungiidae*, *Oculinidae*, *Merulinidae*, *Mussidae*, *Pectiniidae*, *Caryophylliidae*, *Dendrophylliidae*. *Aust Inst Mar Sci Monogr Ser* 4:1-459
- Veron JEN, Pichon M. (1982) Scleractinia of Eastern Australia Part IV. Family *Poritidae*. *Aust Inst Mar Sci Monogr Ser* 5:1-159
- Veron JEN, Pichon M, Wijsman-Best M (1977) Scleractinia of Eastern Australia. Part II. Families *Faviidae*, *Trachyphylliidae*. *Aust Inst Mar Sci Monogr Ser* 3:1-233
- Veron JEN, Wallace CC (1984) Scleractinia of eastern Australia. Part V. Family *Acroporidae*. *Aust Inst Mar Sci Monogr Ser* 6:1-485
- Vollmer SV, Palumbi SR (2002) Hybridization and the evolution of reef coral diversity. *Science* 296:2023-2025
- Vollmer SV, Palumbi SR (2004) Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Mol Ecol* 13:2763-2772
- Wallace CC, Willis BL (1994) Systematics of the coral genus *Acropora*: implications of new biological findings for species concepts. *Annu Rev Ecol Syst* 25:237-262
- Weil E, Knowlton N (1994) A multi-character analysis of the Caribbean coral *Montastrea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bull Mar Sci* 55:151-175
- Willis BL, Babcock RC, Harrison PL, Wallace CC (1997) Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs* 16:53-65
- Willis BL, van oppen MJH, Miller DJ, Vollmer SV, Ayre DJ (2006) The role of hybridization in the evolution of reef corals. *Annu Rev Ecol Syst* 37:489-517
- Wolstenholme JK (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria: Scleractinia). *Mar Biol* 144 (3): 567-582
- Wolstenholme JK, Wallace CC, Chen CA (2003) Species boundaries within the *Acropora humilis* species group (Cnidaria: Scleractinia): a morphological and molecular interpretation of evolution. *Coral Reefs* 22:155-166

Angela M. Mojica & Eva Salas

Connectivity: A snapshot on techniques and the role of CRTR Program in the research field

Angela recently completed her Masters degree under Dr. Mark Butler at Old Dominion University in Virginia, USA. Her research project focused on studying the effect of the herbivorous spiny crab (*Mithrax spinosissimus*) on algal communities within the Florida Keys coral reef ecosystems. As part of the Connectivity and Large-Scale Ecological Processes Working Group, the research team investigated the recruitment patterns of Caribbean spiny lobster (*Panulirus argus*) postlarvae in Mesoamerica for use in building a coupled biophysical oceanographic model of lobster larval dispersal. Angela's research interests include coral reefs ecology, connectivity processes, and the use of remote sensing tools for conservation and management.

Eva graduated recently from her Masters degree at Universidad de Costa Rica, in collaboration with the University of Windsor, Ontario. Her research experience is related with coral reef fish ecology in Eastern Pacific and Caribbean coral reefs. Eva has been studying fish community structure, and her recent work with the CRTR has been focused in the connectivity of bicolor damselfish populations in the Caribbean, using molecular tools. She is currently interested in how dispersal patterns and habitat features shape population dynamics of marine organisms, and wants to use that knowledge to improve marine spatial planning in tropical countries.



Connectivity: a snapshot on techniques and the role of the CRTR Program in the research field

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Abstract

The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program, a partnership between the Global Environment Facility and the World Bank, is a long term worldwide initiative seeking to fill critical gaps in coral reef ecosystems knowledge and to use this information to support management and policy of coral reefs. The Connectivity Working Group in particular, studies demographic connectivity of selected coral reef associated species in Mesoamerica. Connectivity refers to the transfer of individuals among geographically separated populations, and how this process influences population resilience, genetic diversity and the extent of population replenishment. Here we present a short review on the most recent approaches to study and measure connectivity in marine populations, and the role of the CRTR Project in the advancement of the field.

Understanding the factors driving the abundance and distribution of marine populations has become a hot topic in the recent past. With major declines in fishery stocks and an increasing demand for ecosystem-based management approaches (Cowen et al. 2006) such as predictive population and fisheries models (Egglestone et al. 1998) and the design of marine reserves (Sale 2002, Jones et al. 2009, Steneck et al. 2009), the identification of spatial scales of population connectivity is imperative. Connectivity refers to the exchange of individuals among geographically separated populations (Cowen & Sponaugle 2009), and how this process influences population resilience, genetic diversity and the extent of population replenishment (Palumbi 2003, Kritzer and Sale 2004). Identifying patterns of connectivity (e.g., supply of adults and larvae into and out of a reserve, larvae retention, exchange of recruits among reserves) among marine protected areas (MPAs) is critical for their design and ultimately their effectiveness in preserving biological diversity, enhancing fisheries yields, and protecting vulnerable life stages of marine species inside the reserve (Agardy 1994; Palumbi 2001, 2003, Mumby et al. 2006, Steneck et al. 2009). This is especially important for reserves applying the no-take concept, whose economic value depend upon their spillover effect, which is the exportation of individuals outside their boundaries where fishing is allowed (DeMartini 1993; Botsford et al. 2001; Hilborn et al. 2004; Kritzer and Sale 2004, Steneck et al. 2009).

For many marine organisms, including those species with higher dispersal potential as juveniles and adults, the pelagic phase constitutes their primary dispersal vehicle for population connectivity (Cowen & Sponaugle 2009). Empirical studies measuring larval dispersal and determining scales of connectivity are limited due to methodological constraints and difficulties capturing real spatial and temporal variations of dispersal distances as a result of variable oceanographic conditions and larval behavior (Cowen et al. 2006). Available data has been collected for few species, mostly those with short larval duration and short dispersal (Sammarco and Andrews 1989; Shanks et al. 2003). The development of biological-physical models to estimate dispersal kernels under multiple scenarios and for multiple species has been an instrumental tool in understanding connectivity (Cowen et al. 2006). Models, however, do not rely exclusively on oceanographic parameters but also on several assumptions about the level of demographic exchange among populations. Biological factors such as larval period duration, larval behavior (e.g., vertical and horizontal migration), adult spawning strategies (e.g., season and frequency), recruitment, and availability and location of suitable settlement habitats are known to mediate overall dispersal kernel (Cowen et al. 2006).

Measuring these connectivity parameters are essential to not only calibrate but also to validate a model's predictions. New techniques have been developed to overcome difficulties obtaining empirical data on connectivity for selected species providing essential information on connectivity.

Recruitment of postlarvae

Recruitment of postlarvae, that is the arrival or supply of planktonic postlarvae to coastal areas (Steneck et al. 2009), is an essential parameter for models to accurately predict ecologically significant scales of connectivity. Levels of recruitment are usually indicative of the number of settlers required to replenish a local population by maintaining the balance between the juvenile and adult mortality (Cowen et al. 2006, Steneck et al. 2009). Despite the potential dispersal of larvae during their planktonic stage, especially those species with long larval periods such as the Caribbean spiny lobster, *Panulirus argus* (Lyons 1980), there are reasons to suspect that such dispersal may be spatially more restricted than anticipated (Jones et al. 1999, Hughes et al. 2000, Largier 2003, Cowen et al. 2006, Steneck 2006, Almany et al. 2007). Determining the factors driving recruitment dynamics of marine coastal species (e.g., spawning strategies and availability, and the location of suitable habitats for settlement) are critical to a better understanding of how larval and postlarval supply affect connectivity processes (Acosta et al. 1997; Eggleston et al. 1998; Cowen et al. 2006). Butler et al (2009) found that recruitment patterns of spiny lobster postlarvae in the Caribbean are highly variable among localities and months, presumably as a result of biological and local oceanographic phenomena; furthermore, it seems that recruitment patterns mirrored fishery catch in some locations. This type of information is critical to better protect, manage and regulate targeted species. Acquiring comparable long term data that truly reflects recruitment patterns can be expensive and labor intensive, especially for species with long larval stages that require large scale monitoring programs. Moreover, recruitment data does not necessarily correlate with adult populations (e.g., postlarvae and juvenile mortality, suitable settlement habitat, predation).

Genetic markers

Genetic markers are natural tags that can be used to estimate levels of population connectivity and determine source locations. Only a few migrants are needed to dissolve genetic structure, so high levels of genetic differentiation are proof of highly restricted connectivity (Palumbi 2003). Some reef-associated species in the Indo-Pacific show significant levels of genetic differentiation at small and large scales (e.g. Planes et al. 1998; Bernardi et al. 2001; Planes and Fauvelot 2002; Magalon et al. 2005; Gerlach et al. 2007), as do some species from the Caribbean like gobiids, (Taylor and Hellberg 2003), suggesting limited levels of connectivity. Suitable genetic markers for studying demographic connectivity require being highly polymorphic and with high mutation rates, to help infer recent events such as larval dispersal (Mora & Sale 2002). Good examples of markers for this purpose are microsatellites (Hancock 1999). The study of genetic variation using classic population genetics can reveal connectivity patterns among populations, but there is limited potential to quantify the actual amount of larval exchange. Recent studies rely on new statistical and molecular tools, such as genotype assignment techniques and parentage analysis in order to quantify migrant fish (Manel et al. 2005). Assignment methods work by assigning or excluding reference populations as possible origins of individuals, based on their multilocus genotypes (Piry et al. 2004). For example, using assignment methods, Carreras-Carbonell et al. 2007, found that a mean of 66% of the black faced blenny *Tripterygion delaisi* recruits settled in their natal population, and Gerlach et al. 2007 determined that 58% of the recruits of the cardinal fish, *Apogon doederleni*, recruited back to their natal reef. Parentage analyses are also very effective, but a large amount of the population needs to be sampled. In this method, individuals are assigned to the most likely parent from a pool of potential parents (Jones and Ardren 2003) Parentage analyses mostly agreed with results of artificial tetracycline marking of panda clownfish *Amphiprion polymnus*, demonstrating the potential for successful connectivity assessments (Jones et al. 2005). Genetic markers are informative natural tags, but are limited when levels of genetic differentiation are low, a common pattern in marine organisms.

Chemistry in calcified structures

Variations in seawater chemistry, salinity and temperature are recorded in the composition of calcified structures, such as otoliths, statoliths and shells (Thorrold et al. 2007). Therefore, if marine environments show high variation in the geochemical signature (Thorrold et al. 2002), it is possible to track the different places that a marine organism has been in its lifetime. By mapping the geochemical signatures of possible source locations, larvae can be tracked back to their natal place, by looking at the chemistry recorded in the calcified structures. This is a natural tag that can be used to infer connectivity. For example, Swearer et al. (1999), using otolith trace element data showed that 44.5 % of bluehead wrasse (*Thalassoma lucasanum*) originated within the waters of the island St. Croix. Juvenile flatfish have been classified to estuarine and coastal habitats based on the elemental composition of their otoliths (Brown 2006). This technique is usually more effective when used in coastal areas with upwellings and rivermouths rather than in open ocean areas, because there is a higher likelihood of finding distinct geochemical signatures. Other challenges to this technique are to cope with temporal variability in water chemistry and to differentiate chemical signatures of the larvae that come from the home location vs. signatures that come from maternal transmission.

Artificial tags

Probably the most effective technique to measure connectivity is the use of artificial tags that, when found, are unequivocal. Studies of larval retention using otolith tagging with tetracycline, have demonstrated 15-60% self-recruitment in *Pomacentrus amboinensis* at Lizard Island, Australia (Jones et al. 1999); and also have shown that 1/3 of the *Amphiprion polymnus* juveniles from Kimbe Bay, Papua New Guinea were retained within a two hectare natal area (Jones et al. 2005). Almany et al. (2007) tagged offspring using maternal transmission of stable isotopes and reported approximately 60% self-recruitment for two coral reef fish species, the vagabond butterflyfish, *Chaetodon vagabundus*, and the orange clownfish *Amphiprion percula* at Kimbe Bay. Tagging studies are costly and logistically difficult when fishes are very abundant and widely distributed in continuous habitat, so studies using indirect, but more logistically feasible techniques, may be more widely applicable, especially for large scale studies using abundant species.

Currently, members of the CRTR Connectivity Working Group are using different approaches to empirically measure demographic connectivity for selected species in Mesoamerica. Areas of research include genetic studies of scleractinian corals and damselfish employing microsatellite markers to estimate connectivity in the Western Caribbean (e.g., Salas et al. 2009), and recruitment patterns of Caribbean spiny lobster (*P. argus*) postlarvae in Mesoamerica for use in building a coupled biophysical oceanographic model of lobster larval dispersal (Butler et al. 2009). A unique feature of the CRTR Connectivity Working Group has been the direct involvement of local management agencies into the research projects. These projects are pioneers in the developing of new approaches and tools to better understand larvae dispersal and connectivity of a variety of marine taxonomical groups. Such empirical studies are necessary to determine research gaps and technique limitations; more importantly, field data can be used as proxy to validate the predictions of current biophysical models, already available for certain fish species in the Caribbean region (Cowen et al. 2006). Hydrodynamic models have become a novel approach to integrate targeted research efforts providing scientist and managers with new tools to improve management decisions. This is especially true in connectivity, a cloudy research field researchers are just beginning to understand.

References

- Acosta CA, Matthews TR, Butler MJ (1997) Temporal patterns and transport processes in recruitment of spiny lobster (*Panulirus argus*) postlarvae to south Florida. *Mar Biol* 129:79-85
- Agardy MT (1994) Advances in marine conservation: the role of marine protected areas. *TREE* 9:267-270
- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742-744
- Bernardi G, Holbrook SJ, Schmitt RJ (2001) Gene flow at three spatial scales in a coral reef fish, the three-spot dascyllus, *Dascyllus trimaculatus*. *Mar Biol* 138:457-465
- Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144-150
- Brown JA (2006) Classification of juvenile flatfishes to estuarine and coastal habitats based on the elemental composition of otoliths. *Estuarine, Coastal and Shelf Science* 66:594-611
- Butler, MK, Mojica AM, Sosa-Cordero E, Millet M, Sanchez-Navarro P, Maldonado MA, Posada J, Rodriguez B, Rivas CM, Oviedo A, Arrone M, Prada M, Bach N, Jimenez N, Matthews T, Paris Claire, Cowen R (2009) Patterns of spiny lobster (*Panulirus argus*) postlarval recruitment in the Caribbean: a CRTR Project. *Proc Gulf Caribb Fish Inst* 'in press'
- Carreras-Carbonell J, Macpherson E, Pascual M2 (2007) High self-recruitment levels in Mediterranean littoral fish population revealed by microsatellite markers. *Mar Biol* 151:719-727
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522-527
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443-466
- DeMartini E E (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fish Bulletin* 91:414-427
- Eggleston DB, Lipcius RN, Marshall Jr LS, Ratchfordl SG (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Mar Ecol-Prog Ser* 174:33-49
- Gerlach GG, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef. *Fish larvae Proc Natl Acad Sci* 104:858-863
- Hancock JM (1999) Microsatellites and other simple sequences: genomic context and mutational mechanisms In: Goldstein DB, Schlötterer C, Eds. *Microsatellites: Evolution and applications*. Oxford University Press. p 1-9
- Hilborn R, Stokes K, Maguire JJ, Smith T, Botsford L, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood GP, Sainsbury K, Stegansson G, Walters C (2004) When can marine reserves improve fisheries management?. *Ocean Coastal Management* 47: 197-205
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivkyj NA, Pratchett JE, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between adults, fecundity, and larval recruits. *Ecology* 81:2241-2249
- Jones AG, Ardren WR (2003) Methods of parentage analysis in natural populations. *Molecular Ecology* 12:2511-2523
- Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402: 802-804
- Jones GP, Planes S, Thorrold S (2005) Coral reef fish larvae settle close to home. *Current Biology* 15:1314-1318
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, Van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28(2):307-325
- Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: From Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131-140
- Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecol App* 13:71-89
- Lyons WG (1980) Possible sources of Florida's spiny lobster population. *Proc Gulf Caribb Fish Inst* 33:253-266
- Magalon H, Adjeroud M, Veuille M (2005) Patterns of genetic variation do not correlate with geographical distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. *Molecular Ecology* 14:1861-1868
- Manel S, Gaggiotti OE, Waples RS (2005) Assignment tests: matching biological questions with appropriate techniques. *TREE* 20:136-142
- Mora C, Sale PF (2002) Are populations of coral reef fish open or closed? *TREE* 17: 422-428
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98-101
- Palumbi SR (2001) The ecology of marine protected areas In: Bertness M, Gaines SD, .
- Hay ME, Ed. *Marine ecology: the new synthesis*. Sinauer, Sunderland, Massachusetts, USA. p509-530
- Palumbi SR (2003) Population genetics, demographic connectivity and the design of marine reserves. *Ecological Applications* 13:146-158
- Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GeneClass2: A Software for Genetic Assignment and First-Generation Migrant Detection. *J Heredity* 95:536-539
- Planes S, Parroni M, Chauvet C (1998) Evidence of limited gene flow in three species of coral reef Fishes in the lagoon of New Caledonia. *Mar Biol* 130:361-368
- Planes S, Fauvelot C (2002) Isolation by distance and vicariance drive genetic structure of a coral reef Fish in the Pacific Ocean. *Evolution* 56:378-399
- Salas E, Molina H, Walter RP, Heath DD (2009) Local and regional connectivity in a Caribbean reef fish. *Mar Bio Online* first November 2009
- Sale PF (2002) The science we need to develop for more effective management In: Sale PF, Ed. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic press. San Diego, CA. p361- 376
- Sammarco PW, Andrews JC (1989) The Helix experiment: Differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnol Oceanogr* 34(5): 896-9 12
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:159-169
- Steneck RS (2006) Is the American lobster, *Homarus americanus*, overfished? A review of overfishing with an ecologically based perspective. *B Mar Sci* 78(3): 607-632
- Steneck RS, Paris CB, Arnold SN, Ablan-Lagman MC, Alcalá AC, Butler MB, McCook, Russ GR, Sale PF (2009) Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. *Coral Reefs* 28:367-378
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799-802
- Taylor MS, Hellberg M (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* 299:107-109
- Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swearer SE, Neigel JE, Morgan SG, Warner RR (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *B Mar Sci* 70:S291-S308
- Thorrold SR, Zacherl DC, Levin LA (2007) Population connectivity and larval dispersal: using geochemical signatures in calcified structures. *Oceanography* 20: 80-89



Spotlight on:
Rollan Geronimo

Masters student Rollan Geronimo is keen to see the results of research taken up by end users of coral reef systems – in particular the local fisherfolk. “I always try to link my research work to direct applications and recommendations for coastal resource managers,” he says.

Through his work with the Modeling and Decision Support Working Group, Rollan is focused on decision support tools and modeling of the Bolinao-Anda reef complex. The reef faces stressors include destructive fishing, excessive harvesting, sedimentation, and pollution. Rollan’s studies have contributed to the development of a systems-dynamics tool to predict the carrying capacities of reef habitats. When applied to the reef systems near Pangasinan towns, the FISH-BE tool can highlight the effect of various stresses on the reef system and the need for intervention to reduce their impact on the reef and fish populations.

Rollan is also compiling, processing and analyzing available biophysical, fisheries and socio-economic data on the complex from the last decade to determine if events such as the 1998 massive bleaching, and the establishment of Marine Protected Areas and other management interventions are impacting on the reef fish. Initial analysis show increasing fish biomass from 2003 to 2006 and changes in fish density during this time. These trends may be a partial indication of the positive impacts of protection. Evidence such as this provides a strong justification for implementing marine protection measures. Rollan has participated in several workshops on fisheries with local community members, fisherfolk, local government officials, non-government organisation representatives and other scientists which has reinforced his commitment to implementation of research findings.



Spotlight on:

Rachel Ravago-Gotanco

Schools of young rabbitfish make a sparkling spectacle as they cast a shadow across the seagrass flats of Bolinao. From March to May each year, the sight excites the local fisherfolk as juvenile rabbitfish provide a significant resource when they arrive to settle on the reef flats. But where have they come from, where are they going, and why does it matter? As part of her PhD studies, Rachel Ravago Gotanco is focused on these very issues. The rabbitfish (*Siganus fuscescens*) population faces long term threats because they are widely harvested before maturity. If the species is better understood, conservation and management efforts will be more effective.

With the cooperation of local people who provide samples of both adults and newly settled juveniles, Rachel is using molecular techniques to study the connectivity of the rabbitfish populations of the Philippine Archipelago. Examination of genetic differences between populations reveals important information about the distances rabbitfish travel and their seasonal movements. This spatial and temporal data helps tell the story of how the fish populations are connected and provides details of population dynamics. This information underpins conservation and management efforts.

"There have been significant historical changes in the rabbitfish population, but very little is known about what is really going on," says Rachel. "I am looking at factors which influence these changes, the connectivity between populations and the population size. By tracking the distribution of genes among rabbitfish populations, historical and contemporary links can be inferred, which can be useful in predicting reactions and population trajectories in the face of environmental stressors.

"Molecular biology offers powerful new conservation and management tools. The amazing biodiversity of the Coral Triangle has lots of scope to apply this new knowledge – and feeds my curiosity."

Pablo Saenz-Agudelo

Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios



Pablo from Colombia, finished his undergraduate studies in biology in Colombia at the Universidad de Antioquia in August 2004. He then did a Masters degree in Coastal Oceanography in France at the Pierre et Marie Curie University from which he graduated in June 2007. Pablo then enrolled in a joint PhD program between the Ecole Pratique de Hautes Etudes (France) and James Cook University (Australia), under Dr. Serge Planes¹ (EPHE) and Prof. Geoffrey Jones (JCU) co-supervision. He is located in the Centre de Biologie et d'Ecologie Tropicale et Méditerranéenne in Perpignan University campus (South of France on the Mediterranean Coast, near the Spanish frontier). His PhD program focused on the study of coral reef fish connectivity, using a genetic approach. The model species is the panda clownfish *Amphiprion polymnus* and the study site is in Papua New Guinea. Pablo's main scientific interests are marine population dynamics, and connectivity and evolutionary ecology.



Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios

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Abstract

The application of spatially explicit models of population dynamics to fisheries management and the design marine reserve network systems has been limited due to a lack of empirical estimates of larval dispersal. Here we compared assignment tests and parentage analysis for examining larval retention and connectivity under two different gene flow scenarios using panda clownfish (*Amphiprion polymnus*) in Papua New Guinea. A metapopulation of panda clownfish in Bootless Bay with little or no genetic differentiation among five spatially discrete locations separated by 2–6 km provided the high gene flow scenario. The low gene flow scenario compared the Bootless Bay metapopulation with a genetically distinct population ($F_{ST} = 0.1$) located at Schumann Island, New Britain, 1500 km to the northeast. We used assignment tests and parentage analysis based on microsatellite DNA data to identify natal origins of 177 juveniles in Bootless Bay and 73 juveniles at Schumann Island. At low rates of gene flow, assignment tests correctly classified juveniles to their source population. On the other hand, parentage analysis led to an overestimate of self-recruitment within the two populations due to the significant deviation from panmixia when both populations were pooled. At high gene flow (within Bootless Bay), assignment tests underestimated self-recruitment and connectivity among subpopulations, and grossly overestimated self-recruitment within the overall metapopulation. However, the assignment tests did identify immigrants from distant (genetically distinct) populations. Parentage analysis clearly provided the most accurate estimates of connectivity in situations of high gene flow.

Introduction

Marine coastal habitats are often discontinuous and species distributions can be fragmented into spatially discrete populations. The dynamics of these populations can potentially be influenced by self-recruitment or local retention of juveniles within populations, and by connectivity, the degree to which these populations are linked by dispersal (Warner & Cowen 2002; Sale et al. 2005). Levels of self-recruitment within and connectivity among populations on ecological timescales are key factors affecting the persistence of marine metapopulations and their resilience to local disturbance (Armsworth 2002; James et al. 2002; Hastings & Botsford 2006). Optimal design of spatially explicit management strategies for marine species, including marine protected areas (MPA), is also contingent on the extent of population connectivity (Lockwood et al. 2002; Hastings & Botsford 2003; Sale et al. 2005). In benthic-oriented marine species which are often relatively sedentary as adults, population connectivity largely occurs during a larval phase that extends from reproduction to the completion of the settlement process (Cowen et al. 2007). While an increasing number of methods for estimating population exchange on ecological timescales are available, the accuracy of the different methods and the degree of concordance among them are seldom known.

Population genetics is the most widely used approach for making inferences about dispersal and connectivity in marine organisms (Planes 2002; Van Oppen & Gates 2006; Hellberg 2007). Estimates of connectivity based on gene flow are also being used to inform the design of marine protected area networks (e.g. Palumbi 2003). However, while clearly a suitable tool for measuring gene flow on evolutionary timescales, population genetics cannot always distinguish between contemporary and historical gene flow. Standard estimates of migration among populations are increasingly inaccurate at scales where there may be limited population differentiation (Hedgecock et al. 2007). Estimates of dispersal also rely heavily on theoretical models of population structure, such as Wright's island model, which are based on many assumptions that may often be violated in natural populations (Hedgecock et al. 2007). Given that successful management may be reliant on good estimates of population exchange between local populations and successive generations, the accuracy of different approaches needs to be evaluated.

The recent proliferation of molecular and statistical tools has led to the application of genetic tools to provide direct estimates of connectivity in marine populations (Manel et al. 2003). These genetic approaches focus on the assignment of individuals to populations of origin (assignment methods) (Carreras-Carbonell et al. 2007; Underwood et al. 2007) or to specific parents (parentage analysis). (Gerber et al. 2000; Rodzen et al. 2004; Jones et al. 2005; Castro et al. 2006) Direct estimates of retention and connectivity using assignment tests or parentage analysis can be applied using hypervariable molecular markers such as microsatellites. In assignment methods, an individual is assigned to the most likely source population, based on the expected frequency of its multilocus genotype in various putative sources. The typical assumptions of this approach are that all potential source populations are defined in advance, sampled randomly and do not depart from Hardy-Weinberg or linkage equilibrium. Newer statistical approaches that use maximum likelihood and Bayesian methods involve fewer assumptions and provide higher assignment accuracy (Manel et al. 2005). While it has also been suggested that these approaches are more effective when migration is low ($Nm < 5$) (Waples & Gaggiotti 2006) and consequently genetic structure is high (Underwood et al. 2007), the accuracy of assignment techniques at identifying natal origins at small spatial scales has rarely been examined.

In parentage analysis, individuals are assigned to one single parent or parent pair usually using a likelihood-based approach to select the most likely parent from a pool of potential parents (Jones & Ardren 2003). The main constrain of this approach is that parental allocation success declines dramatically as the proportion of sampled candidate parents drop (Marshall et al. 1998). However, methods have recently been developed that allow to deal with incomplete sampling (Gerber et al. 2003; Duchesne et al. 2005). In addition, parentage analysis assumes that there is random mating in the population. This assumption of panmixia is often violated in wild populations at larger spatial scales, but to our knowledge, no empirical studies have tested for the consequences of this violation when parentage models are used to study natural populations.

Coral reef environments are extremely patchy and resident populations of reef fishes can be spatially segregated at small spatial scales, from kilometres to 10s of kilometres (Hellberg 2007). Although fishes have pelagic larval durations that may last weeks to months, recent empirical evidence suggests a high degree of local retention of larvae (Jones et al. 1999; Swearer et al. 1999; Paris & Cowen 2004; Jones et al. 2005; Almany et al. 2007). Standard population genetic techniques vary in their ability to estimate self-recruitment and connectivity at these small spatial scales (Planes 2002), and the application of assignment tests and parentage analysis has been limited (Baums et al. 2005; Gerlach et al. 2007; Underwood et al. 2007). Jones et al. (2005) directly estimated levels of self-recruitment in a clownfish by combining parentage analysis and chemical tagging and found similar results with the two methods. More interestingly, they highlighted that parentage analysis can provide high-resolution connectivity information and direct estimates of dispersal distances at the individual level. However, while promising, the effects of violations in model assumptions require further investigation.

The aim of this study was to evaluate and compare estimates of self-recruitment and connectivity from assignment tests and parentage analysis under two different scenarios of gene flow. First, we considered a high gene flow scenario using genetic data from five spatially discrete subpopulations of the panda clownfish *Amphiprion polymnus* in Bootless Bay, Papua New Guinea. Then, we considered a low gene flow scenario by adding a data set from a genetically distinct population (Schumann Island) located more than 1500 km away in the Bismark Sea (Jones et al. 2005). As dispersal between the two locations is extremely unlikely, pooling the two locations provided a means to evaluate the effect of violating the assumption of a panmictic population when classifying parent-offspring relationships.

Materials and methods

Study species and site

The panda clownfish (*Amphiprion polymnus*) is a southeast Asian endemic fish that lives in close association with discrete aggregations of two species of anemones (*Stichodactyla hadonni* and *Heteractis crispa*) that occupy sandy habitats associated with coral reefs (Fautin & Allen 1992). Each anemone is usually occupied by one breeding pair and up to eight smaller subadults and juveniles. The female (the largest individual) lays demersal eggs on the upper surface of shells or dead coral next to the anemone. The embryos develop over a period of 6–7 days before hatching (Fautin & Allen 1992) and late stage larvae settle into anemones after a pelagic larval phase lasting 9–12 days (Thresher et al. 1989).

We used genetic data from two separate population systems in Papua New Guinea. The first system was located at Bootless Bay, nearby Port Moresby (Fig. 1) and consisted of a metapopulation of five discrete subpopulations with no individuals found in adjacent sand or coral habitats. Each population was confined to a discrete ~1-ha patch of shallow sand and sea grass separated from the other subpopulations by 2 to 6 km. At each site, an exhaustive search for all anemones colonized by *A. polymnus* was made. A total of 85 anemones and 281 adult and subadult *A. polymnus* were distributed among the five subpopulations (Fig. 1).

The second system was located at Schumann Island (Kimbe Bay, New Britain) over 1500 km to the northeast of Bootless Bay. Genetic data from Schumann Island published by Jones et al. (2005) were used to compare the utility of assignment tests and parentage analysis to correctly assign juveniles to geographically distant populations. The Schumann Island population consisted of 40 anemones and 85 adult *A. polymnus* confined to a 1-km² sand flat adjacent to the island.

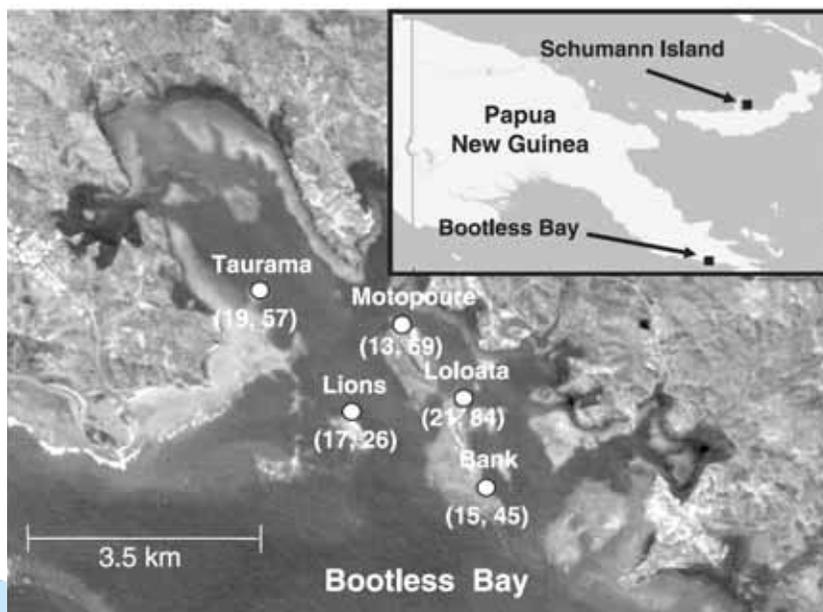


Figure 1. Satellite image showing the sites of five subpopulations of *Amphiprion polymnus* within Bootless Bay. The number of anemones and *A. polymnus* (adult and subadult) at each site are indicated in brackets. Inset: location of Bootless Bay and Schumann Island study locations in Papua New Guinea.

Sampling and genotyping

A total of 458 individuals (281 adults and subadults and 177 juveniles), representing between approximately 85% and 95% of each of the subpopulations, were sampled after extensive searches at each of the five sites. All resident fish (adult and subadult individuals) from the five sites were sampled in December 2005. Each individual was captured on SCUBA using hand nets, fin clipped underwater on site, and then released on the same anemone as captured. All juveniles present at each anemone were captured in December 2005, and at three additional times (January, April, and June 2006). All samples were preserved in 95% ethanol and returned to the laboratory for subsequent genetic analyses. The genetic data set for Schumann Island comprised 158 individuals (85 adults and 73 juveniles). Adults were finclipped in June 2003, and all juveniles settling over a 3-month period between August and October 2003 were sampled (see Jones et al. 2005 for details).

Details of genotyping procedure are described in (Quenouille et al. 2004). After DNA extraction, three multiplex polymerase chain reactions (PCR) were performed per individual, using fluorescently labelled primers to process 11 microsatellite loci containing a mixture of dimer and tetramer repeats. PCR products were processed on a Beckman Coulter sequencer CEQ 8000 Genetic Analysis System and the resulting electropherograms were scored manually. Uncertainties were resolved by re-amplification and comparison. Alleles were scored as PCR product size in base pairs. None of the 637 individuals screened shared the same diploid genotype. Allelic frequencies, allelic patterns and expected heterozygosities under Hardy–Weinberg equilibrium were calculated in genalex version 6 (Peakall & Smouse 2006). Tests for Hardy–Weinberg and linkage disequilibrium were conducted using GenePop 3.4. (Raymond & Rousset 1995) and significance levels were adjusted with sequential Bonferroni corrections for multiple tests with $P < 0.05$.

A table describing the number of samples, number of alleles, observed and expected heterozygosities for each adult and juvenile group of the 10 other loci are shown in Table S1, Supporting Information (online). While heterozygote deficits were present in at least one site at 3 of the 10 remaining loci, consistent heterozygote deficits were detected across all sites only for one locus (loc 2). This deficit suggested the presence of null alleles and consequently, this locus was also excluded from all subsequent analysis. All nine remaining loci were considered statistically independent since no linkage disequilibrium between loci pairs was observed after Bonferroni correction. One locus was excluded because of difficulties during genotyping.

Population structure

We used F-statistics via analysis of molecular variance (AMOVA) to measure the proportion of total genetic variation that is geographically structured within Bootless Bay, and between Bootless Bay and Schumann Island. This analysis was performed in genalex version 6 (Peakall & Smouse 2006) and partitioned the amount of genetic variation between regions (Bootless Bay and Schumann Island), among sites and within sites with respect to different alleles (FST). For this analysis, only the genotypes of adult and subadult individuals were used (juveniles were excluded). Tests for statistical significance for all estimates were based on 104 random permutations, and significance levels were adjusted with sequential Bonferroni correction for multiple tests. In order to facilitate comparison with other studies, standardized pairwise FST values were estimated using the AMOVA framework as described in Meirmans (2006). Finally, to visualize these genetic relationships among sites, a genetic distance matrix derived from the pairwise FST estimates was used to construct a principal coordinate analysis (PCA) graph in genalex.

Assignment tests

Assignment of juveniles was carried out using GeneClass2 (Piry et al. 2004) under the Bayesian assignment method of Rannala & Mountain (1997). This method performs better in assigning/excluding individuals to their correct population of origin than other likelihood-based and distancebased methods (Cornuet et al. 1999). Adult and subadult genotypes of each of the five sites from Bootless Bay and Schumann Island site were used as reference populations. Juveniles from all sites were then either assigned or excluded from each of the populations. We used the Monte Carlo resampling algorithm ($n = 10\,000$) of Paetkau et al. (2004) to generate statistical thresholds to decide if juveniles could be assigned or excluded. Juveniles were considered immigrants when the probability of been assigned to any population was lower than 0.05 (type I error). When a juvenile showed probabilities of assignment greater than 0.05 to only one population, it was assigned to that population. Finally, when a juvenile was assigned to more than one population (with $P > 0.5$), it was left unassigned.

Introduced error	Simulations	
	Error estimation (percentage)	
	Type I	Type II
0.01	38 ± 4.8	0.1 ± 0.3
0.001	5.8 ± 1.2	8.1 ± 1.3
0.0001	1.9 ± 0.5	8.8 ± 1.3
0	1.4 ± 0.3	9.3 ± 1.8

Table 1. Effects of variation of LOD score introduced error on parentage assignments for the Bootless Bay population. Four different error frequencies were evaluated. For each frequency, the number of assignments in relation with the number of mismatches per assignment is presented as well as the estimation of type I and II statistical errors based on 30 simulations of the parentage test

Parentage analysis

Parentage analysis was performed using famoz (Gerber et al. 2003). The program is based on the calculation of LOD (log of the odds ratio) scores for parentage relationships and the construction of statistical tests for parentage assignment. These tests are based on simulations that generate offspring from genotyped parents (Ho: the most likely parent is the true parent) or from allele frequencies in the population (Hi: the most likely parent is not the true parent). famoz allows for the introduction of an error rate in the LOD score calculation that takes genotyping errors and null alleles into account (Gerber et al. 2000). It has been shown that introduction of this error, even if it underestimated the true error rate, can reduce type I and type II errors related to the parentage tests (Gerber et al. 2000; Morrissey & Wilson 2005). We evaluated four different error rates to choose the best compromise between introduced error and type I and type II statistical errors. An error rate of 10⁻³ yielded the lowest statistical type I and type II errors using the Bootless Bay data set (Table 1) and was used for all parentage analysis. Tests evaluations were carried out using the software option 'parentage test simulation'. Thirty test simulations were made for each error rate in order to evaluate mean type I and type II statistical errors.

To test the effect of violating the assumption of a single panmictic population, parentage analysis was carried out as follows: first, Bootless Bay and Schumann Island were analysed separately. Second, both data sets (Bootless Bay and Schumann Island) were pooled together. For each analysis, allelic frequencies were estimated from the corresponding adult and subadult genotypes and these estimations were assumed to be close to the real population allele frequencies (Gerber et al. 2003). For each analysis, simulations of sets of 104 new recruits were made under the two possible hypotheses and subsequent statistical tests were constructed to decide whether a given parent would be selected as the true parent or true parent pair. The distribution of the simulated LOD scores under the two hypotheses was plotted and the intersection between them was used as the threshold decision value (individuals with LOD scores above the threshold value were accepted as true parents).

Finally, because the presence of full sib or half sib relationships can significantly bias parentage analysis (Marshall et al. 1998; Jones & Ardren 2003), all subadults less than 50 mm standard length were excluded from the analysis. While size at the beginning of sexual maturity is not known for *A. polymnus*, individuals of a congeneric species (*Amphiprion clarkii*) under 50 mm are sexually immature (Hattori & Yanagisawa 1991), and therefore subadults of this size are more likely to be either full or half sibs of juveniles than to be parents.

Effect of number and level of polymorphism of loci used

To explore the sensitivity of each method to the number of loci used, we repeated the analyses excluding the two and four least polymorphic loci and the two and four most polymorphic loci from the data set. Then we compared the percentage of assigned, unassigned and excluded juveniles at each case for assignment tests. In the same way, we compared the statistical error (type I and type II) in parentage analysis by simulating parentage tests when two or four loci were excluded.

Table 2. (A) Pairwise *F_{ST}* estimates between sites for *Amphiprion polymnus* at Bootless Bay and Schumann Island. Estimates in bold indicate significance based on 104 permutations after sequential Bonferroni corrections ($P < 0.05$ for all significant comparisons). (B) Standardized pairwise *F_{ST}* values estimated using the AMOVA framework (Meirmans 2006)

A	Bootless Bay					B	Bootless Bay				
	Bank	Lions	Loloata	Motupore	Taurama		Bank	Lions	Loloata	Motupore	Taurama
Bank	—					Bank	—				
Lions	0.007	—				Lions	0.029	—			
Loloata	0.006	0.005	—			Loloata	0.022	0.020	—		
Motupore	0.007	0.000	0.003	—		Motupore	0.029	0.000	0.013	—	
Taurama	0.026	0.017	0.021	0.016	—	Taurama	0.109	0.078	0.091	0.067	—
Schumann	0.111	0.099	0.104	0.101	0.092	Schumann	0.498	0.483	0.495	0.462	0.459

Results

Population structure

The AMOVA partitioned 9% ($F_{ST} = 0.095$) of the genetic variation between Bootless Bay and Schumann Island which was significantly different from zero ($P < 0.001$). Genetic variation among sites within regions was 1% ($F_{ST} = 0.011$) of the total variance and it was also significantly different from zero ($P < 0.001$). For the low gene flow scenario, pairwise F_{ST} comparisons showed significant differences for Schumann Island with all the Bootless Bay sites (F_{ST} values ranging from 0.092 to 0.111 — Table 2A). For the high gene flow scenario within Bootless Bay, the Taurama site showed small but significant differentiation from the other four sites (Lions, Loloata, Bank and Motupore) with F_{ST} values ranging from 0.016 to 0.026. We found no significant genetic differentiation among individuals at Lions, Loloata, Bank and Motupore. The F_{ST} PCA plot (Fig. 2) showed a close relationship among Bootless Bay sites, with Taurama been slightly separated. Schumann Island was clearly genetically distinct from all Bootless Bay sites, reflecting its geographical separation.

Assignment tests

Low gene flow. The assignment method was able to exclude all juveniles sampled in Bootless Bay as being immigrants from Schumann Island with a probability $\geq 95\%$ (Table 3). Likewise, all juveniles from Schumann Island except one were excluded from being immigrants from Bootless Bay ($P \geq 95\%$). However, the one juvenile from Schumann Island was incorrectly assigned to Bootless Bay (Loloata site) with low probability ($P = 0.08$).

High gene flow. Within Bootless Bay, 13 juveniles (7%) had a probability greater than 0.05 of belonging to only one of the five sites and were assigned to that site. A further 146 individuals (82%) had a probability greater than 0.05 of belonging to more than one of the five sites within the bay (but were excluded from Schumann Island) and were assigned to the Bootless Bay metapopulation as a whole. In addition, 15 juveniles (8.5%) had a probability lower than 0.05 of belonging to any site and were designated as being immigrants. Finally, four juveniles had a probability greater than 0.05 of belonging to either Schumann Island or Bootless Bay and were left unassigned. Within Schumann Island, 60 juveniles (70%) were assigned as having originated from the Schumann Island population, while 24 (28.2%) were excluded from both Bootless Bay and Schumann Island populations and designated as immigrants. One individual was assigned to both Schumann Island and Bootless Bay and was left unassigned.

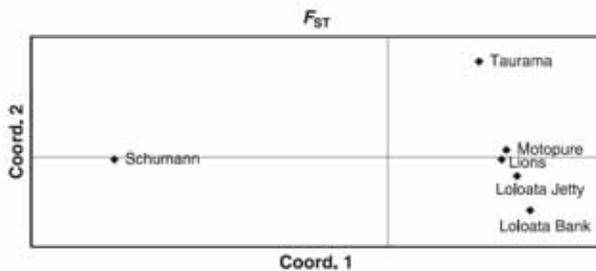


Figure 2. Plots of principal coordinate analysis calculated in genalex from standardized distance matrix of pairwise F_{ST} estimates between sites: the first two axes explain 99% of variation.

Table 3. Results of assignment analysis with GeneClass2. Juveniles were assigned to one of the six possible sites (sample size in brackets) if the likelihood of their genotype occurring in that site was greater than 0.05, when compared to a distribution of 104 simulated genotypes from that site. Juveniles that had a likelihood superior than 0.05 were considered to have originated from one of the sampled sites. Probability of belonging to the assigned population is given in brackets. If an individual's likelihood was greater than 0.05 for more than one of Bootless Bay sites, it was assigned to Bootless Bay as a single unit (all five sites). If the likelihood was greater than 0.05 for both Bootless Bay and Schumann Island, it was left unassigned. Juveniles with a likelihood less than 0.05 in all sampled sites were assumed to be immigrants

Sampling site	Assigned population					Bootless	Sch	Immigrants	Unassigned
	Ba	Li	Lo	Mo	Ta				
Ba(28)	0	1 ^(0.34)	1 ^(0.06)	1 ^(0.16)	1 ^(0.08)	24	0	1	1
Li(16)	0	1 ^(0.06)	0	0	0	13	0	2	
Lo(45)	0	0	0	2 ^(0.10) (0.12)	0	40	0	3	
Mo(59)	0	1 ^(0.15)	0	2 ^(0.14) (0.21)	2 ^(0.24) (0.42)	47	0	4	3
Ta(28)	0	0	0	0	1 ^(0.08)	22	0	5	
Sch(73)	0	0	1 ^(0.08)	0	0	0	51	21	1

Ba, Bank; Li, Lions; Lo, Loloata; Mo, Motupore; Ta, Taurama; Sch, Schumann.

Parentage analysis

Low gene flow. Parentage analysis was not robust to the deviation in panmixia introduced by pooling samples from Bootless Bay and Schumann Island (Fig. 3). For the pooled data set, 39 out of 44 (88.6%) juveniles assigned to parents in Bootless Bay (B) were reassigned there. Five individuals previously assigned to Bootless Bay were excluded, while 10 new juveniles from one of the five sites within Bootless Bay were assigned to Schumann Island. Also, one individual from Schumann Island was assigned to a parent from Bootless Bay (Fig. 3a). When the Schumann Island data were tested separately (S), 23 out of 75 juveniles (31.5%) were assigned to one of the 85 sampled parents. When these data were pooled with the Bootless Bay data (B + S), only 15 juveniles assigned when the Schumann Island data were run independently were again assigned a parent from Schumann Island. Additionally, 31 individuals were assigned within Schumann in this test and two juveniles from Schumann Island were assigned to parents in Bootless Bay (Fig. 3b).

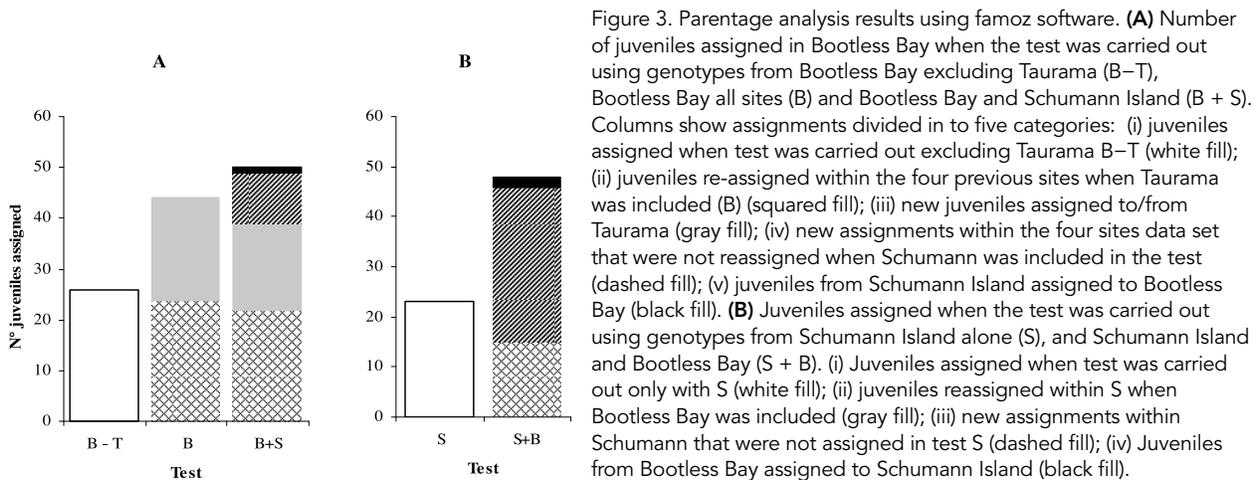


Figure 3. Parentage analysis results using famoz software. **(A)** Number of juveniles assigned in Bootless Bay when the test was carried out using genotypes from Bootless Bay excluding Taurama (B-T), Bootless Bay all sites (B) and Bootless Bay and Schumann Island (B + S). Columns show assignments divided in to five categories: (i) juveniles assigned when test was carried out excluding Taurama B-T (white fill); (ii) juveniles re-assigned within the four previous sites when Taurama was included (B) (squared fill); (iii) new juveniles assigned to/from Taurama (gray fill); (iv) new assignments within the four sites data set that were not reassigned when Schumann was included in the test (dashed fill); (v) juveniles from Schumann Island assigned to Bootless Bay (black fill). **(B)** Juveniles assigned when the test was carried out using genotypes from Schumann Island alone (S), and Schumann Island and Bootless Bay (S + B). (i) Juveniles assigned when test was carried out only with S (white fill); (ii) juveniles reassigned within S when Bootless Bay was included (gray fill); (iii) new assignments within Schumann that were not assigned in test S (dashed fill); (iv) Juveniles from Bootless Bay assigned to Schumann Island (black fill).

High gene flow. We examined the possible effect of the slight genetic differentiation among sites in Bootless Bay on the outcome of parentage analysis by analysing the data set with and without the site (Taurama) that was genetically distinct from the other four sites. When parentage analysis was conducted using the four sites within Bootless Bay excluding Taurama (B-T), 26 out of 149 juveniles were assigned to genotyped parents from these sites. When individuals (adults and juveniles) from Taurama were included in the analysis (B), 24 of the assigned juveniles from the previous analysis (92%) were reassigned to the same parents. The LOD scores (3.22 and 3.27) of the two juveniles that were not assigned to parents in the pooled analysis were, however, close to the threshold decision value (3.2). An additional 20 juveniles were assigned to parents from Taurama when this site was included.

Number of loci and degree of polymorphism

We tested the effect of reducing the number and quality of loci for the assignment test under the low gene flow scenario, and for parentage analysis under the high gene flow scenario. The performance of both methods under the opposite scenario was already unsatisfactory and therefore we did not consider the alternative scenarios further. From the nine loci from our data set, we chose the four loci with the lowest number of alleles as low polymorphic loci (loci: 65, 120, 61 and 55. Increasing number of alleles respectively). Likewise, the four loci with the highest number of alleles were selected as the high polymorphic loci (loci: 10TCTA, 79, 3GATA and 44. Decreasing number of alleles respectively) (see Table S1 for details on number of alleles per loci).

Removing two and four low polymorphic loci had relatively little impact on results from the assignment test compared to results when high polymorphic loci were excluded (Fig. 4a). The proportion of juveniles assigned to the population where they were sampled dropped by 6.4% when excluding two low polymorphic loci and by 6.8% when excluding four low polymorphic loci. When excluding two and four high polymorphic loci, juveniles assigned to the population where they were sampled dropped by 13.6% and by 40% respectively. The proportion of juveniles left unassigned (with a probability of assignment > 0.05 to both populations) changed little when two or four low polymorphic loci were excluded compared to when all loci were used. On the other hand, as many as 42.8% of the juveniles was unassigned when the four high polymorphic loci were excluded. The percentage of juveniles excluded from both populations (with a probability of assignment < 0.05 to both populations) did not change dramatically in any of the four cases.

In parentage analysis, the effect of excluding high and low polymorphic loci was similar as in assignment tests (Fig. 4b). Excluding two low polymorphic loci had no significant effect on error rates. Excluding four low polymorphic loci had an increase in error rate similar to when two high polymorphic loci were excluded. Finally, excluding four high polymorphic loci resulted in dramatic increase of type I error (~57% of wrong assigned parents). For both cases, excluding two high polymorphic loci had an effect similar as when excluding four low polymorphic loci.

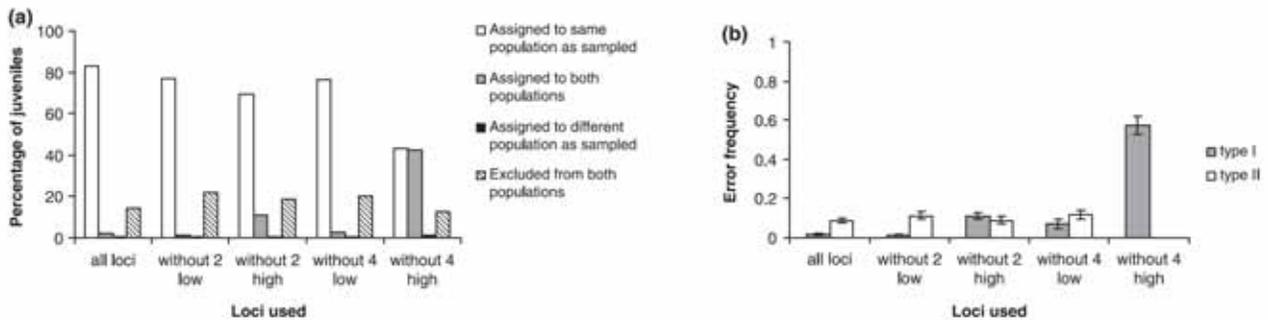


Figure 4. (a) Assignment test results under the low gene flow scenario (Bootless Bay vs. Schumann Island) using different sets. (b) Parentage analysis error rate estimates under the high gene flow scenario using different sets of loci (estimated by test simulations in famoz for each case). The lines on each bar represent the standard deviation after 30 test simulation replicates. The different sets of loci used were two low, two lowest polymorphic loci (loci 120 and 65); four low, four lowest polymorphic loci (loci 120, 65, 55 and 61); two high, two highest polymorphic loci (loci 10TCTA and 79); and four high, four highest polymorphic loci (10TCTA, 79, 3GATA and 44).

Discussion

We have demonstrated that the ability of different genetic techniques to identify natal origins of juvenile coral reef fish depends critically upon the levels of genetic structure within and among focal populations. Standard measures of population differentiation revealed the two distinct gene flow scenarios tested in this study. On one hand, gene flow was extremely limited ($F_{ST} \sim 0.1$) between Schumann Island and Bootless Bay populations of *Amphiprion polymnus*. The result was not surprising that the populations were located in different ocean basins separated by over 1500 km and that the pelagic larval duration of this species is 9–12 days (Thresher et al. 1989). Similar F_{ST} values have also been described for different populations of the same genus (*Amphiprion melanopus*) with similar geographical separation (Doherty et al. 1995). While there may be some gene flow on evolutionary timescales, this is likely to be of little relevance to local population replenishment or management. On the other hand, within the Bootless Bay we found little evidence for genetic structure among subpopulations at five sites 2–6 km apart. However, one of the sites (Taumara) was significantly different from the four other sites in the bay even though F_{ST} values were small. This was an unexpected result, given its proximity to the other populations, although it is perhaps the most isolated of the five subpopulations (Fig. 1). Another possible explanation is that the small genetic difference could be due to stochastic variability in reproductive success of past recruitment episodes (Orsini et al. 2008) rather than reproductive isolation of Taumara from the other Bootless Bay sites. Further information is needed to distinguish between these hypotheses.

Low gene flow scenario

We expected the assignment test to perform well when classifying individuals from well-differentiated populations given previous results from simulated data (Cornuet et al. 1999; Waples & Gaggiotti 2006) and from empirical studies on populations with strong genetic differentiation (Underwood et al. 2007). Our assignment tests between Bootless Bay and Schumann island populations also support this conclusion. Out of 244 juveniles classified, almost all were assigned to the regional population where they were collected. Only one juvenile from Schumann Island was assigned to the Bootless Bay population, although the assignment probability of this juvenile was fairly low (0.08) and close to the decision threshold (0.05). Given the distance between the populations, we consider this individual to be wrongly assigned by the test. Alternatively, parentage analysis was not robust to the deviation in panmixia that results from assigning parentage across two differentiated populations. When pooling both populations together, the proportion of parents assigned by both tests (each population separately and both populations pooled) was relatively low (89.6% for Bootless Bay and only 65.2% for Schumann Island). Also, a considerable number of juveniles

that were not assigned when the test was carried out within each population were assigned when the two populations were pooled (20% at Bootless Bay and 67% at Schumann Island). These new assignments were mostly to parents in the same population as the juveniles were collected in, although three juveniles were also assigned to parents in the other population. Given that levels of self-recruitment at Schumann have independently been confirmed in larval tagging studies (Jones et al. 2005), these additional parent-offspring relationships are most likely errors. Parentage analysis assumes that all offspring and parents in the data set belong to the same population and LOD scores are estimated using this population's allele frequencies (Gerber et al. 2000). Our results show clearly that significant changes in allele frequencies have major effects on parentage assignments. It is noteworthy that in our study, changes in allele frequencies on parentage assignments increased the number of wrong assignments in higher proportions than they excluded correct assignments (considering that almost all assignments obtained under each separate test were correct). These results suggest that parentage analysis is not appropriate for low gene flow scenarios, where analytical methods such as assignment tests appear to have greater utility.

High gene flow scenario

The degree of population differentiation in Bootless Bay was clearly insufficient for assignment tests to discriminate among subpopulations. The tests failed to assign most of the juveniles to any one of the five subpopulations. Only a small number of individuals were assigned to only one of the sites (13 juveniles) compared to the number of juveniles assigned to at least two sites within the bay (146). Overall, the numbers of recruits assigned to the Bootless Bay metapopulation and to Schumann Island were gross overestimates relative to the parentage analysis. In Bootless Bay, given that Taurama had a small but significant genetic signal, we expected that assignment probabilities from or to this site would be greater than to the other sites. However, we found no difference between the assignment probabilities from juveniles assigned to Taurama and juveniles assigned to the other four sites. Also, from the 13 juveniles assigned to only one site, only three were assigned to the same site as the juveniles assigned by parentage analysis at this level.

The level of accuracy of assignment tests in our study may be lower than those recorded in the literature. For example, using simulated data Cornuet et al. (1999) showed that F_{ST} values as low as 0.01 could yield to ~40% accurate assignment with this method. Carreras-Carbonell et al. (2007) using microsatellite data on *Tripterygion delaisi* in the northwest Mediterranean Sea had a similar problem when attempting to assign individuals to populations that were not genetically different, leaving ~30% of fish with unknown origins unassigned.

Parentage analysis can be considered as the method of choice for estimating retention and connectivity in small, spatially discrete, but genetically similar populations. Unlike assignment tests, they produce high-resolution patterns of self-recruitment and dispersal, and estimates of self-recruitment that have been independently tested in *A. polymnus* using larval marking (Jones et al. 2005). Although local genetic heterogeneity was a potential problem, the slight modification of allele frequencies caused by including and excluding the most genetically distinct site at Bootless Bay (Taurama) had little effect on our estimates of parentage within the four other subpopulations. Results for two juveniles apparently produced by parents from Bootless Bay when the analysis was carried out without Taurama were reversed when Taurama was included. These individuals had LOD scores close to the threshold value and therefore the probability that the identified parent is the right parent is just slightly superior to that of identifying a wrong parent from the population by chance. There were also missing alleles in the genotypes of these juveniles and we therefore suspect that changes in allele frequencies when including Taurama in the analysis had no significant consequences. This is encouraging because evidence of genetic structure at fine-spatial scale is more common than previously thought in natural populations (Fredsted et al. 2005; Neville et al. 2006; Zamudio & Wicczorek 2007).

The overall levels of self-recruitment and immigration for the two populations as estimated by assignment tests and parentage analysis were very different (Table 4). Assignment tests found 159 juveniles (90.3%) were returning to Bootless Bay populations, and in Schumann Island, the self-recruitment estimate was 70%. Parentage analysis, on the other hand, generated self-recruitment estimates of 25% and 31.5% in Bootless Bay and Schuman Island populations, respectively. We believe that estimations of recruitment at this scale based on assignment tests should be treated with caution. When estimating recruitment in marine environments at an ecological level with genetic tools, we assume that the genetic population is larger and extends further than the demographic population under study. Dispersal can maintain genetic homogeneity

over relatively large distances (Fauvelot & Planes 2002) and assignment tests may classify juveniles from the larger genetic population to the local population of interest. The discrepancy between self-recruitment estimates from assignment tests and parentage analysis for Bootless Bay and Schumann Island suggests that close to 65% and 40% respectively of juveniles assigned by GeneClass2 originated from nearby, genetically similar populations. It is also possible that our parentage analysis has underestimated self-recruitment, because other members of the local populations have yet to be discovered. Other studies of clownfish have shown estimates of self-recruitment as high as 60% (Almany et al. 2007).

The assignment method performed by GeneClass2 has the advantage that it takes in to account the possibility of not having sampled all potential populations (Piry et al. 2004). Using this procedure, we found that 8.5% of the new recruits sampled in Bootless Bay and 28.2% of new recruits from Schumann Island came from distinct genetic populations that we failed to characterize. Even if the origin of these juveniles cannot be established, the fact that they were excluded from all sampled populations means that their population of origin is likely to be distant and genetically distinct from the other incorrectly classified individuals, which are likely to have dispersed from nearby populations. The genetically distinct individuals could have travelled long distances before settling on the anemones and therefore correspond to the tail of the distribution of recruitment vs. geographical distance. As this information cannot be obtained using parentage analysis, assignment tests may represent a useful technique for defining the tail end of the dispersal kernel. The complementary use of the two techniques may be the best way to define the dispersal kernel as a whole.

Number and polymorphism of loci used

Simulation studies have shown that for a given level of differentiation, adding loci usually improves the ability to assign individuals correctly among populations (Cornuet et al. 1999; Waples & Gaggiotti 2006). We found that the quality of loci had a more significant effect than simply the number of loci used. Simulation results have shown that low polymorphic loci produced less accurate assignments than high polymorphic ones (Waples & Gaggiotti 2006), and our results confirmed this situation. This is not surprising since high levels of polymorphism are related to high mutation rates. As gene flow increases, highly polymorphic loci are more informative because new alleles are constantly being generated within subpopulations and shorter times of isolation are needed to detect small population differentiation. At the same time, in parentage analysis, exclusion probabilities are strongly conditioned by the genotypes of the reported relatives, by the frequency of alleles and by the number of loci (Jamieson & Taylor 1997). These exclusion probabilities increase with the number of loci used and their level of polymorphism. In our study, parentage error rates increased more when high polymorphic loci were excluded than they did when low polymorphic ones were excluded, demonstrating again that quality of the loci used is more important than quantity.

Table 4. Comparison of the different estimates obtained with each of the two methods under the high gene flow scenario

Method	Within sites self-recruitment	Local connectivity	Overall self-recruitment	Immigrants/unassigned
Bootless Bay				
Assignment	2.2%	5.1%	90.3%	8.5%/2.2%
Parentage	10.0%	15.0%	25.0%	75.0%
Schumann				
Assignment			69.9%	28.8%/1.4%
Parentage			31.5%	68.5%

Conclusions

While assignment tests perform well at spatial scales over which populations show large genetic differentiation, parentage analysis appears to be a better choice for estimating dispersal at smaller scales among genetically similar populations. Using genetic methods such as assignment tests when trying to measure connectivity at ecologically relevant scales where migration is high enough to maintain genetic homogeneity remains challenging because these methods still have relatively little power under these circumstances. Parentage analysis on the other hand performs well in conditions of high gene flow. However, incomplete sampling of potential parents can be a major drawback. New likelihood approaches such as the one used in this study need further evaluation to assess this problem. Both techniques appear to lead to overestimates of self-recruitment when applied at scales over which assumptions of the approaches are violated. As parentage analysis appears to be robust to small deviations from panmixia, there may be some intermediate level of differentiation at which both techniques provide useful results. Parentage becomes increasingly difficult to apply as the scale of the study and size of the population increases because the accuracy of assignments relies heavily on the fraction of potential parents sampled. However, more research is needed to explore these new likelihood-based parentage methods to quantify their performance under different parental sampling scenarios. Ultimately, a combination of both parentage and assignment tests may be the best way to fully describe dispersal kernels and estimate the scale of demographically important connectivity in marine populations.

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References

- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science*, 316, 742–744.
- Armsworth PR (2002) Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology*, 83, 1092–1104.
- Baums IB, Miller MW, Hellberg ME (2005) Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology*, 14, 1377–1390.
- Carreras-Carbonell J, Macpherson E, Pascual M (2007) High self-recruitment levels in a Mediterranean littoral fish population revealed by microsatellite markers. *Marine Biology*, 151, 719–727.
- Castro J, Pino A, Hermida M et al. (2006) A microsatellite marker tool for parentage analysis in Senegal sole (*Solea senegalensis*): Genotyping errors, null alleles and conformance to theoretical assumptions. *Aquaculture*, 261, 1194–1203.
- Cornuet J-M, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics*, 153, 1989–2000.
- Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner F (2007) Population connectivity in marine systems. An overview. *Oceanography*, 20, 14–21.
- Doherty PJ, Planes S, Mather P (1995) Gene flow and larval duration in seven species of fish from the great barrier reef. *Ecology*, 76, 2373–2391.
- Duchesne P, Castric T, Bernatchez L (2005) PASOS (parental allocation of singles in open systems): a computer program for individual parental allocation with missing parents. *Molecular Ecology Notes*, 5, 701–704.
- Fautin DC, Allen GR (1992) *Field Guide to Anemonefishes and Their Host Sea Anemones*. Western Australia Museum, Perth, Australia.
- Fauvelot C, Planes S (2002) Understanding origins of present-day genetic structure in marine fish: biologically or historically driven patterns? *Marine Biology*, 141, 773–788.
- Fredsted T, Pertoldi C, Schierup MH, Kappeler PM (2005) Microsatellite analyses reveal fine-scale genetic structure in grey mouse lemurs (*Microcebus murinus*). *Molecular Ecology*, 14, 2363–2372.
- Gerber S, Mariette S, Streiff R, Bodenes C, Kremer A (2000) Comparison of microsatellites and amplified fragment length polymorphism markers for parentage analysis. *Molecular Ecology*, 9, 1037–1048.
- Gerber S, Chabrier P, Kremer A (2003) famoz: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. *Molecular Ecology Notes*, 3, 479–481.
- Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences, USA*, 104, 858–863.
- Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. *Ecological Applications*, 13, S65–S70.
- Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences, USA*, 103, 6067–6072.
- Hattori A, Yanagisawa Y (1991) Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environmental Biology of Fishes*, 31, 139–155.

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- Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. *Oceanography*, 20, 70–79.
- Hellberg M (2007) Footprints on water: the genetic wake of dispersal among reefs. *Coral Reefs*, 26, 463–473.
- James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: modeling larval dispersal and retention patterns. *Proceedings of the Royal Society B: Biological Sciences*, 269, 2079–2086.
- Jamieson A, Taylor SS (1997) Comparisons of three probability formulae for parentage exclusion. *Animal Genetics*, 28, 397–400.
- Jones AG, Ardren WR (2003) Methods of parentage analysis in natural populations. *Molecular Ecology*, 12, 2511–2523.
- Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature*, 402, 802–804.
- Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Current Biology*, 15, 1314–1318.
- Lockwood DR, Hastings A, Botsford LW (2002) The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theoretical Population Biology*, 61, 297–309.
- Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18, 189–197.
- Manel S, Gaggiotti OE, Waples RS (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology & Evolution*, 20, 136–142.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, 7, 639–655.
- Meirmans PG (2006) Using the AMOVA framework to estimate a standardized genetic differentiation measure. *Evolution*, 60, 2399–2402.
- Morrissey MB, Wilson AJ (2005) The potential costs of accounting for genotypic errors in molecular parentage analyses. *Molecular Ecology*, 14, 4111–4121.
- Neville HM, Isaak DJ, Dunham JB, Thurow RF, Rieman BE (2006) Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. *Molecular Ecology*, 15, 4589–4602.
- Orsini L, Corander J, Alasentie A, Hanski I (2008) Genetic spatial structure in a butterfly metapopulation correlates better with past than present demographic structure. *Molecular Ecology*, 17, 2629–2642.
- Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*, 13, 55–65.
- Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*, 13, 146–158.
- Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography*, 49, 1964–1979.
- Peakall ROD, Smouse PE (2006) genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, 6, 288–295.
- Piry S, Alapetite A, Cornuet JM et al. (2004) GeneClass2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity*, 95, 536–539.
- Planes S (2002) Biogeography and larval dispersal inferred from population genetic analysis. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. Sale P), pp. 201–220. Academic Press, San Diego, California.
- Quenouille B, Bouchenak-Khelladi Y, Hervet C, Planes S (2004) Eleven microsatellite loci for the saddleback clownfish *Amphiprion polymnus*. *Molecular Ecology Notes*, 4, 291–293.
- Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences, USA*, 94, 9197–9201.
- Raymond M, Rousset F (1995) GenePop (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248–249.
- Rodzen JA, Famula TR, May B (2004) Estimation of parentage and relatedness in the polyploid white sturgeon (*Acipenser transmontanus*) using a dominant marker approach for duplicated microsatellite loci. *Aquaculture*, 232, 165–182.
- Sale PF, Cowen RK, Danilowicz BS et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, 20, 74–80.
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature*, 402, 799–802.
- Thresher RE, Colin PL, Bell L (1989) Planktonic duration, distribution and population structure of Western and Central Pacific Damsel fish (Pomacentridae). *Copeia*, 1989, 420–434.
- Underwood JN, Smith LD, Van Oppen MJH, Gilmour JP (2007) Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology*, 16, 771–784.
- Van Oppen MJH, Gates RD (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, 15, 3863–3883.
- Waples RS, Gaggiotti O (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, 15, 1419–1439.
- Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms and consequences. *Bulletin of Marine Science*, 70S, 245–249.
- Zamudio KR, Wicczorek AM (2007) Fine-scale spatial genetic structure and dispersal among spotted salamander (*Ambystoma maculatum*) breeding populations. *Molecular Ecology*, 16, 257–274.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1 Summary of genetic variation for ten microsatellite loci at five sampling sites in Bootless bay (BA: Loloata Bank, LI: Lion Island, LO: Loloata Jetty, MO: Motopoure Island, Ta: Taurama). N, number of analysed individuals; Na, number of alleles; Ho and He, observed and expected heterozygosity respectively; Fis, inbreeding coefficient, significant values ($p < 0.05$ after Bonferroni corrections) are in Bold capitals

Kirk Kilfoyle

Experimental methods of coral reef restoration: implementing a standardized module intervention and monitoring program in Mexico



Kirk earned a B.S. in marine biology from Texas A&M University at Galveston in 1999, and worked for several years as a field/laboratory technician, scientific diver, and fisheries observer for the NOAA Fisheries Service until returning to school. In 2005 he entered the Master of Science program in marine biology at Nova Southeastern University Oceanographic Center in Fort Lauderdale, FL, working in the Ichthyology laboratory and studying coral reef restoration and artificial reef applications. After graduating in 2008, he decided to remain at NSUOC and enter the PhD program, continuing his research on experimental coral reef restoration.



Experimental methods of coral reef restoration: implementing a standardized module intervention and monitoring program in Mexico

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Coral reef degradation on a global scale has been both well documented and well publicized in recent years (Bryant et al., 1998; Wilkinson, 2008). Coral reefs have always been affected by a wide range of natural disturbances. However, a host of relatively new anthropogenic factors are arguably affecting coral reefs more significantly than the combined forces of most natural impacts, and are increasing in frequency worldwide for a variety of reasons that are generally associated with overexploitation, coastal development, poor land management practices, and climate change (Hughes, 1994; Bryant et al., 1998; Kojis and Quinn, 2001; Moberg and Ronnback, 2003; Bellwood et al., 2004; Wilkinson, 2008; Hoegh-Guldberg et al., 2007). Although reefs have an exceptional adaptive capacity to recover from stresses, both naturally and anthropogenically induced, it is commonly agreed the combined influence of these disturbances is leading to directional changes in the structure of coral reef ecosystems (Wilson et al., 2006), and in many regions of the world the ability to recover is being increasingly pushed to the limit and, perhaps in many instances, well beyond (Bell et al., 2006).

To combat some of these negative impacts, the efficacy and applicability of many different methods of coral reef restoration are being tested for use in the coral reef environment. In regard to natural resource management, the most widely accepted definition of restoration is as follows: the process of assisting recovery, in terms of structure and ecological function, of an ecosystem that has been degraded, damaged, or destroyed, to a close approximation of its condition prior to disturbance (Davis and Slobodkin, 2004; Precht and Robbart, 2006). However, reef restoration is a science still very much in its formative stages, and as such there remains much to be learnt about restoring these complex ecosystems. Despite best intentions, most restoration projects have fallen short of returning damaged areas to their original condition prior to disturbance, resulting in more of an 'enhancement' or 'rehabilitation' rather than true 'restoration' (Moberg and Ronnback, 2003).

In some cases, the greatest restoration success may be achieved by simply allowing natural recovery to run its course. Certain reefs exist in regions with minimal anthropogenic impact and ideal water quality, and possess relatively high levels of natural resilience, high rates of coral recruitment, and a high degree of connectivity with other healthy reefs (Connell, 1997; Quinn and Kojis, 2006). If the natural structural framework is left intact, these reefs have a high likelihood of recovering on their own. However, in most cases some of the key conditions conducive to natural recovery are diminished or lacking altogether. If direct intervention is not applied in such cases following an anthropogenic disturbance, one or more of several results may occur. The coral reef ecosystem may not recover on its own (Pratt, 1994), and may shift to an alternate and/or less-desirable state (Hughes, 1994; Bellwood et al., 2004; Edwards and Gomez, 2007), or may take an exceptionally long time to recover and cause varying negative socio/economic impacts. Due to the fact that mechanisms of coral reef recovery and patterns of relative abundance and succession on coral reefs remain poorly understood (Hughes and Connell, 1999), it stands to reason that given slow rates of natural recovery and increasing levels of anthropogenic stress, some method of intervention (such as restoration) seems both well justified and increasingly essential in many cases. Thus, one of the major debates in reef restoration is centered on when, where, and how much direct intervention is warranted, and how best to apply limited resources following reef degradation.

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To address some of these questions, scientists and concerned individuals have been developing new ideas and techniques to improve the knowledge-base of coral reef restoration. Some actions, such as stabilizing shifting substrates or rebuilding reef framework, can assist in accelerating the process of natural recovery by creating conditions which are favorable to settlement of reef-building corals, in turn making the area more attractive to reef fishes and other mobile reef inhabitants. Enhanced complexity and heterogeneity of reef substrate has been shown to provide greater selection of niche availability and refuge from predation (Duedall and Champ, 1991; Perkol-Finkel et al., 2006) and has been shown to have positive effects on species richness, abundance, and size distribution of both reef fish (Figure 1) and invertebrate assemblages (Gittings, 1988; Hixon and Beets, 1989; Hixon and Beets, 1993; Edwards and Clark, 1998; Spieler et al., 2001; Lindahl, 2003; Zimmer, 2006). Coral cover has also been directly related to abundance of reef fishes (Bell and Galzin, 1984; Sale, 1991), with observed declines in abundance and species richness following loss of live coral cover; indicative of increased mortality and/or movement of fishes to more favorable habitats due to loss of shelter and food resources (Jones et al., 2004; Wilson et al., 2006).



Figure 1. A large aggregation of juvenile grunts (*Haemulidae*) seeking refuge on an artificial reef.

Most reef restoration projects in the past have dealt with the use of artificial reefs (ARs) as potential tools for restoration and rehabilitation (Clark and Edwards, 1999; Seaman, 2000; Spieler et al., 2001; Perkol-Finkel et al., 2006); however, their increasingly popular use for purposes of coral reef restoration in recent years remains a controversial issue. Many commercially available and mass produced AR designs have acquired seemingly unjustifiable reputations as positive drivers of successful reef restoration, often chosen because of their popularity or without regard for underlying ecological rationale (Rinkevich, 2005). Obviously, ARs are inherently 'artificial', and their use automatically removes true 'restoration' from the list of achievable goals. They typically require a conditioning period, during which their substrates become more amenable to colonization by corals and other benthic invertebrates, and it is argued that even 'mature' artificial reefs cannot accurately host a 'natural' coral reef biotic assemblage in even the best of conditions (Pearson, 1981; Reyes and Yap, 2001; Spieler et al., 2001). Multiple studies have examined how structurally complex artificial substrates (typically used for environmental monitoring) are able to replicate certain aspects of the natural environment (eg micro-habitats) and host a natural assemblage of infaunal and meiofaunal organisms (Atilla et al., 2003; Mirto and Danovaro, 2004). Some researchers have theorized that the addition of similar artificial substrates (Figure 2)

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to AR surfaces on coral reefs can mediate predation on meiofauna (Russo, 1987) and assist in the creation of 'more natural' conditions, as well as provide positive spill-over effects on biodiversity and abundance of other associated biota (Robinson and Thomas, 2000; Robinson et al., 2008; Robinson and Messing, 2009). Others researchers are evaluating the efficacy of coral transplantation and new coral 'gardening' methods (Rinkevich, 2000; Epstein et al., 2001; Rinkevich, 2006). The addition of coral transplants has been hypothesized to enhance coral recruitment onto artificial or degraded substrates (Harriott and Fisk, 1988; Oren and Benayahu, 1997; Edwards and Clark, 1998; Epstein et al., 2001; Reyes and Yap, 2001; Epstein et al., 2003; Gleason et al., 2003; Zimmer, 2006). The potential ability to enhance recruitment presumably results from both the settlement of conspecifics near adult colonies and settlement of propagules from the transplants directly onto the nearby un-colonized substrate. Supporting results to date have been minimal and more research is needed in order to further refute or substantiate this theory.



Figure 2. A small sample of novel invertebrate enhancing artificial substrate pad material. Large sections of this material will be attached to the exterior of select experimental ARs.

In an effort to more thoroughly examine some of these techniques, an experimental project was initiated to study the effects of direct restorative intervention on standardized substrate modules (Reefballs™) at the Mesoamerican Center of Excellence in Puerto Morelos, Mexico. This project operates on two main hypotheses: 1) Addition of a novel invertebrate enhancing artificial substrate (Figure 2 and 3) to restoration structure will affect (likely enhance) resulting fish and coral assemblages, as well as enhance the return of a "more natural" coral reef ecosystem; and 2) The addition of coral transplants (Figure 4) to restoration structure will affect (likely enhance) settling dynamics of potential coral recruits and resulting fish assemblages. This study examined multiple recovery parameters as they related to the experimental treatments (controls, artificial invertebrate enhancing substrate pads, and coral transplants), including: rates of coral recruitment, rates of coral growth, rates of coral survival, fish community composition and abundance, non-coral invertebrate composition and abundance, algal growth and major groupings of algae, and diversity and areal coverage of other taxa competing for space. These parameters were monitored bi-annually for a period of three years post-deployment and compared to similar or identical parameters on the adjacent natural reef.



Figure 3. Substrate module with artificial invertebrate enhancing substrate pad treatment applied to the exterior.



Figure 4. An *Agaricia agaricites* coral transplant.

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Field work for this project was completed in September 2009 and final analysis of the data is still pending. Initial results indicate species-specific differences for fish abundance and species richness between controls, artificial substrate pads, and coral transplants. A total of 60 coral colonies from three species ($n=20 \times 3$) were transplanted onto the substrate modules: *Agaricia agaricites*, *Montastrea annularis*, and *Porites astreoides*. Over the three year period, *Porites* and *Agaricia* retained the best overall health and highest growth rates; although results have been confounded by the presence of an aggressive encrusting sponge (*Holopsamma helwigi*), which killed approximately 20% and negatively impacted a further 33% of all transplants (Figure 5). Coral recruitment onto the substrate modules does not seem to have been significantly affected by any of the experimental treatments, although coral recruits/m² appears to be directly correlated with percent coverage by the overgrowing sponge.



Figure 5. A *Montastrea annularis* coral transplant in the process of being overgrown by the encrusting sponge *Holopsamma helwigi*.

The results of this project are intended to bridge some of the information gaps and eliminate much of the inherent guesswork associated with many restoration projects to date, as well as help build an increasingly comprehensive knowledge base for marine resource managers to use in the decision-making process. Currently, there are no proven and established methods of restoring coral reefs that can be applied with any degree of certainty in every situation, regardless of geographic location or the nature and extent of damage (Edwards and Gomez, 2007). Moderate success has been achieved in some localized areas, but methodologies that may appear successful in one region may be completely ineffective in another, and results may even vary within small areas due to the inherent variability of the marine environment. The unprecedented decline in global reef health dictates that more effort must be made on the part of coral reef researchers and managers to enhance our capacity to make decisions that will have relevant and lasting positive outcomes.

3. New tools for understanding and managing coral reef systems

References

- Atilla N, Wetzel MA, Fleeger JW (2003) Abundance and colonization potential of artificial hard substrate-associated meiofauna. *Journal of Experimental Marine Biology and Ecology* 287: 273-287
- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15: 265-274
- Bell JD, Ratner BD, Stobutzki I, Oliver J (2006) Addressing the coral reef crisis in developing countries. *Ocean and Coastal Management* 49: 976-985
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- Bryant D, Burke L, McManus J, Spalding M (1998) *Reefs at Risk - A Map-Based Indicator of Threats to the World's Coral Reefs*. World Resources Institute, Washington D.C., 56 pp
- Clark S, Edwards AJ (1999) An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 5-21
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16(Supplement): S101-S113
- Davis MA, Slobodkin LB (2004) The science and values of restoration ecology. *Restoration Ecology* 12(1): 1-3
- Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent over estimations: 'objective' is not always better. *Marine Ecology Progress Series* 96: 93-100
- Duedall IW, Champ MA (1991) Artificial reefs: Emerging science and technology. *Oceanus* 34(1): 94-101
- Edwards AJ, Clark S (1998) Coral Transplantation: A useful management tool or misguided meddling? *Marine Pollution Bulletin* 37: 474-487
- Edwards AJ, Gomez ED (2007) Reef restoration concepts and guidelines: Making sensible management choices in the face of uncertainty. *Coral Reef Targeted Research and Capacity Building for Management Programme*. St. Lucia, Australia. iv + 38 pp
- Epstein N, Bak RPM, Rinkevich B (2001) Strategies for Gardening Denuded Coral Reef Areas: The Applicability of Using Different Types of Coral Material for Reef Restoration. *Restoration Ecology* 9(4): 432-442
- Epstein N, Bak RPM, Rinkevich B (2003) Applying forest restoration principles to coral reef rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13: 387-395
- Gittings SR, Bright TJ, Choi A, Barnett RR (1988) The recovery process in a mechanically damaged coral reef community: recruitment and growth. *Proceedings of the Sixth International Coral Reef Symposium, Volume 2*: 225-230
- Gleason DF, Brazeau DA, Munfus D (2003) Can self-fertilizing coral species be used to enhance restoration of Caribbean reefs? *Bulletin of Marine Science* 69(2): 933-943
- Harriott VJ, Fisk DA (1988) Coral transplantation as a reef management option. *Proceedings of the 6th International Coral Reef Symposium* 2: 375-379
- Hixon MA, Beets JP (1989) Shelter Characteristics and Caribbean Fish Assemblages: Experiments with Artificial Reefs. *Bulletin of Marine Science* 44(2): 666-680
- Hixon MA, Beets JP (1993) Predation, prey refuge, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63: 77-101
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez ED, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioiols ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences*, Vol. 101, no. 21: 8251-8253
- Lindahl U (2003) Coral reef rehabilitation through transplantation of staghorn corals: effects of artificial stabilisation and mechanical damages. *Coral Reefs* 22: 217-223
- Kojis BL, Quinn NJ (2001) The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bulletin of Marine Science* 69(2): 967-974
- Mirto S, Danovaro R (2004) Meiofaunal colonization on artificial substrates: a tool for biomonitoring the environmental quality on coastal marine systems. *Marine Pollution Bulletin* 48: 919-926
- Moberg F, Ronnback P (2003) Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean and Coastal Management* 46: 27-46
- Oren U, Benayahu Y (1997) Transplantation of juvenile corals: a new approach for enhancing colonization of artificial reefs. *Marine Biology* 127: 499-505
- Pearson RG (1981) Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 4: 105-122
- Perkol-Finkel S, Shashar N, Benayahu Y (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. *Marine Environmental Research* 61: 121-135
- Pratt JR (1994) Artificial habitats and ecosystem restoration: Managing for the future. *Bulletin of Marine Science* 55(2-3): 268-275
- Precht WF, Robbart M (2006) Coral Reef Restoration: The Rehabilitation of an Ecosystem under Siege. In Precht WF (ed), *Coral Reef Restoration Handbook* (pp. 1-24). Boca Raton, Taylor and Francis
- Quinn NJ, Kojis BL (2006) Natural Resilience of Coral Reef Ecosystems. In W. F. Precht (ed), *Coral Reef Restoration Handbook* (pp. 61-75). Boca Raton, Taylor and Francis
- Reyes MZ, Yap HT (2001) Effect of Artificial Substratum Material and Resident Adults on Coral Settlement Patterns at Danjungan Island, Philippines. *Bulletin of Marine Science* 69(2): 559-566
- Rinkevich B (2000) Steps towards the evaluation of coral reef restoration by using small branch fragments. *Marine Biology* 136(5): 807-812
- Rinkevich B (2005) Conservation of Coral Reefs through Active Restoration Measures: Recent Approaches and Last Decade Progress. *Environmental Science and Technology* 39(12): 4333-4342
- Rinkevich B (2006) The Coral Gardening Concept and the Use of Underwater Nurseries: Lessons Learned from Silvics and Silviculture. In Precht WF (ed), *Coral Reef Restoration Handbook* (pp. 291-302). Boca Raton, Taylor and Francis
- Reyes MZ, Yap HT (2001) Effect of Artificial Substratum Material and Resident Adults on Coral Settlement Patterns at Danjungan Island, Philippines. *Bulletin of Marine Science* 69(2): 559-566

3. New tools for understanding and managing coral reef systems

- Robinson J, Thomas J (2000) Measure of mesobenthic diversity: a pilot study using 3-dimensional artificial substrates as a surrogate for natural substrata. Poster session presented at: Crustacean Society Summer Meeting, Puerto Vallarta, Mexico
- Robinson J, Robinson L, Buskirk B, Spieler RE (2008) Effects of a novel invertebrate substrate on assemblages of fish associated with concrete modules. Poster session presented at: 11th International Coral Reef Symposium, Fort Lauderdale, FL
- Robinson J, Messing C (2009) A comparison of mesobenthic amphipod diversity on 3-dimensional artificial substrates versus natural substrates in a shallow coral reef environment. Poster session presented at: Benthic Ecology Meeting, Corpus Cristi, TX
- Russo AR (1987) Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. *Marine Ecology Progress Series* 36: 101-105
- Sale PF (ed) (1991) *The Ecology of Fishes on Coral Reefs*. San Diego, Academic Press: 754 pp
- Seaman WJ (ed) (2000) *Artificial reef evaluation with application to natural marine habitats*. Boca Raton, Taylor and Francis: 246 pp
- Spieler RE, Gilliam DS, Sherman RL (2001) Artificial substrate and coral reef restoration: what do we need to know what we need? *Bulletin of Marine Science* 69(2): 1013-1030
- Wilkinson C (ed) (2004) *Status of Coral Reefs of the World: 2004, Volume I*. Townsville, Queensland, Australia, Australian Institute of Marine Science: 302 pp
- Wilkinson C (ed) (2008) *Status of Coral Reefs of the World: 2008*. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia, 296 pp
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12: 2220-2234
- Zimmer B (2006) Coral Reef Restoration: An Overview. In Precht WF (ed), *Coral Reef Restoration Handbook* (pp. 39-59). Boca Raton, Taylor and Francis



CRTR e-News
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Keeping watch in the Caribbean

Two decades ago coastal development along the Yucatan Peninsula was fixed on Cancun City but, as this location has become Mexico's leading vacation spot, development has slowly made its way to the south. Indeed, Playa del Carmen is now one of the fastest growing cities in Latin-America.

The coral reefs are responsible for Cancun's success. It is vital to the prosperity of the region to ensure their protection in spite of the coastal development.

This setting has allowed for a sampling design project that will test hypothesis on the effect of coastal development and protection status on the health of coral reefs. CRTR student Adán Guillermo Jordán-Garza, together with other Mexican students and colleagues from Cornell University, has participated in a huge sampling effort that covers a set of environmental conditions.

As part of the Disease Working Group, Adán has been working under the tutelage of Dr. Eric Jordán Dahlgren, who leads ecological research on the Mexican Caribbean at the Universidad Nacional Autónoma de México (UNAM) research station in Puerto Morelos.

Now that the first samplings are complete, researchers are turning their efforts to explaining their findings in publications. Interesting results and opportunities are emerging, including the development of a simple deterministic epidemiological model, which Adán, who is particularly interested in the impact of disease on coral populations.

Chris M. Roelfsema

A web based toolkit for using remote sensing to map and monitor marine environments



Chris has been at the University of Queensland (UQ) since 1999, first as a research assistant and currently as a postdoctoral research fellow with the Centre For Spatial Environmental Research. He has a PhD in Coral Reef Remote Sensing (2009), a PG.Dip. in Marine Science (1999), a MSc. Geodetic Engineering (1992), and a BSc in Hydrographic Surveying (1986). Prior to coming to UQ, Chris's experience included a year hydrographic surveying on the North Sea and Scotland; two years developing Geographic Information Systems for the Dutch civil service; and two years as a scuba diving instruction in Jamaica and Malaysia. His special interests include the development and implementation of techniques, integrating field and remote sensing data, for monitoring and management of coral reef and seagrass habitats throughout developing countries; and capacity building of the developed innovative and cost effective techniques, which can be applicable for a range of monitoring agencies.



A web based toolkit for using remote sensing to map and monitor marine environments

www.gpem.uq.edu.au/cser-rstoolkit

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Introduction

Maps derived from airborne and satellite imaging systems provide reliable and cost effective information for monitoring, modeling and managing marine environments. As the number of commercial and free airborne and satellite image types increases, along with easier access to public domain and open-source image processing approaches, the choice of which data and processing approach(es) to use is confusing. To enable technicians, scientists and managers to make the most appropriate selection of data and a processing approach for a specific environment and application, an interactive, web-based toolkit was created.

The aim of the toolkit's is to show managers, scientists and technicians working in marine environments how images collected from satellites and aircraft can be used to map and monitor changes to commonly used indicators of coastal ecosystem health.

The toolkit guides users through the process of selecting remotely sensed data to map a specific biophysical variable in the marine environment, and then outlines the processing and resource requirements and likely costs for implementing such a project. Detailed descriptions are provided for the type(s) of image data required, along with the type of processing approach and requisite personnel, hardware and software. The toolkit also provides examples of different mapping applications, and brief explanations of how remote sensing technologies work, as well as references or resource material.

The web based toolkit

The toolkit can be explored through either the text and tables version or through a graphical user interface (GUI) version (Figure 1). The GUI is structured by a conceptualisation of the different monitoring options, marine environments and biophysical variables to be mapped or monitored.

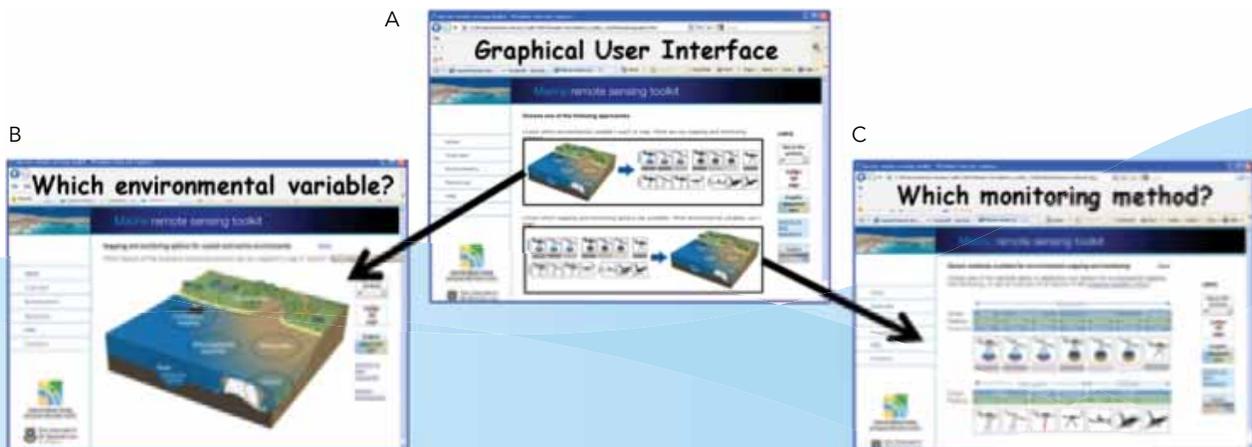


Figure 1. Screen shots of the user interface web based toolkit. Once in the toolkit the user needs to decide (a): to determine a remote sensing monitoring approach for a specific monitoring value (b) or what monitoring value can be monitored with specific monitoring options (c).

3. New tools for understanding and managing coral reef systems

Before assessing what monitoring options are available, the user of the toolkit is advised to complete the user's needs table (Table 1). This table forces the user to define his/her mapping or monitoring needs in the terms that can be used to objectively select suitable image data sets and processing approaches.

Table 1. Example of the User's needs table, which is designed to capture key information on the environment being mapped and the required mapping information to objectively evaluate image data and processing techniques.

Required information to use remotely sensed data for monitoring	Your mapping or monitoring requirements					
	Coastal ecosystem health indicator(s)					
Extent of area to be mapped and monitored	0-50 km ²	50-250 km ²	250-500 km ²	500-5,000 km ²	5,000-50,000 km ²	50,000 km ²
Minimum size of feature to be mapped (i.e. the object you want to see)	extremely fine <5m	fine 5-20m	medium 20-250m	coarse 250-1000m	extremely coarse >1000m	—
Level of minimum measurement precision (i.e. smallest measurable change in % coral cover)	0-5%	5-10%	10-25%	25-50%	anything	—
Level of minimum measurement accuracy (i.e. required acceptable agreement between estimated and actual value of % coral cover)	anything	Low 10-40%	Medium 40-70%	High 70-90%	Very High 90-100%	—
Time period over which maps are to be updated (e.g. annually)	1-24 hours	1 day	1 week	1 month	3 months	3-5 years
Reason for mapping driven by	Once-off project (e.g. design harbour)	Once-off project, but recurring for other sites	Event based (e.g. bleaching, vessel grounding)	Continuous over time (e.g. 3 yearly seagrass cover)	Retrospective (e.g. mangrove dieback)	—
Access to study site	Easy	Only on demand	Difficult - too remote	Difficult - too many different sites	Dangerous (e.g. crocodiles)	no access
Format information is to be delivered as	Tabular, graphic or numeric summary	Hardcopy map	Digital spatial data	—	—	—

Following the user's needs review, the user can choose with the graphical user interface (Figure 1a) which image data and processing options are available for a specific biophysical parameter and environment (Figure 1b); or which biophysical parameter and environment can be mapped or monitored with a specific image data and processing option (Figure 1c).

To assess which image data and processing option can map a specific biophysical variable (Figure 1b) the variable type needs to be selected (e.g. benthic habitat) (Figure 2a). Within benthic habitats the user needs to decide which type of benthic feature needs to be assessed (e.g. coral reefs) and at what spatial scale (e.g. benthic community scale) (Figure 2b). The last step is to determine for what type of water clarity (e.g. clear-turbid) and depth (e.g. sub-tidal shallow) (Figure 2c).



Figure 2. Examples of the selection and option phases of the marine remote sensing toolkit. Once a benthic mapping application (a) is chosen, e.g. coral reef habitat mapping, the level of spatial detail is then set (b), followed by the environment and depth conditions (c). All of these conditions are used to find out what image data and processing options are operational.

Another approach assesses what biophysical can be mapped using a specific sensor. This is achieved by first selecting the sensor type (e.g. airborne multi-spectral) (Figure 1c) and then reviewing the various biophysical variables and environments (Figure 2b). Once one is chosen case studies can be reviewed (Figure 3b) or complete overview is available in the capability matrix (Figure 3c).

3. New tools for understanding and managing coral reef systems

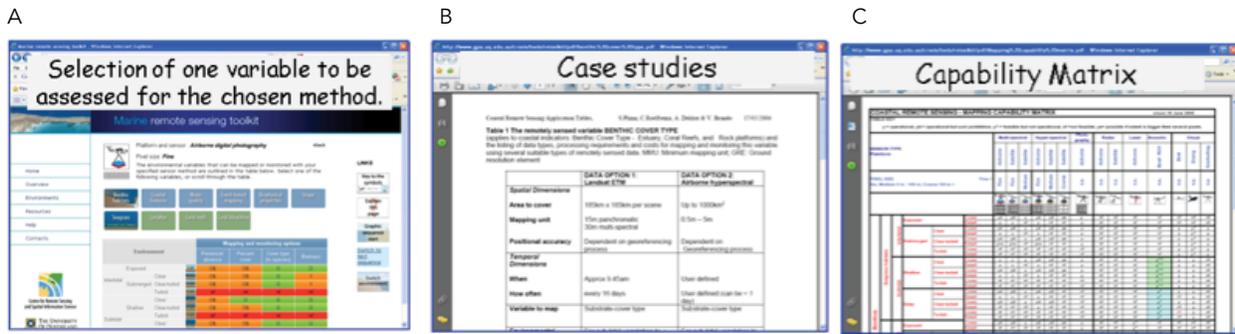


Figure 3. Examples of the selection phase to determine what biophysical parameters can be mapped with a specific sensor type (a). At several points in the toolkit it is possible to review case studies (b) or the the capability matrix (c).

The capability matrix

The core of the web site is a capability matrix which cross-tabulates image and field data sets to specific applications and provides the level of capability for monitoring options to monitor and map a biophysical variable in a marine environment.

The levels of capability able to be assigned to each data set/mapping approach includes: not feasible; feasible but not operational; feasible but needs further research; operational; operational but cost prohibitive and operational depending on the size of the feature to be monitored.

Table 2. An example of the capability matrix which cross-tabulates image and field data sets to specific applications and provides the level of capability for image data and processing options to monitor and map a biophysical variable in a marine environment.

		MARINE REMOTE SENSING - MAPPING CAPABILITY MATRIX											CSER 8 April 2010						
		Table Key: O= operational, O\$ = operational but cost prohibitive, f = feasible but not operational, nf =not feasible, fp=partly feasible, OE=possible if extent is bigger then several pixels																	
SENSOR Type Platform	Passive											Active			Field				
	Multi-spectral			Hyper-spectral			Photo graph	Radar	Laser	Acoustic	Visual								
	Airborne	Satellite	Satellite	Airborne	Satellite	Satellite	Airborne	Airborne	Satellite	Airborne	Boat/ ROV	Boat	Diving	Snorkelling					
PIXEL SIZE	Fine < 5m, Medium 5 m - 100 m, Coarse 100 m >											n.a.			n.a.				
Parameter and environment		Icon											Icon			Icon			
presence/absence	Intertidal	Exposed		Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	nf	nf	nf	nf	
		Submerged	Clear	Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	nf	O	f	O	
			Clear-turbid	Icon	O\$	O\$	O	O	f	nf	O	nf	nf	nf	nf	O	f	O	
			Turbid	Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	O	f	O	
		Subtidal	Shallow	Clear	Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	fp	O	O\$	O
			Clear-turbid	Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	fp	O	O\$	O	
	Turbid		Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	fp	O	O	nf		
	Deep	Clear	Icon	O\$	O\$	O	O\$	f	nf	nf	nf	nf	nf	f	O	O	nf		
		Clear-turbid	Icon	O\$	O\$	nf	O\$	f	nf	nf	nf	nf	nf	f	O	O	nf		
		Turbid	Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	f	nf	O	nf		
	% Cover	Intertidal	Exposed		Icon	O\$	O\$	O	O\$	f	OE	f	nf	nf	nf	nf	nf	nf	nf
			Submerged	Clear	Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	nf	O	f	O
Clear-turbid				Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	nf	O	f	O	
Turbid				Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	O	f	O	
Subtidal			Shallow	Clear	Icon	O	O	O	O\$	f	OE	O	nf	nf	nf	fp	O	O	nf
			Clear-turbid	Icon	O\$	O\$	O	O\$	f	OE	O	nf	nf	nf	fp	O	O	nf	
		Turbid	Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	fp	O	O	nf		
Deep		Clear	Icon	O	O	O	O\$	f	nf	nf	nf	nf	nf	f	O	O	nf		
		Clear-turbid	Icon	nf	nf	O	O\$	f	nf	nf	nf	nf	nf	f	O	O	nf		
		Turbid	Icon	nf	nf	nf	nf	nf	nf	nf	nf	nf	nf	f	nf	O	nf		
Seagrass habitats		Exposed		Icon	O	O	nf	O	nf	nf	fp	nf	nf	nf	nf	nf	nf	nf	
		Clear	Icon	O	O	nf	O	nf	nf	fp	nf	nf	nf	nf	O	f	O		

3. New tools for understanding and managing coral reef systems

The monitoring options include remote sensing data sets that are mostly from passive or active sensors on satellite or airborne platforms. Passive sensors capture an image of the study area by recording reflected sunlight or emitted thermal radiation (e.g. multispectral imaging sensors and thermal sensors), while active sensors provide their own source of illumination to create an image (e.g. Radar and Lidar). This toolkit will also provide alternative options from active sensors deployed from boats (e.g. echo sounders), or visual observations by snorkelers or divers (e.g. photo transect surveys).

The biophysical variables that are derived from the image data and processing options for monitoring can be used to quantify: habitat composition through presence/absence, % cover, cover type, biomass; species composition; the shape of the environment through bathymetry or rugosity; or the concentration of water column constituents (organic, inorganic and dissolved organic) and optical properties; or physical characteristics of water surface, such as temperature, and wave height.

The toolkit will also present solutions for the use of remote sensing in event based monitoring and change detection and analysis. Event based monitoring can be focused on coral bleaching, flood plume mapping, ship grounding, oil spill and impacts of cyclones. The change detection section will discuss the requirements for time series analysis of image data sets and the maps derived from them.

The marine environments to which the toolkit can be applied are: seagrass, coral reefs, mangroves, salt marsh, coastal and oceanic waters. These environments are split in areas that vary in water depth: intertidal exposed or submerged; or sub-tidal shallow or deep waters. A further division is made for the submerged areas in different water clarity regimes, characterised as clear, clear to turbid and turbid water.

The Marine Remote Sensing Toolkit is part of a bigger web-based remote sensing toolkit that has two other sections – terrestrial and atmospheric. Both have identical functionality to the marine section. The three sections represent the area from deep ocean water to inland mountains, and the atmosphere above it. Together, they present a variety of remote sensing applications and monitoring variables for the three environments which will help users to understand and use optical remote sensing.

Resources

Via the help function and resources, the toolkit provides information on:

- How to use the toolkit.
- Case studies, which represent examples of the requirements for: image types; soft/hard ware; knowledge and skills; processing techniques; and cost.
- References to scientific publications, books, websites and reports.
- Explanation of remote sensing fundamentals in marine environments.
- Explanation of processing sequence, field data collection methods, accuracy assessment and interpretation and change detection.

Summary and future work

The toolkit is intended to improve communication in the gap between remote sensing scientists/technicians (the producers) and the wide range of groups using the remote sensing based products (the users). Developing and improving this understanding is essential to enable remote sensing to be used effectively in coastal and marine environments. The toolkit can also be used to educate interested students or professional marine scientists and technicians. Future work will focus on adding case studies and refining the toolkit to create similar resources for terrestrial and atmospheric monitoring and management.

Acknowledgements

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Spotlight on:

Mark Vergara

With 50 per cent of the Philippines' protein sourced from fish, Mark Vergara sees his work at the UP Marine Science Institute as helping to put food on people's tables. Home to the Institute's marine laboratory, Bolinao has one of the largest reef complexes in the Philippines and is one of the most overfished areas. It is now designated as a priority conservation area. Mark's Masters thesis is focused on understanding the coral community structure of the Bolinao Reef Complex, including the composition of reef populations, their spatial organisation and functional relationships. Through field surveys and taxonomic identification, the ecologist is documenting the corals and other marine life in the complex. This will provide baseline data and save time, effort and resources for future researchers studying the reef, including CRTR researchers.

"To study corals effectively, we must be able to identify them correctly," says Mark.

A comprehensive guide to the corals of Bolinao and Western Luzon will be produced and will assist researchers in species identification. As well as identifying individual corals, the research is building a picture of the reef overall using digital photography and modeling techniques. The work is critical to the effective research at Bolinao which in turn will contribute to conservation efforts here and elsewhere in the Coral Triangle.

"So ultimately I am helping to conserve a resource which feeds people which is very rewarding."

Top Shot

In July 2007, Mark Vergara from the University of the Philippines won the International Society of Reef Studies Photograph of the month competition for 'Recent coral bleaching at Inner Talim Point, Batangas, Philippines'. The winning photograph is pictured above.

Deborah Cleland

SimReef and ReefGame: gaming for integrated reef research and management



Deborah is a PhD student at the Fenner School of Environment and Society at the Australian National University. She graduated with a BA/BSc (Hons) from the ANU after completing a thesis focusing on using visual tools, including participatory models and board games, for coral reef and coastal management in the Philippines. Through her PhD, Deborah will continue to examine the utility and potential benefits of using creative techniques to explore alternative livelihood options and locally-based stewardship arrangements in artisanal reef fisheries, as well as the nexus between art and science.



SimReef and ReefGame: gaming for integrated reef research and management

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Abstract

As threats to coastal and ocean systems grow in scale and complexity, the calls for new approaches to research and management grow in volume. The Modeling and Decision Support Working Group (MDSWG) of the CRTR Program has developed two participatory gaming tools that address the need for integrative approaches to coral reef management. SimReef is a regional model and role-play game aimed at policy makers and industry representatives. It simulates coastal development trajectories and trade-offs between environmental, social and economic concerns. ReefGame is a local-level model and board game that helps local people and reef managers explore interactions between livelihoods, reefs and fisheries. We have used these tools successfully in participatory workshops in the Philippines and Mexico. These experiences demonstrate that using games with stakeholders can be a powerful way to educate and involve the public in coral reef management.

Introduction

Globally the health of coral reefs is in decline, largely due to human activity (Pandolfi et al. 2005). Key drivers include climate change, overfishing, tourism, and nutrient and sediment flows from agriculture, mining and towns.

Models are often used in integrated coastal management, to aid understanding, develop scenarios, and explore policy options (Siebenhuner and Barth 2005). Here, we combine models with role-playing games, bringing stakeholders together in a non-confrontational, playful environment (Lynam et al. 2002). The players are given control over certain aspects of a model, so they can make their own decisions and explore different outcomes. Role-playing helps participants (including “experts”) to understand and experience the pressures and constraints felt by others, and allows them to “see” new ways of thinking about a problem (D’Aquino et al. 2003).

The MDSWG has developed two participatory computer games, SimReef and ReefGame, which have been used in workshops in Mexico and the Philippines.

SimReef, Quintana Roo, Mexico

Tourism and coral reefs in Quintana Roo

The arrival of ever-growing numbers of tourists to Quintana Roo, on the Caribbean coast of Mexico, has had a serious impact on the Mesoamerican Barrier Reef system. From about 1975, a wave of mass tourism development has spread outward from the tourist centre Cancun, with annual tourist arrivals now numbering more than 6 million (Daltabuit et al. 2006). Across the state, damage to the reefs caused by human activities has interacted synergistically with natural disturbances, such as hurricanes and coral disease, contributing to the widespread degradation of the reefs (Harborne et al. 2001).

Many industries, communities and families in Quintana Roo are wholly or partly dependent on the ecosystem services provided by reefs, such as coastal protection (Iglesias-Prieto 2009). These groups influence the outcomes of reef management proposals, supporting those they agree with, and blocking those they do not. Improving reef management therefore requires bringing these groups together to create partnerships, share knowledge and, most importantly, negotiate the necessary change in current practices to protect the future of the reefs and the local economy.

SimReef coupled model and role-play game

'SimReef' is a model and coupled role-play game that captures the regional-scale drivers of social and economic change triggered by tourism development in Quintana Roo. The model was kept as simple as possible, so stakeholders could contribute to scenario development, without being presented with a "finished product".

Each group interacts with the SimReef interface, shown on a projector screen. The interface is a schematic representation of the Quintana Roo coastline, showing the location of key ecosystems and human settlements (Figure 1).



Figure 1. Sim Reef Interface

Green = forest, blue = open sea, brown = urban, light blue = lagoon, dark blue = fringing reef, teal = seagrass, pink = temples, grey = cenotes (fresh water holes), pale yellow = scrub and open land, dark yellow = agriculture

The SimReef role-play game mimics real-life negotiation patterns, whilst maximising interactions between groups. The roles represent four major interest groups in Quintana Roo – conservation agencies (public and private), tourism, fisheries and the government (shown as circles in Figure 2 and Figure 3). Each group is given simple goals to structure play and aid strategy formation (indicated in brackets in Figure 2 and Figure 3). For example, the tourism industry's goal is profitability, measured by the income of resorts over each time step.

3. New tools for understanding and managing coral reef systems

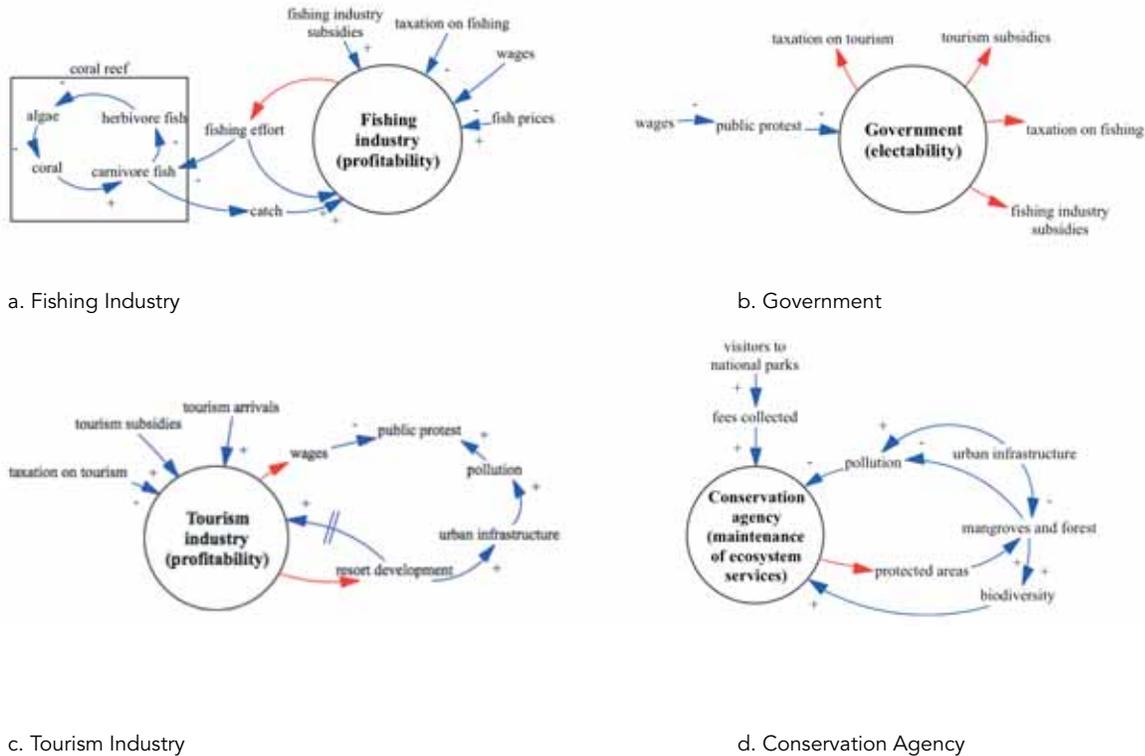


Figure 2. The four roles and their goals, inputs and outputs

The above diagrams illustrate the four roles and their inputs/ outputs, as represented in the SimReef model and role-play game. Positive and negative feedback relationships are marked with +/- signs. Black circles represent the roles discussed in text. Dotted arrows and bold text represent the decisions each role was responsible for (e.g. the Conservation Agency decided the size and location of protected areas).

Every round each group in the role-play game makes decisions about the use of the resources under their control (linked with red arrows in Figures 2 and 3). For example, the tourism role decides the average wage and how many resorts to develop, whilst the fishing role establishes (legal) fishing effort. These decisions then have flow-on environmental and social effects, measured by indicators like 'pollution' and 'public protest'. In turn, these indicators affect the outcomes for the government and the conservation agency. Each group must reach a consensus on their decisions, and negotiate access to funds and approvals through the government. For example, the conservation agency has to obtain permission from the government to establish new protected areas. After reaching consensus, the final decisions are coded into the model. Facilitators then present the results, including whether each group is meeting their established goals.

3. New tools for understanding and managing coral reef systems

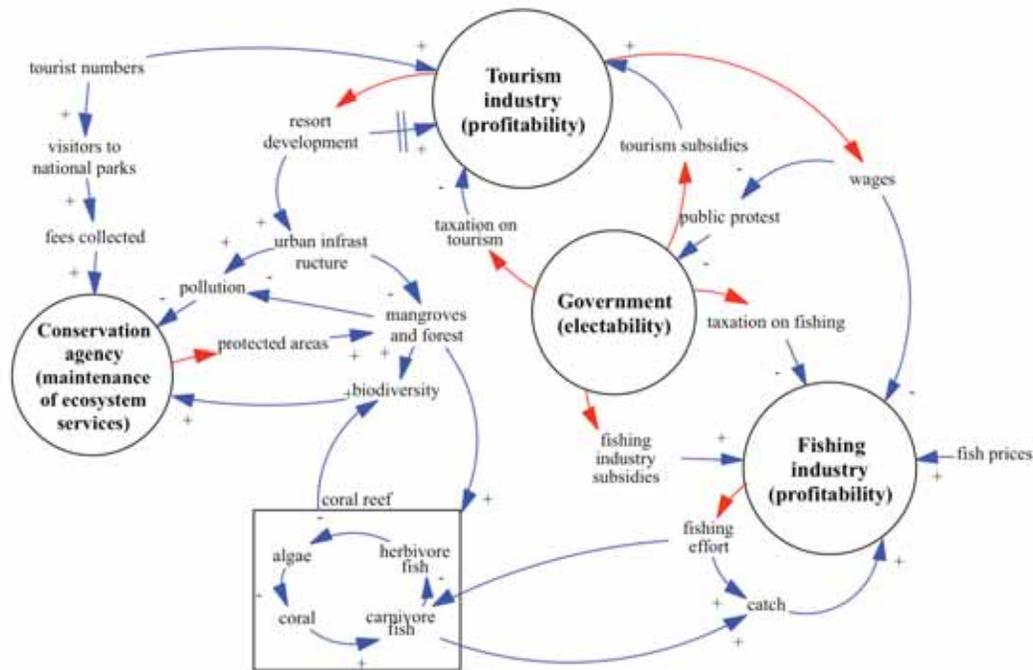


Figure 3. Complete causal loop diagram

The above diagram illustrates the interlinking of the four roles and their inputs/ outputs introduced in figure 2. Positive and negative feedback relationships are marked with +/- signs. Black circles represent the roles discussed in text. Red lines represented the decisions made by each entity

SimReef workshop

SimReef was played at a participatory workshop in Akumal, Quintana Roo, in October 2005. A group of 15 local people participated, representing the federal government's conservation agency, social and marine scientists, a local environmental NGO and an eco-tourism operator. No representatives from the fishing industry were present, although they had been invited. Participants were divided into the four role-play groups, each with a facilitator. Four rounds of the game were played, representing four years. Whilst the model was updated with each round's decisions, the underlying data and assumptions for each of the model's components were presented, so the participants could comment on their perception of the validity of the assumptions, and their recommendations for improving the model. Finally, participants were asked to reflect on the game/model, and its potential for further use as a management tool both in the Quintana Roo context and more generally.

Workshop outcomes

SimReef in Mexico helped to foster relationships and encourage interaction, learning and exchange between researchers and local participants. Introducing fun and play to the participatory context had a particularly positive impact on stakeholder engagement, pointing to some potential for researchers battling stakeholder fatigue.

However, the positive potential of SimReef did not overcome the problems caused by our lack of contact with local stakeholders prior to arriving in Mexico. The outcomes of the workshop were not connected to ongoing projects nor effectively linked to management priorities. Commitment from the individuals and institutions that possess the power to change the behaviours and activities that drive reef degradation is essential. Without this, models and participatory processes in general cannot engage effectively with the structural barriers to improved marine management. These lessons were used to improve design and implementation of the MDSWG's second participatory modeling experiment.

ReefGame, Bolinao, the Philippines

Fishing and reefs in Bolinao

Overfishing is the overwhelming issue for reef management in Bolinao. Falling catches and catch per unit effort are two indicators that target species are close to collapse. Fishing effort needs to be radically reduced if fish stocks are to recover (Meñez et al. 1991; McManus et al. 1992; Licuanan et al. 2006). The burgeoning aquaculture industry, upper-catchment clearing, chemical agriculture and domestic waste streams are also harming the health of the marine ecosystem (Talaue-McManus et al. 2000). Together, these factors mean that the region's growing fisher population is relying on a dwindling resource base that can no longer support the needs of their families. However, limited funds and corruption in the government have meant that little effective management action has been taken (Graham and Sol 2004).

ReefGame coupled model and role play game

ReefGame aims to help fishers understand how overfishing is harming both their livelihoods and the reef, and to start discussions about what could be done. At the same time, we hoped to increase understanding of the fishers' behaviour and livelihood choices as their catches declined.

Unlike SimReef, where users interact directly with the computer interface, ReefGame is primarily a board game. Participants playing in pairs are given a particular fishing identity – with a boat, a family size and ongoing expenses that they have to pay each round. There is also a role for a banker/fish buyer.

Two identical game boards represent a coastal area with an offshore island, made up of sea and land cells and bearing a schematic resemblance to the coast of Bolinao (see figures 4 and 5). Habitat cards are distributed on the sea cells, showing where mangrove, seagrass, coral-dominated reef and algae-dominated reef are located. Designated land cells have livelihood icons, initially one for each of the different activities available (e.g. carpentry and taxi-driving).

Half the participants play around each board. Using both boards means that groups are kept small and different conditions and scenarios can be applied to each. Scenarios include Marine Protected Area implementation, introduction of different livelihoods and migration possibilities, and natural disasters.



Figure 4. Game board showing fisher and habitat tokens



Figure 5. Fishers playing ReefGame

In each round of the game, each pair either goes fishing (by moving their token to any sea cell) or works for a wage in another occupation (the corresponding land cell).

The computer model accompanying ReefGame calculates each pair's catch and income. Fishers receive fish tokens that represent catch biomass. Fish tokens are swapped for money tokens, which are used to track each pair's income (or debt). After players receive their gross earnings, the banker collects family expenses from each player.

ReefGame workshop

Twenty fishers played ReefGame at a one-day participatory workshop in Bolinao, the Philippines in September 2007. We have also used ReefGame as an educational tool in undergraduate and postgraduate workshops at different venues around Australia and the Philippines.

Workshop outcomes

The Philippines workshop demonstrated that models and games are powerful community education and outreach tools, eliciting rich responses and discussion from participants. Facilitators commented that workshop attendees interacted enthusiastically and naturally with the game and each other. This is in stark contrast to interview and focus groups they had experienced, where 'information extraction' was the sole purpose, creating a stilted one-way interrogation. Participants were also pleased about experiencing something different from the 'typical' workshop setting with butcher's paper and PowerPoint presentations. Most also identified that the workshop had helped them build relationships with peers and learn about reef function and management.

Further research

Together with an extended team based at the University of the Philippines, MDSWG members secured funding from the David and Lucille Packard Foundation through the Ecosystem Based Management (EBM) Tools Network to run participatory modeling workshops in 5 different towns throughout the Philippines in 2010. These workshops will have a strong emphasis on multi-sectoral integration to help find sustainable alternative and supplementary livelihoods for the artisanal fishers who are dependent on reefs. Thus, we will continue the approach initiated with SimReef and continuing with ReefGame in using models and games to improve outcomes of participatory modeling workshops for people and management.

Conclusion

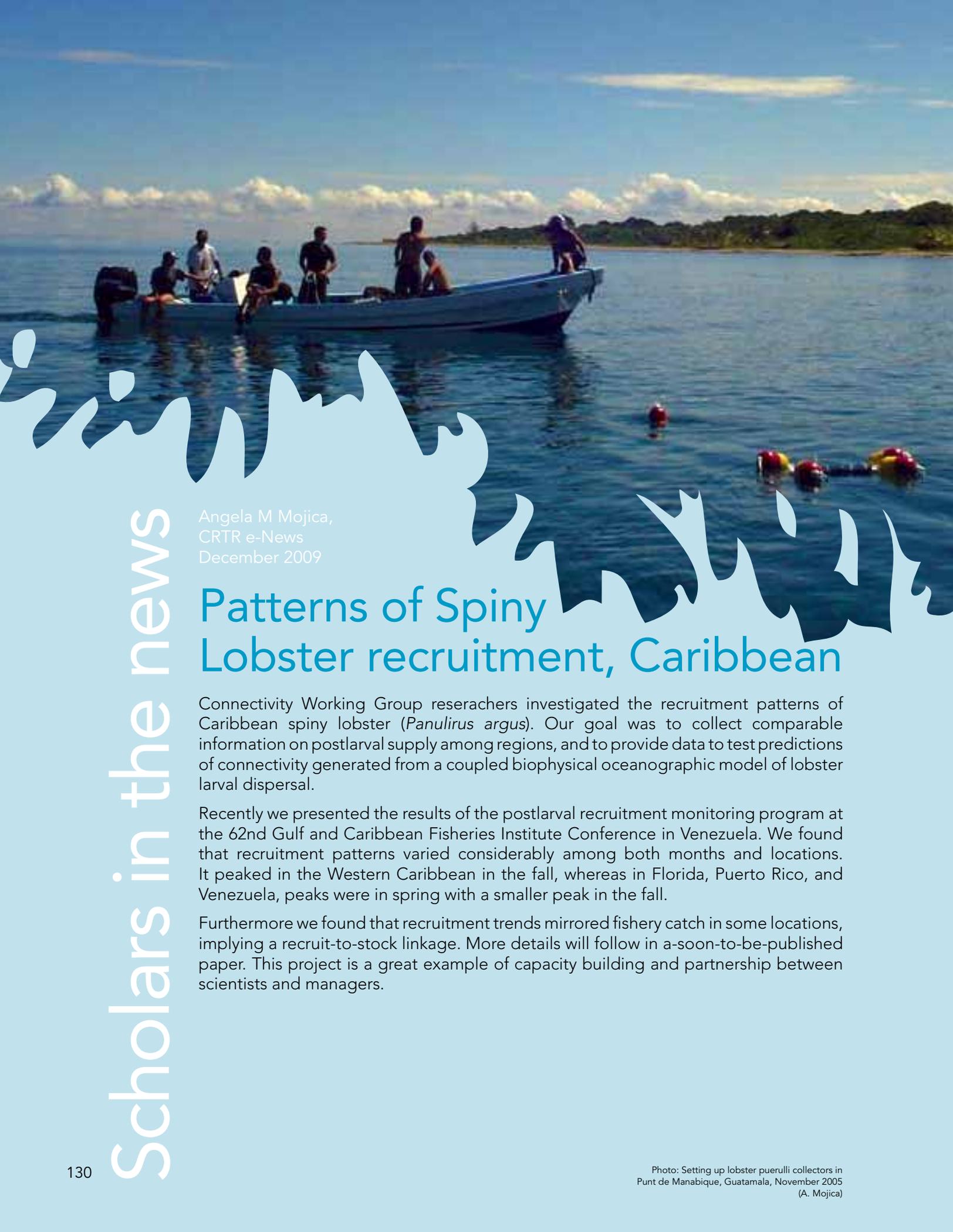
SimReef and ReefGame have very different foci and target audiences, but both were able to elicit creative and interactive responses from key stakeholders. Thus far, gaming has been a valuable tool to build relationships and conduct social research. Moreover, it shows promise as a decision support tool for marine managers. The SimReef workshop demonstrated the dangers of neglecting the traditional concerns of participatory research, particularly local power relationships and the integration of the researchers with the local community and decision-making processes. However, we have drawn a number of important lessons from these experiences, and have incorporated stronger and more direct links to management decisions in our current work.

Acknowledgements

Deborah Cleland would like to thank all participants of SimReef and ReefGame workshops most sincerely for their time and energy. Abbie Trinidad (Conservation International) and Porfirio Alino (Marine Science Institute, University of the Philippines) provided expert advice and support in the development of ReefGame and also facilitated the Bolinao workshop. This work was largely completed as part of Deborah Cleland's honours research, supervised by David Dumaresq, convener of the Human Ecology Program, Fenner School of Environment and Society, ANU. Aspects of this research were presented at the International Coral Reef Symposium in Fort Lauderdale, USA in 2008 and the World Oceans Conference in Manado, Indonesia in 2009. Some material from this paper has also been adapted from a paper by Cleland et al, REEFGAME: exploring the dynamics of subsistence fishing communities, submitted to Simulation and Gaming in September 2009.

References

- Cleland D, Wyborn C (in press) Using visual methods to explore conflicts in land and seascape management. In: Brown VA, Harris J, Smith M (eds) Tackling wicked problems: using the transdisciplinary imagination. Earthscan, London,
- D'Aquino P, Le Page C, Bousquet F, Bah A (2003) Using self-designed Role-Playing Games and Multi-Agent Systems to empower local decision-making process for land use management: The SelfCormas experiment in Senegal. *Journal of Artificial Societies and Social Simulation* 6: <http://jasss.soc.surrey.ac.uk/6/3/5.html>
- Daltabuit M, Vázquez LM, Cisneros H, Ruiz G (2006) El Turismo Costero en la Ecorregión del Sistema Arrefical Mesoamericano. Universidad Nacional Autónoma de México, Cuernavaca, Morelos
- Graham J, Sol N (2004) Rethinking Governance, Social Conflict and Livelihood Choices: Stories from Prieto Diaz, Philippines The Commons in an Age of Global Transition: Challenges, Risks and Opportunities the Tenth Conference of the International Association for the Study of Common Property Oaxaca, Mexico
- Harborne AR, Afzal DC, Andrews MJ (2001) Honduras: Caribbean Coast. *Marine Pollution Bulletin* 42:1221-1235
- Hardin G (1968) The Tragedy of the Commons. *Science* 162:1243-1248
- Iglesias Prieto R (2009) Groundwater pollution and the importance of coral reefs in the protection of the coastal zone The Fifth GEF Biennial International Waters Conference, Cairns, Australia
- Licuanan WY, Aliño P, Campos WL, Castillo G, Juinio-Meñez MA (2006) A Decision Support Model for Determining Sizes of Marine Protected Areas: Biophysical Considerations. *The Philippine Agricultural Scientist* 89:507 - 520
- Lynam T, Bousquet F, Le Page C, D'Aquino P, Barreteau O, Chinembiri F, Mombeshora B (2002) Adapting science to adaptive managers: spidergrams, belief models and multi-agent systems modeling. *Conservation Ecology* 5: <http://www.consecol.org/vol5/iss2/art24>
- McManus JW, Nañola CL, Reyes RB, Kesner KN (1992) Resource ecology of the Bolinao coral reef system International Center for Living Aquatic Resources Management, Manila
- Meñez LAB, McManus LT, Jimenez JF, Rivera CA, Concepcion J, Luna Cz (1991) Survey of the coral reef resources of the Western Lingayen Gulf, Philippines ICLARM
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are U.S. Coral Reefs on the Slippery Slope to Slime? *Science* 307:1725-1726
- Siebenhuner B, Barth V (2005) The role of computer modeling in participatory integrated assessments. *Environmental Impact Assessment Review* 25:367-389
- Taluae-McManus L, Clemente RS, Gomez E, Licuanan W, McGlone D, San Diego McGlone ML, Siringan FP, Villanoy CL (2000) Synthesis Report. In: Institute MS (ed) Economic Evaluation and Biogeochemical Modeling of Lingayen Gulf in Support of Management for Sustainable Use



Angela M Mojica,
CRTR e-News
December 2009

Patterns of Spiny Lobster recruitment, Caribbean

Connectivity Working Group researchers investigated the recruitment patterns of Caribbean spiny lobster (*Panulirus argus*). Our goal was to collect comparable information on postlarval supply among regions, and to provide data to test predictions of connectivity generated from a coupled biophysical oceanographic model of lobster larval dispersal.

Recently we presented the results of the postlarval recruitment monitoring program at the 62nd Gulf and Caribbean Fisheries Institute Conference in Venezuela. We found that recruitment patterns varied considerably among both months and locations. It peaked in the Western Caribbean in the fall, whereas in Florida, Puerto Rico, and Venezuela, peaks were in spring with a smaller peak in the fall.

Furthermore we found that recruitment trends mirrored fishery catch in some locations, implying a recruit-to-stock linkage. More details will follow in a soon-to-be-published paper. This project is a great example of capacity building and partnership between scientists and managers.



CRTR e-News
June 2009

Nong sets sights on Thai corals

Australasian CoE-sponsored postgraduate student Narinratana (Nong) Kongjandtre has spent three months in Thailand, continuing her experiments on coral hybridization.

Nong's February-April stint follows two years research into coral spawning patterns in Thailand and her previous research of coral hybridization potential which started in 2008. With assistance from several local groups Nong says this year she repeated last year's experiment, following the different timing of coral spawning at various locations in the Gulf of Thailand.

In February she conducted her experiment at Sichang Island, Aquatic Resources Research Institute, Chulalongkorn University and in March she collaborated with Dr Potchana Boonyanate and Anchalee Chankong from Eastern Marine and Coastal Resources Research Centre (EMCOR).

At EMCOR, Nong helped train the local staff with the priori experiment to culture coral larvae, nursing the juveniles in order to donate to the reefs at Monnai Island.

Before she returned to Australia, Nong collaborated with Dr Monthol Ganmanee at King Mongkut's Institute of Technology's Chumphon campus and Srisakul Piromvarakorn, from James Cook University.

Says Nong: "With the support of the CRTRAustralasian CoE, together with collaboration and knowledge from other organisations and researchers in the country, hopefully, we can improve the conditions of coral reefs in Thailand."

Georgina Gurney

Integrated models of natural and human systems: a critical component of environmental management



Georgina has recently completed her Honours thesis at the University of Tasmania, Australia, in 2009. She received First Class Honours for her research which focused on modelling coral reef ecological processes at a local scale, and examined associated socio-economic dynamics. She is a member of the Modeling and Decision Support Working Group and graduated with a Bachelor of Science from the University of Tasmania, majoring in Marine, Freshwater and Antarctic Ecology in 2007.



Integrated models of natural and human systems: a critical component of environmental management

Georgina Gurney

University of Tasmania, Australia

Introduction

Over the past century, the impact of humans on the natural world has reached unprecedented levels on a global scale, with ecosystems experiencing greater rates of anthropogenic change in the past 50 years than in any other period of human history (Millennium Ecosystem Assessment 2005). These human-driven alterations to biotic and abiotic systems are substantial and threaten biological diversity, disrupt climatic patterns and adversely affect ecosystem services that humans depend upon (Vitousek et al. 1997, Alberti et al. 2003). In addition, the present momentum of human population growth and economic development will almost certainly lead to further anthropogenic pressure on nature. It follows that environmental management strategies aiming to lessen the adverse impacts of humans on nature are an urgent and growing priority. Ultimately, 'environmental' management is a product of human decision making and requires alteration of human behaviour to be effective (Mascia et al. 2003). Therefore, to successfully reach environmental management targets, it is imperative to understand the complex interactions between socio-economic and bio-physical systems.

Modeling is well-placed as a tool to facilitate the integration of human and natural elements as complex dynamical systems, allowing prediction of non-linear behaviours and an understanding of the processes that govern these dynamics (Larocque et al. 2006). Furthermore, modeling can be used to predict and assess the outcomes of alternative management strategies. Thus, the focus of this paper is to illustrate the importance of integrated models of human and natural systems for environmental management, to briefly highlight the challenges for interdisciplinary collaboration, and to suggest future directions.

1. Why integrate human and natural systems?

The practical application of ecological models in support of policy advice has often been limited because they frequently do not address the socio-economic dimension of the problem, i.e. they often ignore the economic, political and institutional factors related to environmental management (Stern 1993, Drechsler and Wätzold 2007, Perrings 2007). The need for interdisciplinary integration is increasingly being recognised by a wide range of actors including managers and policy makers in government and non-government agencies and academia in various disciplines (Fox et al. 2006). While some facets of environmental management can be sufficiently understood under a solely ecological framework, the large majority of environmental management problems and almost all of their potential solutions require an interdisciplinary approach (Kinzig and Starrett 2003, Ostrom et al. 2007, Liu et al. 2007a). For example, estimating the size of a protected area necessary to ensure conservation of a threatened species may be purely the domain of ecology, but selecting between alternative sites will require interdisciplinary collaboration (Wätzold et al. 2006). This is because while all alternative sites may be equally appropriate in terms of ecology, they may not be in terms of the socio-economics and thus, will deliver different conservation outcomes.

Disciplines, such as anthropology, may be able to identify conservation-orientated cultural beliefs, values and laws that are suitable to act as the basis for formal environmental management policy. Social sciences offer valuable insights into how resource use rights, monitoring and compliance strategies mould individual use of, and hence the state of, the protected area (Mascia et al. 2003).

Ultimately, the need for environmental management policy arises due to human activities and the policy itself is a product of human decisions, requiring alteration of human behaviour to be effective (Mascia et al. 2003). Thus, to effectively manage the environment, it is crucial to understand how social and economic drivers, such as cultural values, legal frameworks, markets and demographics, mould interactions between humans and nature, and anthropogenic decisions to protect or exploit a resource. Unless ecology and socio-economics are integrated, management recommendations which are approached by one discipline may often fail to present a paramount management strategy, in terms of both the ecological outcome and the most efficient use of financial resources.

Given that the consequences of management decisions are so important, it is useful to illustrate this point with three examples. The first two examples deal with the inclusion of socio-economic elements into investigations that are usually the domain of ecologists; the first integrates economics with ecology while the second focuses on ecological and sociological aspects. The third example demonstrates the benefit to management of considering ecological factors in a traditional economic analysis.

While the selection and design of reserve sites has traditionally been purely a subject of ecology, Ando et al. (1998) found that integrating economic costs (in this case land prices) into ecologically based selection algorithms for reserve areas, resulted in optimal conservation policy. Accounting for heterogeneity in land prices resulted in better efficiency in terms of either the extent of protected land given fixed funds or the amount of expenditure in protecting a fixed land coverage. Ando et al. (1998) argued that to achieve the same conservation outputs using purely ecological models would cost up to 80% more. In another example, Skonhofs et al. (2002) demonstrated that by considering various stakeholders' social and economic needs in their model, including those related to hunting, tourism and conservation, they were able to minimise conflicts in considering alternative management scenarios for the chamois, a mountain ungulate, in the French Alps. They found that management recommendations generated by the model were different when focusing on a wide range of values, rather than solely on the conservation value. While the development of management plans for endangered species usually falls under the domain of ecology (Skonhofs et al. 2002), this study demonstrates that a holistic approach can result in the development of optimal management strategies, in this case ensuring the least amount of conflict among the diversity of stakeholders and thus increasing the likelihood of management success (Watzold et al. 2006).

Including ecological aspects into analyses which are usually the domain of economists has also been demonstrated to be beneficial to management outcomes (Drechsler et al. 2007). For example, assessing the cost-effective spatial differentiation of environmental policy tools is traditionally an economist's problem (Watzold et al. 2006). But as Watzold et al. (2006) points out, the benefit functions usually included in an economist's analysis are typically founded on abstract supposition and fail to include many benefit functions relevant in the context of nature conservation. However, as Watzold and Drechsler (2005) reveal, there are some benefit functions for biodiversity management that are based on ecological theory, which have not been considered by economists in the past. This study uses a simple ecological-economic model to examine how different types of benefit and cost functions affect cost-effectiveness of spatially differentiated conservation instruments. The inclusion of ecological elements (in this case, biodiversity benefits) resulted in management recommendations distinctly different to those portrayed by economic models (Watzold and Drechsler 2005).

As exemplified by these three examples, disciplinary and interdisciplinary approaches to the same environmental management conundrums may produce very different results. Management recommendations produced through disciplinary research are often suboptimal compared to results from more integrated approaches, and for this reason, may fail to be taken up by managers at all (Watzold et al. 2006). Although the biology is often correct in disciplinary solutions, environmental management interventions based on biology alone can fail to achieve desired outcomes (Mascia et al. 2003) and this is often attributed to 'policy failure' (Watzold et al. 2006). However, disconnectedness between biological knowledge and success in environmental management is increasingly being recognised as 'science failure' in which the primary shortcoming is the lack of consideration of socio-economic elements (Mascia et al. 2003, Watzold et al. 2006).

2. How common are integrated models of natural and human systems?

As illustrated above, integrated socio-economic and ecological models are integral in understanding the dynamics of the world as a human-dominated landscape, and thus provide an invaluable tool for environmental management. However, while the benefits of using these models for environmental management purposes are clearly substantial, this form of modeling is far from being an established approach (Drechsler and Watzold 2007, Schultz et al. 2007, Cooke et al. 2009, Hong et al. in press). Liu et al. (2007a) purport there have been some studies using integrated models to address management problems but these are few, with modeling largely being the domain of disciplinary activity. A literature search using Scopus (a large, multidisciplinary database) supports this view (Figure 1a). I used Scopus to search literature from the past two decades (excluding 2009) in order to assess the number of published studies of ecological models, economic and sociologic models and integrated models of ecology, and

3. New tools for understanding and managing coral reef systems

economics or sociology, or both. Papers were found by running three searches in the title or the keywords for either 'model' or 'model(l)ing' and other appropriate keywords as follows: (1) for ecological models, the key words were 'ecosystem' or 'ecological', (2) for socio-economic papers, the key words were 'economic', 'sociologic' or 'socio-economic', and (3) for integrated papers, the keywords were 'ecological-economic', 'socio-ecological' or 'interdisciplinary'. These keywords were chosen after scanning the keywords and titles of forty modeling articles. The results show clearly that models of human systems and models of ecological systems are much more common than interdisciplinary studies which account for only 2.5% of modeling papers (Figure 1a).

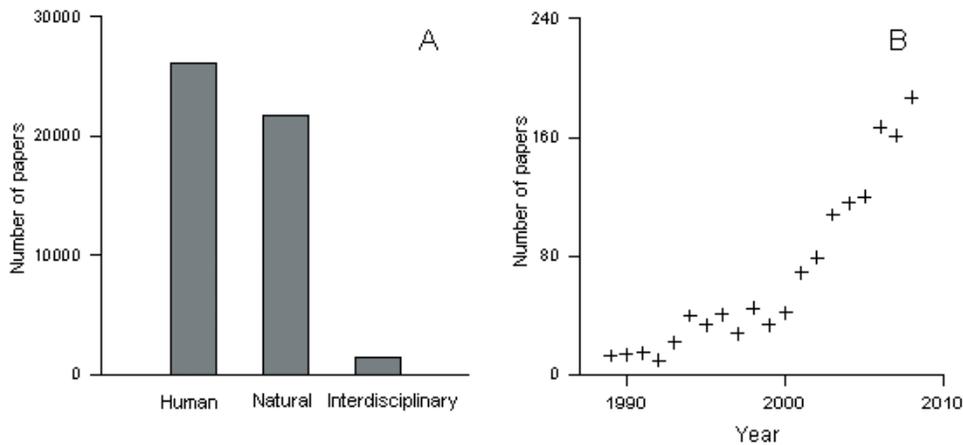


Figure 1. The number of papers published in the last 20 years that include modeling dealing with human, natural or interdisciplinary systems (A). The number of papers published in the last 20 years that include modeling of interdisciplinary systems (B). Both literature searches were undertaken with Scopus.

Furthermore, several authors assert that due to lack of long-term data sets for coupled human and natural systems, the majority of integrated models are theoretical rather than empirical, using conceptual diagrams rather than quantitative models (Liu et al. 2007a, Hong et al. in press). Therefore, there is a significant paucity of both the number of studies integrating natural and human components and suitable empirical information to inform these studies. Given the limitations of disciplinary approaches for management, this is clearly a gap in the current research. It seems abundantly clear that data collection and modeling under an integrated framework would be highly beneficial and should be a priority focus area.

Effort and interest in coupled models is gaining momentum, however, with a clear increase in the number of published works over the past two decades (Figure 1b). Despite the relative paucity of studies, integrated models of varying structure have been shown to be successfully applicable at different scales across an array of ecosystem types and at different levels of economic development (Liu et al. 2007b, Cooke et al. 2009).

3. Challenges for the development of integrated models

While the benefits of integrated natural and human systems modeling to environmental management is significant and well recognised, it is still a far cry from being an established approach (Watzold et al. 2006, Drechsler et al. 2007, Cooke et al. 2009). Two acknowledged hurdles for the proliferation of integrated models are: institutional barriers and difficulties in integrating multi-disciplinary approaches to modeling. In Fox et al.'s (2006) survey of scientists of multiple disciplines on barriers to integration, the most common perceived barriers were (1) lack of common vocabulary, (2) discouragement of interdisciplinary collaboration by traditional academic reward systems, (3) lack of funding for interdisciplinary work and (4) limited opportunities for interdisciplinary collaboration.

3.1 Institutional barriers

Generally the existing structure and incentives of research institutions encourage disciplinary research rather than multidisciplinary research (Stern 1993, Drechsler and Wätzold 2007). Disciplinary research is typically more rewarding in terms of career prospects and attracts more funding than interdisciplinary research (Stern 1993, Drechsler and Wätzold 2007). Therefore, for the further development of integrated modeling, there needs to be a move toward research structures that facilitate communication and collaboration between disciplines. This might include sufficient funding and incentives, and opportunities for publication that are beneficial for multiple disciplines.

3.2 Difficulties of integrating multi-disciplinary approaches to modeling

The second hurdle deals with the challenge of combining different approaches to modeling, both in terms of the inherent mindset of researchers from different disciplines and the mechanics of combining disciplinary modeling techniques, which are typically of different structure and scale. Within each discipline, scholars are educated to examine and frame research questions in different ways and hence, when investigating a management problem they are likely to have dissimilar focuses and design different experiments (Armstrong 2007, Drechsler et al. 2007). The perspective of an ecologists is generally 'conservation at whatever cost', while an economist is 'conservation subject to cost' (Watzold et al. 2006). Thus, the first challenge for collaboration between disciplines when developing an integrated model, is finding a common focus and aim.

Given that mathematical models are a commonly used tool for research in multiple disciplines (particularly ecology and economics), it is often assumed models from different disciplines can be easily merged (Drechsler et al. 2007). However, each discipline generally has a dissimilar approach to modeling which may impede communication and integration of knowledge. Models typically differ in terms of the underlying mathematical techniques, level of complexity and consideration of spatial and temporal scales (Veldkamp and Verburg 2004, Drechsler et al. 2007). This is illustrated by Drechsler et al.'s (2007) survey of 60 ecological, economic and ecological-economic models related to biodiversity management. They found that all economic models were formulated and solved analytically (the model is completely described by equations) and tended to be of a general nature and of low complexity. Conversely, while the vast majority of ecological models addressed specific problems, as a whole, they were less homogenous than economic models. Around 25% of the ecological models had algorithmic formulation (flow charts or if-then rules were used), but the majority were analytically structured and of these, the results were obtained in three ways: (1) numerically (by determining eigenvalues in a matrix model), (2) via simulation (simulating population dynamics incrementally) and, (3) analytically (by solving equations for equilibrium solutions) (Drechsler et al. 2007). In terms of complexity (which was judged on number of parameters), a substantial number of ecological models were rather simple, while some were highly complex and this reflects their use for different purposes. Another important difference between the two disciplines is the way in which they deal with spatial heterogeneity and temporal dynamics. Drechsler et al. (2007) found that a greater proportion of ecological models were dynamic when compared with economic models, with temporal and spatial scales featuring to a much greater extent. When scales are considered, economic models are typically spatially or temporally differentiated at a large scale (ie regions or periods with different conditions), while ecological models are spatially or temporally explicit on a small scale (locations or time periods considered explicitly) (Watzold et al. 2006, Drechsler et al. 2007).

Thus, there are distinct differences in the way in which modeling is approached and carried out by different disciplines and subsequently a common understanding of modeling and scales must be achieved to facilitate integrated modeling. An increased understanding as to why these differences arise, will aid modellers in determining the appropriate approach to integrated modeling (Watzold et al. 2006, Drechsler et al. 2007). To illustrate this, Watzold et al. (2006) point out that if the differences in modeling techniques arise due to 'cultural' differences (ie differences in education), then a shift in the mindset of scholars would ease the integration of the two disciplines. However, if these differences in modeling technique occur because socio-economic and ecological systems need to be modelled differently, it has significant implications for developing the approach to integrated modeling. Thus, further research must be undertaken with the aim of uncovering the reasons behind the disparities in ecological and economic modeling.

Conclusion

The large majority of environmental management problems and almost all of their potential solutions, have bio-physical and socio-economic dimensions. Thus, as this paper has exemplified, integrated modeling is a crucial tool for successful environmental management, in terms of both the ecological outcome and the most efficient use of financial resources. However, integrated modeling is far from being an established approach and this is largely due to the dual challenges of institutional barriers and difficulties in integrating multi-disciplinary approaches to modeling. Hence, to facilitate the future development of integrated models, it is vital that institutional structures encourage communication and collaboration between disciplines. Further research into uncovering the reasons behind disparities in ecological and economic modeling would also improve the likelihood of successful collaboration. While the costs of achieving these recommendations and using integrated modeling are substantial, the implications of not doing so, such as unproductive and cost-ineffective management, are likely to be much larger.

References

- Alberti, M., J. Marzluff, E. Sculenberg, G. Bradley, C. Ryan, and C. Zumbrunnen. 2003. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience* 53:1169-1179.
- Armstrong, C. W. 2007. A note on the ecological-economic modeling of marine reserves in fisheries. *Ecological Economics* 62:242-250.
- Cooke, I., S. Queenborough, E. Mattison, A. Bailey, D. Sandars, A. Graves, J. Morris, P. Atkinson, P. Trawick, R. Freckleton, A. Watkinson, and W. Sutherland. 2009. Integrating socio-economics and ecology: a taxonomy of quantitative methods and a review of their use in agro-ecology. *Journal of Applied Ecology* 46:269-277.
- Drechsler, M., V. Grimm, J. Mysiak, and F. Wätzold. 2007. Differences and similarities between ecological and economic models for biodiversity conservation. *Ecological Economics* 62:232-241.
- Drechsler, M. and F. Wätzold. 2007. Ecological-economic modeling for the sustainable use and conservation of biodiversity. *Ecological Economics* 62:203-206.
- Fox, H., C. Christian, J. Nordby, O. Pergams, G. Peterson, and C. Pyke. 2006. Perceived Barriers to Integrating Social Science and Conservation. *Conservation Biology* 20:1817-1820.
- Hong, B., K. Limburg, J. Erickson, J. Gowdy, A. Nowosielski, J. Polimeni, and K. Stainbrook. in press. Connecting the ecological-economic dots in human-dominated watersheds: Models to link socio-economic activities on the landscape to stream ecosystem health. *Landscape and Urban Planning*.
- Kinzig, A. and D. Starrett. 2003. Coping with Uncertainty: A Call for a New Science-Policy Forum. *Ambio* 32:330-335.
- Larocque, G. R., D. A. Mauriello, R. A. Park, and J. E. J. Rykiel. 2006. Ecological Models as Decision Tools in the 21st Century: Proceedings of a conference organized by the International Society for Ecological Modeling (ISEM) in Quebec, Canada, August 22-24, 2004. *Ecological Modeling* 199:217-218.
- Liu, J., T. Dietz, S. Carpenter, M. Alberti, C. Folke, E. Moran, A. Pell, P. Deadman, T. Kratz, J. Lubchenco, E. Ostrom, Z. Ouyang, W. Provencher, C. Redman, S. Schneider, and W. Taylor. 2007a. Complexity of coupled human and natural systems. *Science* 317:1513-1516.
- Liu, J., T. Dietz, S. Carpenter, C. Folke, M. Alberti, C. Redman, S. Schneider, E. Ostrom, A. Pell, J. Lubchenco, W. Taylor, Z. Ouyang, P. Deadman, T. Kratz, and W. Provencher. 2007b. Coupled human and natural systems. *Ambio* 36.
- Mascia, M., J. Brosius, T. Dobson, B. Forbes, L. Horowitz, M. McKean, and N. Turner. 2003. Conservation and the social science. *Conservation Biology* 17:649-650.
- Ostrom, E., M. Janssen, and J. Anderies. 2007. Going beyond panaceas. *Proceedings of the National Academy of Sciences of the United States of America* 104:15176-15178.
- Perrings, C. 2007. Future challenges. *Proceedings of the National Academy of Sciences of the United States of America* 104:15179-15180.
- Schultz, L., C. Folke, and P. Olsson. 2007. Enhancing ecosystem management through social-ecological inventories: lessons from Kristianstads Vattenrike, Sweden. *Environmental Conservation* 34:140-152.
- Skonhoft, A., N. Yoccoz, and N. Stenseth. 2002. Management of chamois (*Rupicapra rupicapra*) moving between a protected core area and a hunting area. *Ecological Applications* 12:1199-1211.
- Stern, P. 1993. A second environmental science: human-environment interactions. *Science* 260:1897-1899.
- Vitousek, P., H. Mooney, J. Lubchenco, and J. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494-499.
- Wätzold, F. and M. Drechsler. 2005. Spatially uniform versus spatially differentiated compensation payments for biodiversity-enhancing land-use measures. *Environmental and Resource Economics* 31.
- Wätzold, F., M. Drechsler, C. Armstrong, S. Baumgärtner, V. Grimm, A. Huth, C. Perrings, H. Possingham, J. Shogren, A. Skonhoft, J. Verboon-Vasiljev, and C. Wissel. 2006. Ecological-economic modeling for biodiversity management: potential, pitfalls and prospects. *Conservation Biology* 20:1034-1041.



In December 2007, the Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program held a forum for 55 postgraduate and postdoctoral students in coral reef studies from 20 countries. CRTR Future Leaders Forum aimed to develop a network of future leaders in marine and coral reef ecosystem research and management; to build their capacity to understand global issues impacting on reefs; and to develop new knowledge and skills to assist them in their future current and roles.

Out of this forum, the CRTR Future Leaders Network was established to foster and encourage linkages between young scientists across countries and areas of coral reef research. This anthology presents a snapshot of their research and achievements during Phase One of the CRTR Program.

For information regarding the Future Leaders Network, or to reach the network, contact the CRTR Project Executing Agency, Global Change Institute, University of Queensland, Australia:

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The CRTR Program is a partnership between the Global Environment Facility, the World Bank, the University of Queensland (Australia), the United States National Oceanic and Atmospheric Administration (NOAA) and approximately 50 research institutes and other third-parties around the world.