PROJECT FINAL REPORT

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Executive summary

The management of coral reef ecosystems for the 21st century requires not only the continued understanding of the natural dynamics of this ecosystem but also the interaction between people and coral reefs. The important services that reefs provide to fisheries, tourism, and coastal defences are under threat from increased extraction, developing and climate change. The EU Project FORCE (Future of Reefs in a Changing Environment) sought to understand the dynamics of reefs, the complex dependencies of people and reefs, and provide management tools to help achieve better outcomes for people and the environment. Researchers from 20 organisations in 10 countries within Europe, the Caribbean, Australia and North America came together to address this complex challenge.

After 4 years the project has generated 48 papers, and further manuscripts are in preparation. The variety of models developed has extended our ability to forecast the structural and dynamical properties of Caribbean reef ecosystems. By improving our knowledge on the impact of disturbances on ecosystem functioning, these models provide meaningful insights into climate change research. We discovered that local reef management of both herbivorous fish and water quality is not only important for ensuring the future function of reefs but essential. Moreover, switching to the more optimistic greenhouse gas emissions' scenarios (e.g. RCP2.6) is vital – along with local management – to maintain positive reef growth towards the end of this century. Re-evaluating earlier assessments of the state of Caribbean reef the project discovered crucial flaws that made them overly pessimistic at 10% mean coral cover. Our revised estimate now doubles this at an average 20% cover therefore our recommendation of habitat-specific measurements for monitoring Caribbean coral reefs when incorporated into existing monitoring programs such as AGRRA will assist in more effective reef state analyses. The identification of a single, simple indicator (parrotfish) to determine fish populations will also be consequential to monitoring reef ecosystems. The research on the valuation of coral reef fish resources for fisheries versus tourism provide economic justification for investment in reef fish conservation to avoid significant economic losses from stock declines and to even increase current gains in the region. Tools were developed to assist with a diverse range of issues ranging from incorporating climate change impacts into the design of marine reserve networks, identifying separate fish stocks just from morphometric measurements and providing livelihoods diversification frameworks to regional organisations. Research into people's perceptions of future of reef ecosystems highlighted that locally focused reef management minimally distracted by external issues (e.g. climate change blame) is essential for community engagement. Identifying social networks that shape information communication will influence how science and policy is shared with stakeholders, for example, in St. Kitt's information is government-centralised whereas non-government organisations are key information brokers in Honduras. FORCE research provided the necessary maps and spatial information used in negotiating the recent designation of the largest marine protected area in eastern Honduras. In Belize we carried out the first ever attempt to model and map the future resilience of coral reefs and evaluate the degree to which marine reserves could enhance resilience. Our results have now been incorporated into the Belize government's program to extend its network of protected areas. We also contributed to the European Commission's 2013 submission to the UN Convention on Biological Diversity. We produced 8 policy and management briefs and worked with managers in developing the publication, '*Towards Reef Resilience and Sustainable Livelihoods: a handbook for Caribbean reef managers'* which is available in English and Spanish, and supported by an online webGIS of data that can be used to help conservation planning.

Context and objectives

The Future of the Reefs in a Changing Environment: an ecosystem approach to managing Caribbean coral reefs in the face of climate change or FORCE project (www.force-project.eu) was 7th Framework Programme collaborative project which commenced in January 2010 and ended in May 2014. This multi-disciplinary project brought together researchers from the natural and social science disciplines to understand the causes of change in reef health and improve the management of Caribbean reefs. FORCE research teams represent 20 organisations, located in 10 countries within the Caribbean, Europe, USA as well as Australia.

Caribbean coral reefs provide a wealth of ecosystem services but experience pressure from a multitude of anthropogenic sources which are expected to increase as human populations rise and climate change drives a rapid change in physical environments. Practical management measures are needed to help reefs cope or adapt to these changing conditions. Management involves altering human behaviour in the hope that it influences the natural environment of reefs. By combining natural and social sciences, the FORCE project has a rare opportunity to identify the management strategies and governance structures needed to maintain functioning reefs, their biodiversity, and the livelihoods of people that benefit from them.

The FORCE project was developed in response to recognition that the coral reefs in the Caribbean are being subjected to a wide range of pressures driven by changing patterns of reef use, wider economic development and climate change. As a result, the state of the reefs in the Caribbean has, in general, been on a long-term path of decline. Therefore, a key thread that runs through the project is that of the challenge to support the efforts of coral reef stakeholders in the region to understand and respond to these changes.

The first objective was to understand the ultimate and proximate causes of change in Caribbean coral reef environments. In order to manage any threat it is imperative to understand it. Reef research for the most part has focused on understanding the proximate causes of change to the health of reefs. These proximate causes include coral bleaching, algal blooms, coral disease, a massive die-off of the sea urchin *Diadema antillarum*, sedimentation, ocean acidification and damage from hurricanes. Coral reef researchers generally concur on the proximate or immediate drivers of reef degradation, however several critical issues have remained unclear. Gaps still exist in our understanding of many ecosystem processes, yet modelling studies suggest that some processes exert a more profound impact on ecosystems than others. With this in mind, the FORCE project proposed to study ecological processes for which little is known yet their potential ecosystem impacts could be considerable.

Understanding of some reef processes is limited and even less is known about the combined effects of multiple sources of disturbance. Reef managers face the challenge of responding to many problems which act simultaneously and over several scales. Providing insight into the combined effects of disturbance requires combined ecological modelling. Given the sensitivity of corals to rising sea surface temperatures, ecological models are required that can integrate many processes and predict the response of reefs to future changes in

climate. The project's ecological modelling of multiple stressors helps to explain the relative impact of different proximate drivers of coral reefs and illuminate the response of reefs to combinations of drivers, such hurricane disturbance and coral bleaching.

A better understanding of proximate drivers leads to greater insight of reef dynamics. Yet it is vital that the ultimate causes of such problems, which include overfishing, overpopulation, inappropriate coastal development, destructive fishing practices, land-based pollution such as fertilisers, corruption and poor governance are also understood (Sale 2008). The importance of understanding the ultimate drivers of reef health cannot be overstated because many of the opportunities to improve reef management are tied intimately to people's behaviour and expectations. Obtaining a comprehensive understanding of the links between ultimate and proximate drivers of reef health requires a merging of social and natural sciences. In particular, social science methods can link coral reef ecosystem science to governance, which important for managing human behaviour in an ecosystem context. The FORCE project combined research on current governance states, livelihood dynamics, and biophysical processes to understand how these ultimate and proximate causes act either independently or link to influence the state of reef ecosystems in the Caribbean.

The second objective of the FORCE project was to assemble a region-wide management toolbox. The management intervention measures available to Caribbean coral reef managers are often limited in that they are patchy and unconsolidated. Managers do not have access to a comprehensive source of coral reef ecosystem management options on a range of issues. These management tools include measures used to develop policies, such as ecological models and governance frameworks, and initiatives taken to control human behaviour such as fisheries regulations, coastal zone management regulations, marine reserves, ecosystem restoration, and livelihood diversification strategies.

Additionally coastal management traditionally, has focused on a small, select number of commercially valuable reef fisheries, such as lobster and conch. This species-specific management has relied on fishing gear and effort restrictions, as well as the limitation of harvest sizes but the scope needs to be much broader to accommodate other reef species, particularly herbivores which are important reef grazers. Even though the expansion of marine reserve initiatives in the early 21st century was a step forward, the total coverage of reserves is still considered insufficient and reserve design initiatives need to consider incorporating other factors such as vulnerability of some corals to bleaching based on their location and larval connectivity of important reef-building corals and commercially viable fish species. Based on the ecological and social research the project aimed to collate and distribute a handbook that incorporated the most recent research that can contribute to management actions for fisheries such as reef fish population indicators and marine reserve design algorithms for planning. As part of the toolbox other resources such as a web GIS with new layers on wave exposure, biogeographical regimes and maps of connectivity coupled with the ecological model of Caribbean reef ecosystems would be made available to managers.

While many tools are widely used, new scientific developments offer scope to strengthen their weaknesses, adapt their design, and improve their overall effectiveness. During the FORCE project, we proposed to investigate and develop the extension of fisheries regulations to consider the management of major herbivores, provision of a framework for enhancing livelihood diversification, and stratification of the location of marine reserves with respect to the likelihood of coral bleaching and the provision of new bioindicators.

Third, the project investigated both the efficacy of management tools and the governance constraints to successful implementation. Reef management tools work in several different ways. Some, like reef restoration using laboratory-reared corals, are a direct means of treating a symptom (lack of natural corals) but do not necessarily address the cause of the problem (the reason why so few corals exist). Others attempt to mitigate the cause of the problem, such as coastal mangrove regulations to reduce the input of sediments onto reefs. Some issues benefit from several tools being used together such as reducing macroalgal blooms by limiting nutrient runoff along with conserving herbivorous fishes. With a diversity of problems facing reefs, and tools available to address these varied issues, it is difficult to identify the efficacy of individual management tools. Efficacy is the ability of a management tool to improve the future trajectory of reef health (corals, fish or both) on the condition that the tool is implemented effectively. The efficacy of a tool can be determined in several ways, through feedback from the experience of practitioners, and from the simulation of impacts of a tool within an ecological model. The FORCE project proposed to investigate the efficacy of management tools for improving reef health.

Although a tool might have the efficacy to address a particular issue if implemented appropriately, many coral reef management initiatives lack the financial or human capacity for effective implementation. Some tools, such as marine reserves, are likely to be successful if local stakeholders take ownership of the process, particularly where funds for enforcement are limited. There are, therefore, a number of constraints to the implementation of management tools, and many can be traced to economics and governance structure. Governance is the principal mechanism for managing human behaviour through government policies, regulations, incentives, and informal community-based activities. Unfortunately there are constraints that lead to failure of government processes and policies. These constraints are expected to be common when governments are faced with the complex trade-offs inherent in an ecosystem approach to coral reef management. Through the field research in countries representing varying gradients of social and economic conditions, and levels of marine resource dependency, FORCE project proposed to identify the governance constraints to the implementation of management tools.

The final aspect of the project centred on the communication of recommendations, and outputs to a range of users. The user group ranges from policy makers in donor agencies (e.g. Pew Charitable Trust), to government and non-governmental practitioners of reef management, to stakeholders in local communities. At a stakeholder level, it is important to convey not only the magnitude of the problems facing coral reefs but also that local actions can play an important role in mitigating stress on reefs or assisting people to adapt to a new environment. Such information is critical for generating participation in and support for reef management and even instigating local action. At the next level, in order to increase management effectiveness of reefs and subsequently the health of reefs in the future,

management practitioners need to take ownership of the tools being provided by the project,. The project would utilise and create opportunities such as a reef managers' workshop for practitioners to provide recommendations on the development of the tools, particularly the reef manager's handbook and the interface of the webGIS. Through the ecological and social science field research within the region, practitioners would be engaged and encouraged to provide feedback on the development of tools as well as the method of communicating the project's research results.

Main results

The ten Work Packages (WP) of the project cover a diverse range of social science and ecological research on processes related to coral reef ecosystems and its management.

WP1 Governance of coral reefs

Reef management is often pursued without consideration of the broader governance structures within which it must take place. The principal aim of WP1 was to develop a systematic process for quantifying the complexity of marine governance in a variety of societal contexts. Four countries: Barbados, St Kitts and Nevis, Honduras, and Belize, were selected, which represented a gradient of wealth, population, industry, natural resources and geography. This enabled broad inferences to be drawn about human dependency on marine resources and management and governance structures that other parts of the Caribbean region can draw lessons from. By replicating four detailed case studies, snapshots of the wider Caribbean have been obtained and some of the geo-political and bureaucratic complexity captured.

Proximate and ultimate drivers of reef health

Changes to the health of reefs can be caused by drivers acting directly on the reef (proximate drivers; e.g. coral bleaching, sedimentation, algal blooms) or drivers which may be physically removed from the reef (ultimate drivers; e.g. coastal development, poverty, poor governance). Management of coral reefs typically focuses on the proximate drivers, those that act directly on the reef. However, understanding the ultimate drivers is key to improving management. Developing a common understanding of the threats to reefs among those responsible for their management is a critical step towards more integrated and effective management. FORCE research compared perceived drivers of reef health among reef managers and policy makers (n=110) in the four case study countries.

Interview data were coded to identify perceived links between reef health proximate drivers (37), and ultimate drivers (79), creating a set of links that identified each separate relationship in the causal chains affecting reef health. Drivers were categorised into 31 themes. Some similarities were identified among respondents' perceptions but statistically significant differences in perceptions were also found among countries. Commonalities demonstrated a broad appreciation of the wide range of proximate and ultimate drivers of Caribbean coral reef health, many of which are shared across the countries studied. Differences may be due to country-specific threats to reefs and specific local management, in addition to differences in the background and awareness of respondents.

Reef management may be improved by acting on this information to help develop policies through: 1) identification of the complex ultimate drivers underpinning the proximate causes of reef degradation; 2) building a common understanding of drivers

between people that use reefs and those responsible for managing them. For example, divergence in managers' and resource users' perceptions of drivers of reef health may lead to a lack of support for management and lack of compliance with management measures.

Social network analysis

In the Caribbean, many actors are involved in or related to reef use, research, management, and decision-making. Organizations that can bridge such diverse actors have been associated with enhancing adaptive capacity and achieving better management outcomes. Social network analysis (SNA) is a tool that can be used to identify brokers, or actors in bridging positions. Information-sharing networks in coral reef governance were investigated using SNA alongside qualitative research methods to identify actors in these brokerage roles and the function of the bridges they provide. Representatives (n=262) from multiple sectors, including local and national government, NGOs, community organizations, and resource user groups from 12 communities across four Caribbean countries were interviewed to determine their roles in reef governance.

Results identified actors that hold significant brokering positions in the information networks. Function of these bridges is significantly correlated to resource users' (n=545) perceived opportunity to participate in decisions made about coral reefs. Data exploration revealed that using SNA in this manner can help further the understanding of the roles and effectiveness of these organizations and can lead to better support of bridging organizations to facilitate collaborations for enhanced reef management outcomes.

Reef-related information sharing networks showed different patterns of interactions among the four countries studied: in St. Kitts, information sharing was highly centralised around a single government department responsible for marine resources; in the Bay Islands of Honduras, fishing and tourism resource users were primarily exchanging information with local NGOs in charge of managing MPAs and had virtually no contact with government agencies; Belize, by comparison, had high levels of information sharing between resource users, local NGOs, and government agencies; in Barbados, patterns of interactions similar to Belize were occurring, however fewer actors were involved, local NGOs were absent, and the overall number of interactions was much lower.

Future scenarios

Livelihoods dependent on Caribbean coral reefs face uncertain futures that have been scientifically articulated in other parts of the project. Predictions of future population, climate and environment are relatively well developed in global and regional models. In contrast, limited studies identify corresponding future behaviours in threatened societies as ecosystem services are lost. Future scenario workshops provide systematic processes to capture perceived drivers of change within different reef contexts, to aid

managers in their decision-making about potential policies and relevant actions they can consider to tackle different issues arising from alternative future scenarios.

The social implications of future challenges were explored during 10 successful workshops with communities in four Caribbean countries and territories. In each workshop, four divergent scenarios were described concerning two critical future uncertainties; whether local reefs are a) subject to community or top-down management and b) relatively healthy or unhealthy, based on a regional scale. Four additional identical workshops were delivered to national policy makers in each country in January 2014, and the results were contrasted with community perceptions.

Scenario work generated unique comparative data. Comparison of community scenario matrices highlighted differences in communities' abilities to see and shape their own futures. Varying adaptive and participatory capacities and visions of viable future governance were apparent. National workshops largely reflected the geo-political context of each nation, and an emphasis on external threats was apparent in each case. The disparity of perceptions and foci between governance levels leads to some interesting implications for management.

WP2 Livelihoods and coral reefs

Coral reef ecosystems underpin the fisheries and tourism sectors that are the mainstay of many livelihoods around the Caribbean. These reefs are being negatively impacted by a multitude of stressors, from overfishing and pollution, to coastal development and climate change. The ability of people living in coastal communities to cope with changes is hampered by few alternative food and employment options. In addition, there is increasing pressure on coral reef ecosystem resources from factors including increasing populations, rising fuel prices and structural changes in global tourism. Natural disasters and more frequent and severe weather conditions are also having a negative impact on coastal areas. Coastal communities, whether in small island development states or in isolated coastal areas of larger countries, often have limited economies of scale to allow for economic diversification to help avoid these pressures. Consequently, dependency on coastal resources can be very high and as a result, both reefs and coastal livelihoods suffer.

Caribbean Reef Livelihoods Framework for managers and researchers

The *Caribbean Reef Livelihoods Framework* is a research framework which is intended to act as a guide and analytical device; providing a structure to help understand how the multiple elements influencing people's lives come together. Critically it helps to understand how livelihoods at the household or community level interact with the wider social, political, economic and cultural context within which they live. This Framework was applied in eight communities, in four countries (Honduras, Belize, St

Kitts and Nevis, and Barbados) to understand some of the similarities and differences in reef dependency between those communities.

The research found that dependency on reefs was mainly and most visibly concerned with fishing and tourism, although the reef also provides coastal protection, a service which is less well understood. The studies also identified interconnectedness between tourism, fisheries and coastal protection, which has implications for reef management strategies. This interconnectedness indicates that change to fisheries, which is often viewed as an immediate necessity in terms of policy change, is so closely related to tourism that the two services should be considered together in the face of climate change. The Caribbean Reef Livelihood Framework has enabled a better understanding of the complexity of the relationships between reefs and livelihoods in ways that indicate that responses to climate-induced changes in reef dependency need to respond to that complexity if the diversity of stakeholders' needs is to be addressed.

Dependency of local communities on coral reef resources and their vulnerability and responsiveness to change in those resources

Throughout the Caribbean, people depend on coral reefs in varied ways: for income, for food, for coastal protection and for maintaining the health of the wider marine and coastal environment. This means that any change in coral reef resources, or in the way that people are able to use coral reef resources, can affect the livelihoods of many people throughout the region.

We aimed to improve our understanding of the ways in which people depend on reefs, and how they are affected by different changes to their access to reef resources. Field studies were carried out in coastal communities with varying levels of dependence on fisheries and tourism in Barbados, Belize, St Kitts and Nevis and Honduras. The qualitative research provides a detailed understanding of the relationships that people have with reefs and how their lives are being affected by change. It goes beyond the social, economic and demographic statistics so often informing policy and brings to light the personal relationships that people have with their environment, their neighbours and the wider society. This provided a unique and very relevant opportunity for coastal people to voice their opinions and concerns to the policy makers and institutions that govern their lives.

The findings of this field work highlighted the many different dimensions of dependency on reefs, which include income-generation, food supply, the generation of opportunities in tourism, coastal protection and the social and cultural significance of coral reefs for some communities. Changes that affect these different forms of dependence, whether they are seasonal, unexpected shocks or changes that take place over generations, can pose significant challenges to people, households and communities.

The findings of the research emphasised the increasing importance of tourism, using local coral reefs or beaches strongly linked to coral reefs, in people's livelihoods throughout the Caribbean. While tourism generates many opportunities, not everyone is in a position to take advantage of them, because they lack the education, skills and capital that are required to capture the benefits of tourism. Coastal fishing, often on or near coral reef areas, continues to play an important role for many people, either as a main source of income, as a supplement to work in other sectors, or as a periodic fall-back when times are hard, tourism declines or other livelihood opportunities are lacking. However, both inshore fishing and coastal tourism depend upon many of the same natural resources and cannot be deemed as sustainable substitutes in the face of climate change.

A systematic approach to coastal livelihood enhancement and diversification in the Wider Caribbean

For coral reef management to be effective, it is important to ensure that reef-users are able to find alternatives ways of making a living that will allow them to adapt to living in a better managed environment. The research identified some of the key factors that help people to adapt better to change, whether that change is the result of new coral reef management measures, changes in the wider economy or shocks and trends such as natural disasters and personal crises. These findings contribute to designing better initiatives for coral reef management that take account of the needs of local coral reef users and enable them to take advantage of the new opportunities that healthy reefs can provide, and adapt to the changes in their livelihoods that management might require.

We produced a review of the literature on livelihoods and reefs entitled *People and Reefs in the Caribbean: a Review of Knowledge* which helped to identify some of the key challenges that coral reef managers have faced in trying to integrate livelihood change into their management efforts. The field research carried out within communities in the four study countries, provided an extensive set of examples of how processes of livelihood change have played out on the ground, whether they were the result of personal or local initiatives or of externally-supported programmes.

Quantification of the value of reef fish for two industries – fishing and tourism

The negative effects of habitat degradation and unsustainable fishing on Caribbean reefs have already been felt in many areas, endangering the livelihoods of dependent individuals. This research examined the economic benefits that Caribbean coastal communities currently derive from the direct use of coral reef fishes, namely within the reef fishing and dive tourism industries. It provides estimates of how future change could affect the flow of benefits to resource users. In an attempt to capture some of the regional diversity, interviews were conducted in three types of communities; i) those

dependent on reef fishing, ii) those dependent on reef tourism and iii) those dependent on a mixture of the two and in each of three contrasting countries: St. Kitts and Nevis, Honduras and Barbados. Given the uncertainty associated with the future of coral reefs, hypothetical scenarios were used to examine the potential adaptive responses of individuals in the diving and reef fishing industries to future changes in the sizes and abundance of reef fishes.

For the nine study sites, estimated annual net revenues ranged from US$0.03-0.95 million from reef-associated fishing and US$0-11.1 million from dive tourism per community (Purchasing Power Parity, PPP dollars). For the fishing industry, factors such as export market access, the presence of marine protected areas, and attributes of individual fishers were strongly associated with reef-related revenues. For the dive industry, community location, target markets and operational costs were some of the main factors identified as associated with revenue.

WP3 Physical environments of Caribbean reefs

The objective of WP3 was to describe and categorize the environmental regime that coral reefs experience around the Wider Caribbean using remote sensing products, in situ datasets and regional ocean models. WP3 has produced a suite of GIS layers describing the environmental regimes that coral reefs experience across the Wider Caribbean. The maps summarize information related to bathymetry, wave exposure, hurricane incidence, sea surface temperature, turbidity, rainfall, sea surface salinity and incident radiation. Connectivity GIS layers for five important species in the Caribbean (two species of coral and three species of fish) were also produced.

WP4 Ecological status of Caribbean reefs

The ecological field team conducted surveys at 129 forereef sites in 12 different Caribbean Countries, Honduras, Belize, Curaçao, Bonaire, Jamaica, Barbados, Dominican Republic, Antigua, St. Lucia, St. Vincent and the Grenadines, Panamá and Costa Rica. At each site, researchers surveyed the benthic and fish communities and rugosity.

The status of Caribbean coral reefs and importance of habitat-specific measurements

During our surveys we noticed that there were two types of forereefs, those mostly built by *Acropora* spp. and *Orbicella* spp. which have the potential for high habitat complexity and 'gorgonian plains' which historically have had little live coral and are typically found in areas of higher wave exposure. Our Caribbean-wide analysis showed that combining habitats that historically have little coral cover, with those habitats that have exhibited significant reef development such as *Orbicella* reefs, can produce biased estimates of coral cover, benthic and fish composition. The mean coral cover at *Orbicella* reefs was ~24%, more than double that of gorgonian plains and previous reports for the region. Therefore distinguishing between forereef habitats before any

type of analysis, is necessary to accurately report a baseline for future research and/or monitoring.

According to the data, the current status of *Orbicella* reefs in the Caribbean showed a relatively high coral cover (>40%) in countries like Bonaire, Panamá and Barbados. The coral composition in Bonaire and Barbados consisted of mostly reef-building species, such as *Orbicella* spp. and *Montastraea cavernosa*, while the principal species observed on Panama's reefs were the weedier corals, particularly *Agaricia lamarcki* and *Agaricia agaricites*. Overall, the shift to weedier species has not occurred at many *Orbicella* reefs in our survey. At many of the sites the highest cover was by an important framework builder, *O. faveolata*.

At 94% of the *Orbicella* sites, mean coral cover was well above 10%, a level considered to be beyond which reef accretion might fail to outweigh erosion (Perry et al. 2013). Model predictions suggest that positive carbonate budgets are still feasible throughout this century provided that local and global stressors are managed and when coral cover starts at around 20% (Kennedy et al. 2013). Taking a 20% coral threshold, 64% of the sites surveyed meet this target, implying that there is considerable scope for continued ecosystem function in the Caribbean.

The benthic biogeography of Caribbean coral reefs

Caribbean reefs are generally considered biogeographically homogeneous at a regional scale. Based on using the species richness of corals, we assessed reefs along 546 transects positioned within the same forereef habitat (*Orbicella* reefs). We use three different benthic species assemblages (corals, sponges and octocorals) and three different community attributes to examine their degree of sensitivity to spatial scale. Our initial findings suggest that species richness of coral assemblages, generally the target of biogeographical studies, is the most insensitive taxa and community attribute to large-scale spatial patterning. Other metrics such as species scale-dependent diversity were the most sensitive metrics to spatial scale, with each assemblage responding differently to spatial patterning and environmental drivers. We also saw indications of a strong biogeographic signal in the basin. However, the large variability observed at the site scale highlights the relevance of local ecological drivers such as reef structure (rugosity) and wave exposure shaping the assemblages, and might suggest the contribution of localized anthropogenic disturbances within the region.

Resilience of Caribbean coral reefs based on the current benthic structure and recruit density

We identified country similarities according to coral cover and algal cover. The results showed that the reefs surveyed could be categorised into three groups based on an 87% similarity: A) Dominican Republic, Saint Lucia, and Saint Vincent and Grenadines; B)

Belize, Honduras and Jamaica; and C) Curaçao and Bonaire. Antigua reefs join groups A and B with 82% of similarity; and Barbados is 82% similar to group C. Costa Rica and Panama reefs are dissimilar between themselves and among the groups. The above groups are not statistically different based on ecoregion classification proposed by Spalding et al. (2007); however these groups are statistically different based on physicochemical provinces classification proposed by Chollett et al. (2012).

Coral cover was negatively correlated with macroalgae cover. However, some surveyed reefs showed low coral cover in a wide range of macroalgal cover (low or high). Reefs with the highest coral cover had macroalgal cover below 20%. These results could indicate that other factors are influencing coral cover in Caribbean reefs.

Coral recruits' composition in Caribbean reefs were mainly represented by three genera: *Agaricia*, *Porites* and *Siderastrea*. Average recruit density varied significantly among countries. Brooding coral recruits were more abundant in most of the countries, compared with spawning coral recruits. These differences are not statistically significant for adult coral cover. Comparing coral cover and recruit density, we have a positive relation for brooder species, but there are no differences for spawner species.

WP5: Ecological processes on coral reefs

WP5-R5 aims to address gaps in our understanding of coral reef ecological processes, particularly where processes are expected to influence ecosystem dynamics strongly. WP5-R5 focuses on underlying ecological processes and proximate drivers of reef degradation. The main objectives were to explore processes affecting benthic community structure. In particular we focussed on processes involved in natural coral recovery, nutrification, bioerosion, the effects of habitat structure on biodiversity (reef fish and benthic organisms) and fish populations in no-take marine reserves.

Investigate the processes of natural coral recovery

Healthy reefs produce more and better coral offspring

The reproductive success of biological populations and species is assumed to be determined by energetic tradeoffs between the number of offspring produced and their individual size. The best offspring size is often determined by environmental conditions, though models describing reproductive tradeoffs often ignore how parental condition is shaped by the environment and can in turn limit reproductive investment. Furthermore, reproductive investment is most directly limited by the energy used for reproduction, though this is rarely measured directly. We examined reproductive tradeoffs in corals from an energetic perspective. Corals produce variable numbers and sizes of offspring and invest large amounts of lipid energy into reproduction allowing us to directly test theories related to energy investment tradeoffs in reproduction. Our assessments spanned five species, two populations, three years, and multiple life histories, providing

a robust dataset for understanding reproductive patterns on multiple relevant scales. Across species, we found that energetic lipid content and fecundity tended to be higher in populations in intact reef communities compared to those on declining reefs. We also noted a link between physiological differences and reproductive patterns between sites. Differences in the body size of coral larvae and energy content were greatest among individuals and species, though were remarkably similar across populations. Our findings suggest that differences in physiological state can lead to disparity in reproductive output that is not necessarily adaptive for the coral. When such differences emerge among conspecifics on population scales it can have implications for connectivity and regional resilience, especially when coupled with differences in life history traits that influence dispersal potential.

Effects of larval size and planktonic stress on the survival and performance of Caribbean coral larvae

When juvenile corals must tolerate harsh environments early in life, the disproportionate success of certain phenotypes across multiple early life stages will dramatically influence adult community composition and dynamics. In many species, large offspring have a higher tolerance for stressful environments than smaller offspring. We have a poor understanding of whether the benefits of increased parental energy investment carry over after juveniles escape harsh environments or progress to later life stages (latent effects). We therefore investigated whether parental effects and latent effects interactively influence offspring success in two stony coral species under harsh abiotic conditions. Larvae of both species were sorted by size class and exposed to relatively high-temperature or low-salinity conditions. Survivorship was quantified for six days in these stressful environments, after which surviving larvae were placed in ambient conditions and evaluated for their ability to settle and metamorphose. We subsequently assessed long-term post-settlement survival of one species in its natural environment. We found that large offspring size did enhance offspring performance in each species. However, large offspring size within a species did not reduce the negative effects of harsh larval environments. The coral species that produces larger offspring was more, not less, prone to negative hidden environmental effects. We conclude that, within species, large offspring size does not increase resistance to latent effects. Comparing between species, larger offspring size does not confer greater robustness, and we instead propose that other life history characteristics such as larval duration better predict the tolerance of offspring to harsh and variable abiotic conditions.

Coral recruitment depends on the presence of nearby adults

We tested the central predictions of the Janzen-Connell model on swimming larvae and settled polyps of the common Caribbean coral *Orbicella faveolata*. The Janzen-Connell model states that host-specific biotic enemies (pathogens and predators) promote the coexistence of tropical tree species by causing distance- or density-dependent mortality

of seeds and seedlings. In our field experiment, coral settler mortality was higher near coral adults (density-dependent), especially in locations down-current from adult corals. However, survival of a coral settler did not increase with distance to adult corals, revealing the influence of fluid dynamics around adult corals in structuring spatial patterns of settler mortality. Microbial analyses around adult coral heads revealed that marine microbial communities (one potential cause of settler mortality) follow the same spatial patterns. A complementary field experiment indicated that settler mortality can be 2.3–3.0 times higher near adults of the same species vs. near adult corals of other genera, or in open reef areas. In four laboratory experiments, swimming coral larvae were exposed to water collected near adult corals of the same species, near other coral genera, and in open areas of the reef. Microbial abundance in these water samples was manipulated with filters and antibiotics to test whether the cause of mortality was biotic (i.e., microbial). Juvenile survivorship was lowest in unfiltered water collected near the same species, and survivorship increased when this water was filter sterilized, collected farther away, or collected near other adult coral genera. This is the first time the Janzen-Connell principles are revealed in a marine ecosystem and in an animal. This has important implications for coral diversity in the Caribbean, as the distribution of adult corals across a reef can influence the spatial pattern of juvenile survival. When rare coral species have a survival advantage, coral species diversity per se becomes increasingly important for the persistence and recovery of coral cover on tropical reefs.

Delayed rather than direct impacts cause suboptimal performance of coral larvae after an oil spill

Oil spills are one of the most readily-visible human-caused spills of a toxic substance into the environment, yet we still know relatively little about the delayed effects of crude oil on marine organisms. When a small oil spill occurred on Curacao in August 2012 we took the opportunity to examine the effects of crude oil on coral larvae. Many species of corals use the sea surface for fertilization and dispersal before coral larvae move to the seafloor for settlement. Given this reproductive strategy, coral species whose spawning events coincide with the occurrence of spills may be particularly affected by oil or other forms of chemical pollution at the water surface. Moreover, exposure of organisms to harmful agents can have delayed negative effects that persist over lifetimes. We tested coral larval performance in water collected from the spill site, where oil was still visibly present, and in oil-contaminated seawater that we created in the lab. During the exposure to oil-contaminated water, we found very little instantaneous or direct effect of oil on the survival of larvae of two species of stony corals. However, we found that the ability of larvae to successfully settle and metamorphose after they were exposed to oil-contaminated water decreased by an order of magnitude in one coral species and by more than 50% in the other species. Furthermore, the latent effects of oil on one species led to over 50% mortality after larvae were moved to normal seawater. These results show that organisms with pelagic

life cycles, such as corals, can experience mortalities long after a direct exposure to oil. These latent negative effects of oil spills are often ignored during impact assessments, so that high mortalities of marine species can go unnoticed. This opportunity provided results which contribute to understanding other potential stressors on the performance of coral larval fitness.

Diseases in crustose coralline algae (CCA)

Crustose coralline algae (CCA), rock-hard calcareous red algae are important for coral reefs because they provide a substrate that the larvae of many reef organisms, especially some hard reef-building coral recruits favour for settling and growing on. Our research and experiments on Curacao concluded that CCA diseases varied considerably in time and space on the island of Curaçao. They were more abundant on reef flats than reef slopes and had a higher prevalence during the warm/rainy season. We found a positive link between temperature and CCA disease occurrence and highlighted the importance of stressors interactions to better understand disease dynamics. We also found that diseases affected all crustose coralline algae species. Thus they have the potential to cause major declines in CCA abundance coupled with shifts in species composition, particularly in shallow waters. Laboratory bioassays with healthy and diseased CCA showed that diseases can affect coral larval settlement behavior. Coral larvae did not settle on diseased and recently dead surfaces of the CCA species *Hydrolithon boergenesii* known to act as a coral settlement cue, but readily settled onto healthy surfaces, suggesting that diseases could affect coral recruitment in the natural environment.

Post-settlement mortality of corals, sediments and algal dynamics

Turf algae are becoming a dominant component of coral reef communities around the world and may affect the post-settlement mortality of corals. To assess the impact of turf algae on corals, we investigated the effects of increased nutrients (eutrophication) on the interaction between the Caribbean coral *Orbicella annularis* and turf algae at their growth boundary. We found that turf algae cause visible (overgrowth) and invisible negative effects (reduced fitness) on neighbouring corals. Corals can overgrow neighbouring turf algae very slowly, but turf algae overgrew corals at a higher rate when nutrients were experimentally increased. We also used PAM fluorometry (a common approach for measuring a colony's ''fitness'') to detect the effects of turf algae on the photophysiology of neighboring corals. Turf algae always reduced the effective photochemical efficiency of neighbouring corals, regardless of nutrient and/or herbivore conditions. At ambient nutrient levels, traditional conservation measures aimed at reversing coral-to-algae phase shifts by reducing algal abundance will not necessarily reduce the negative impact of turf algae on local coral communities.

Benthic cyanobacterial mats

Benthic cyanobacterial mats are impacting coral reefs worldwide. However, the sources and transport by which nutrients stimulate these mats are unclear. We have identified organic matter degradation as a mechanism of nutrient supply with consecutive growth impulse for benthic cyanobacterial mats on coral reefs. Organic matter stimulates growth of coral-damaging cyanobacterial mats, even without elevated nutrients in the seawater. Coastal urbanization and hydrodynamics affect the accumulation of particulate organic matter on the seafloor, which subsequently fuels the growth of these unwanted mats. Our results suggest that organic matter is a major threat to coral reef health and should be included in monitoring and management plans.

Benthic cyanobacterial patches were dominated by either *Blennothrix glutinosa*, *Oscillatoria bonnemaisonii* or *Lyngbya majuscula* on Curacao. Those mats fixed notable amounts of nitrogen. A maximal areal rate of nitrogen fixation for a brown mat dominated by *O. bonnemaisonii* is one of the highest reported in coral reefs worldwide.

The mats excreted large amounts of dissolved organic carbon (DOC) in the light and especially in the dark. It is well documented that DOC excreted by macroalgae, is deleterious for corals. The DOC measured on cyanobacterial mats was much higher than previously reported for macroalgae over a 24-hour period. As these cyanobacterial mats are increasingly observed in mass occurrences, we argue that the DOC release from cyanobacterial mats may form a serious threat for coral reefs and additionally could contribute to the nitrogen pool on the reef which is often a limiting growth factor for corals.

Fate of nutrients entering coral reefs from land

We developed a new experimental setup to quickly detect by fluorimetry nutrient limitation in macroalgae and seagrasses. We found that the brown alga *Lobophora variegata*, which is often associated with the degradation of coral reefs, was limited by both nitrogen and phosphorus.

Looking at the molecular nitrogen fixation potential of turf algae on a degraded and less degraded reef site in Curacao we found that the total amount of nitrogen fixed by turf algae is substantial. This fixation was higher during the day and in the upper 10 meters but was unaffected by the level of eutrophication. As turf algae are currently dominating many reefs around the world, and because they are present throughout the year, our results indicate that they may play an important role within the nitrogen cycle on the reef.

We also measured the rates of nutrient uptake of the major reef phototrophic organisms, including corals, macroalgae, turf algae, benthic cyanobacteria and phytoplankton. We found that benthic algae and cyanobacteria, which are known to cause nuisance blooms on reefs around the world, are the quickest in capitalizing on

these newly available nutrients. Compared to corals and phytoplankton, benthic algae and cyanobacteria take up nutrients substantially faster. Undoubtedly, this may have consequences for the competitive interactions among these reef organisms. Benthic algae and cyanobacteria are more likely to out-compete the slow-growing corals when more nutrients become available on the reef, for example via sewage discharge or coastal construction near the reef.

We compared our results on rates of primary productivity (PP) of phototrophic organisms with results of a 40 year old survey to determine whether a shift occurred in the main benthic primary producers on the shallow reef. Historically, corals were the main contributors, yet nowadays according to our calculations turf algae are the main primary producers. We also found that the total primary productivity of the reef (based on abundance data from corals, benthic algae and cyanobacteria) decreased during the past four decades. This may have affected the functioning of the food web with less energy being transferred to herbivores.

Objective 3 Algal-driven increase in bioerosion on reefs

Increased bioerosion mediated by coral-algal phase shifts and dissolved organic matter (DOM)

In many Caribbean reefs the cover of benthic algae increases at the expense of hard coral cover. We explored the non-intuitive consequences of increased algal cover on reef bioerosion through algal production of dissolved organic carbon (DOC). We found that benthic macroalgae release more DOC than corals and that this DOC produced by algae is highly dependent on light availability. This may be one of the reasons why DOC concentration in water around some Curacao reefs significantly decreases by ~50% from May-June (high light intensities) to November (lowest light intensities). Increase in algal cover and substantial DOC release from benthic algae imply that the supply of DOC to the benthos is increasing. We also discovered that the benthic community is exposed to large variations in DOC concentration. We therefore studied the impact of increased benthic DOC on the process of reef bioerosion by sponges. Specifically we found that two different but common coral-excavating (i.e., bioeroding) sponge species (*Cliona delitrix* and *Siphonodictyon* sp.) were capable of taking up natural DOC. Remarkably, their diet consisted of more than 75% of DOC. Indirect evidence from stable isotope samples suggest that algal-derived DOC might be part of their diet as also appears to be the case for open reef and coral reef cavity sponges. The general increase of algal-derived DOC detected on Curacao reefs may stimulate sponge abundance and excavation rates, with potential consequences on the architecture of the coral framework and associated quality of the reef habitat.

Biodiversity and the structure of coral reefs (rugosity, coral cover and algal cover)

The decline of complex reef-building coral species such as *Acropora* and *Orbicella* and transition to stress-tolerant, less complex 'weedy' species such as *Agaricia* or *Porites*, has led to increasing homogenisation of benthic composition and flat reefs now comprise 75 % of Caribbean reefs compared to 20 % in the 1970s (Alvarez-Filip et al. 2009). A precedent exists to expect significant declines in Caribbean biodiversity as reef structure degrades over time. Data were collected on fish community composition and coral reef structural complexity from 11 countries around the Caribbean. Several methods were employed: one to allow for large scale comparison of fish communities, one to control for habitat variability, and one to collect data on fish behaviour. The surveys conducted for this component represent an important dataset because it has minimised traditional variability in data collected by multiple researchers using dissimilar methods in different locations at different scales.

These data have so far been used to elucidate the importance of complexity to coral reef fish communities, within each country and across the Caribbean basin. Results reveal high complexity reefs in the Caribbean at present may not necessarily have the greatest fish species richness, but should still be a priority for conservation and management as they may support specialist species or higher biomass. Complexity may be less important to coral reef fishes in areas of high algal dominance, and the models employed reveal the role of multiple variables in determining fish communities. Structural complexity has been shown to be important to a wide range of marine organisms in different habitats, but to the best of our knowledge this is the first study to assess the importance of complexity to many of these taxonomic groups as well as total faunal species richness at this scale on coral reefs. This research provides an exposition of the role of complexity on total reef faunal richness, which incorporates multiple taxa-specific relationships. The richness of most taxa investigated declined at lower complexity levels, except for sponge richness which increased. Fish or coral species richness may be useful to identify key conservation areas with the priority to maintain ecosystem structure and function, as diversity provides an insurance against environmental fluctuations.

Objective 5 Recovery of fish populations in no-take marine reserves

Simple reef fish population condition indicators

We set out to identify simple indicators of the effects of fishing: indicators that could be implemented under the data-poor and resource-limited conditions in which most reef fishery managers operate in the Caribbean. We examined the relationships between proxies of fishing and simple fish metrics derived from entire fish communities (i.e. fish abundance, fish biomass, fish mean weight, species richness) or specific fish assemblages (i.e. density, mean fish weight and biomass of parrotfishes and commercial species such as snappers and groupers) within and across locations in the Caribbean To

conduct these analyses, we used the Caribbean-wide standardised fish and reef survey data available through the Atlantic and Gulf Rapid Reef Assessment (AGRRA) initiative as well as data from fish surveys in Barbados.

With regard to the fish metrics derived from entire fish communities, our results have clearly demonstrated that mean fish size is the most useful for assessing fishing pressure on today's Caribbean coral reefs. With regard to the fish metrics derived from specific fish assemblages metrics, we have further demonstrated that parrotfish mean size is an excellent and simple indicator of fishing effects, which performs much better than conventionally used metrics derived from snappers and groupers, given that this species group is now relatively rare on today's reefs as a result of pervasive overfishing across the region.

WP6 Impacts of climate change on corals

Objective 1: Characterisation of the effects of chronic and acute thermal stress on corals (coral bleaching)

Seasonal differences in coral physiology

We studied seasonality in symbiont content, pigmentation and metabolic rates in four coral species; *O. annularis, O. faveolata, M. Cavernosa and P. strigosa.* Our results revealed significant differences in seasonality among species but some general trends. In agreement with previous studies, we found that the number of symbionts is higher in winter than in summer. However, these differences do not appear to impact calcification rates, which remained similar throughout the seasons. We found no clear responses of pigmentation to season. Detailed monthly monitoring studies revealed some interesting new results. Where previous studies report only one seasonal minimum for symbiont content and pigmentation in mid-summer, we found a second minimum during the transition from winter to summer, coinciding with increasing water temperature and increasing light exposure. In general, *M. cavernosa* showed the lowest symbiont content and smallest seasonal variation, whereas, *P. strigosa* and *O. annularis* showed the greatest.

Characterization of coral optics

The four species of coral studied demonstrated high efficiency for absorbing light but small but significant differences in efficiency among species. For example, *O. faveolata* and *P. strigosa* exhibited 6% lower maximum absorptance (87-88% of incident light) than *O. annularis* and *M. cavernosa* (93-94% of incident light). However, *O. faveolata* required less pigmentation to reach this maximum indicating that it is very efficient at collecting light at low pigmentation but is more heavily impacted by the packaging effect. The lowest pigment absorption efficiencies were exhibited by *M. cavernosa* and *P. strigosa,* with the former requiring high pigment concentration to achieve maximum absorption and the latter having a low absorptance maximum.

Characterization of coral photobiology and photoprotection capacity

Our study found no differences among species in relation to photosynthetic performance. The estimated minimum photosynthetic requirements of photosynthesis confirmed that the four coral species are highly efficient at trapping light, but also at using light. As light stress is a critical process to explain the effect of thermal stress, we examined potential differences among species in the capacity for photoprotection *M. cavernosa* and *O. faveolata* showed a large capacity to absorb excess light. This ability strongly reduces the capacity of both species to maintain high photosynthetic rates under low light conditions. By contrast, *O. annularis* and *P. strigosa* showed lower ability to absorb excess light, and presented higher photosynthethic turnover under lower light conditions. *P. strigosa* is the species that accumulates faster photodamage with increasing light, but also has a more effective repair mechanism that maintains photosynthetic activity

Direct and combined effect of light, thermal stress and low pH on coral physiology

Experimental studies revealed that a moderate decrease in water pH did not significantly affect the physiology of the four species examined. However, thermal stress of +2ºC 10 days caused significant impacts on coral photosynthesis and calcification. The interaction between the two stressors exacerbated the effect caused by thermal stress. Considering predictions for future ocean scenarios in relation to warming and acidification, this study concludes that scleractinian corals, and consequently coral reefs, are strongly threatened by global change due to negative effects on photosynthetic physiology and calcification.

Objective 2 Effects of ocean acidification on coral calcification and linear extension rate

Impact of temperature on coral skeletal density and linear extension rate

For this study we wanted to assess the effects of increasing sea surface temperature on the calcification rates of common Caribbean corals. We found that for all species on all reefs, calcification rate is negatively correlated with annual average sea surface temperature SST. The impacts are not uniform across species however. In *Orbicella* spp. the strength of the negative relationship is significantly lower than in *Porites astreoides*, *Pseudodiploria strigosa* and *Siderastrea siderea*. Moreover, *Pseudodiploria strigosa* and *Siderastrea siderea* are more sensitive to temperature increase than *Porites astreoides* and *Orbicella* spp. Our results demonstrate that the effects of climate change, specifically the increase of SST will have differential impacts on different coral species, and this variability could have significant ecological repercussions. For example, species such as *P. astreoides* and *S. siderea* which invest extra calcification resources into faster growth may reduce their ability to compete for space on the reef when SST increases. *Orbicella* spp. and *P. strigosa* on the other hand invest extra calcification resources into making denser skeletons may instead increase their susceptibility to physical and

biological breakdown. Overall, these differences in response could have significant impacts on competition, mortality and community structure

Objective 3 Multiplicative effects of physical stress on corals

Species-specific thresholds of dissolution for Caribbean corals

Ongoing ocean acidification (OA) is rapidly altering carbonate chemistry and projected climate change scenarios could have deleterious consequences for coral reefs due to reductions in their calcification-dependent growth.The first stage of our study considered how ocean acidification and reduced carbonate concentration affects coral reef calcification, through the reduced ability of corals to calcify and/or increased dissolution of existing coral skeletons. A number of studies measure net calcification rates (NC) in corals in response to ocean acidification but this does not always consider the proportions of 'real' (gross) calcification (GC) versus gross dissolution. This study measured both gross and net calcification rates for a tropical scleractinian coral under potential conditions of ocean acidification. Colonies of the Western Atlantic coral *Porites porites* were incubated under normal and reduced pH conditions, to simulate ocean acidification and their calcification rates were measured. We demonstrated that at ambient pH, widely used alternative measures of total calcification yield comparable results as long as experiments are conducted over short-time spans and/or conditions are maintained constant. Our results showed no change, over short incubation periods in the gross calcification rates of *P. porites* under a range of pH conditions that are predicted to prevail in the ocean by the end of the century.

In the second phase of the study we experimentally compared the responses of two reef building corals (*Porites porites* and P*orites astreoides*) to the synergistic effect of pH and temperature. Our results show differential response to treatments between the two coral species with respect to photosynthesis and respiration, calcification, and microbial community. *P. porites* (and *P. astreoides* in a lesser extent) showed significantly lower photochemical yields at the higher temperature (31°C) and a higher photochemical yield at normal (8.1) pH. The microbial community structures hosted by *P. porites* shifted significantly with increased temperature. Microbial communities in *P. astreoides* shifted significantly in response to decreased pH and increased temperatures, both separately and synergistically.

Mesocosm experiments on effects of pH, temperature, nutrients, light and flow on coral growth and skeletal density

Although the effects of individual factors on coral growth have been described, the interplay between different factors remains largely unknown. Understanding this complexity is of importance to predict the development of coral reefs as the environment continues to change.

We conducted five studies aimed at understanding multiple factor effects on coral growth. Three of these studies focused particularly on the role of dissolved oxygen in relation to other factors such as the availability of organic food, pH, water movement and alkalinity under daytime and night-time conditions (light/dark).

The presence or absence of organic food (zooplankton) affected the results considerably: whereas feeding enabled a higher capacity to calcify in light, feeding completely suppressed calcification in darkness, regardless of the level of dissolved oxygen. This effect was ascribed to a decrease of the internal pH in the coral tissue due to acidifying digestive processes that take place after zooplankton uptake.

One experiment included multiple effects of nutrients, pH and water movement on the growth of the Caribbean keystone species *Porites porites*. We found an antagonistic effect of nutrient enrichment on pH; both nutrients and pH inhibited coral growth, but the effect of pH was less severe under nutrient enrichment.

From our experimental results, it became apparent that the balance between photosynthesis and calcification can be disturbed by changes in oxygen saturation, food availability and pH. The magnitude of these effects varies per species. In addition, multifactor effects of pH and nutrification were found to have an antagonistic effect (nutrification tempering the negative effect of ocean acidification) on calcification in *Porites porites*, which is in contrast to earlier research on another Caribbean species. Hence, differential responses to stress on natural coral reefs may not only result in slower reef development but may also lead to changes in species composition.

WP7 Integrated modelling of processes and drivers

Synergistic impacts of global warming on the resilience of coral reefs

In the past three decades, many Caribbean coral reef ecosystems have undergone a profound community change from coral to macroalgal dominated. With relatively few corals capable of rapid growth, and a paucity of herbivores, fleshy macroalgae have increased in abundance on Caribbean reefs. Moreover, grazing levels have often been reduced further by the fisheries exploitation of the remaining herbivores. However, the consequences of global warming have become one of the greatest concerns for the future of coral reefs. Corals usually tolerate only a narrow range of sea surface temperatures (SST), and therefore, rising SST may exert both a chronic and acute impact on reef ecosystems.

We studied the complex effects of rising SST on the resilience of Caribbean coral reefs, questioning how acute and chronic stresses may interact to drive future coral cover and reef resilience. Using a spatially-realistic model of coral populations, we simplified the reef ecosystem to represent two groups of corals that have different life histories but contribute significantly to the state of present-day Caribbean coral reefs: the *Orbicella annularis* complex and *Porites astreoides*.

We simulated the response of each coral to a scenario of climate change representing high greenhouse gas emissions, i.e. “business as usual” (RCP8.5). Using an experimental approach we assessed the separate and combined effects of the chronic and acute thermal stresses on reef state and resilience, asking whether the two stresses (treatments) interact synergistically, additively, or antagonistically. For each treatment, 100 replicate simulations were run for 50 years.

Under a baseline scenario where corals are not affected by any thermally-induced perturbations, coral cover invariably increases over time and reefs are fully resilient (i.e., probability of recovery is certain). The addition of acute disturbances, i.e., bleaching events as predicted under the RCP8.5 scenario, considerably reduces the total cover of corals and progressively erodes reef resilience. A chronic reduction of *P. astreoides* growth rate has a smaller effect on reef state (i.e., coral cover) and resilience compared to acute bleaching. The predicted combined effects of the two stressors closely matched the simulated combined-stressor effect, indicating that the two stressors act additively on reef state, without synergism nor antagonism. On reef resilience however, acute and chronic stresses when combined have a much greater effect than expected. This indicates synergism in the reduction of resilience.

This study provides important insights on the mechanisms that maintain healthy coral reef ecosystems. It also has important implications for reef monitoring, showing that reef state and resilience can respond differently to disturbances. A key difference here is the time scale over which they change. Resilience measures whether there is sufficient recruitment and growth to allow net coral recovery from the current reef state. If a reef moves to a point where the balance between the processes of recovery and natural mortality becomes negative, this will be barely detectable in relation to coral cover because the rate of coral decline might be very low. However, a small change in the coral cover will have a catastrophic and immediate impact on resilience. Thus, resilience can change considerably faster – and earlier – than a change in reef state.

The dynamics of architectural complexity on coral reefs under climate change

Understanding the mechanisms that maintain complex reef architecture is important to envision the future health of reef habitats in an era of climate change.

Central to the creation of the reef architecture is the growth and calcification of hard corals that constitute the primary units of the reef framework. A number of biological and physical agents, however, lead to the erosion of the coral-generated carbonate framework. The balance between these two processes (accretion and erosion) determines the ability of a reef to grow through net carbonate accretion. Recent studies have revealed significant reductions in the ability of Caribbean reefs to sustain a net reef accretion, which raises concerns considering the predicted impacts of climate change on coral growth and calcification.

We developed a mechanistic model of reef topographic complexity for contemporary Caribbean reefs. The model describes the dynamics of corals and other benthic taxa under climate-driven disturbances (hurricanes and coral bleaching), and quantifies the contribution of each coral species to the deformation of the reef surface. The model accurately simulated the decadal changes of coral cover observed in Cozumel (Mexico) between 1984 and 2008, and provided a realistic hindcast of changing topographic complexity over the same period. We then projected future changes (2010-2050) of Caribbean reef architecture in response to global warming. Model simulations indicated a significant decline of architectural complexity due to the combined impacts of bleaching and hurricanes.

Under severe and frequent thermal stress caused by business-as-usual GHG emissions, reefs may dramatically lose structure in the next three decades. Under high frequency hurricane regimes, the same reef habitats may be critically degraded over shorter timescales (< 20 years). Coral mortalities due to bleaching disrupted the development of complex architectures and compromised their ability to recover from hurricane damages. Under this scenario, the ability of Caribbean reefs to maintain functional reef habitats in the short term may depend on the efficiency of local management in sustaining high grazing. As a result, model simulations suggest that with realistic rates of parrotfish bioerosion, high levels of grazing would benefit the reef habitat structure rather than accelerating its degradation. Protecting or restoring parrotfish grazing may help corals recovering from moderate bleaching and hurricanes thus maintaining carbonate production at levels that will offset skeletal erosion. Our results thus support the view of the importance of combining aggressive mitigation of GHG emissions with local interventions aiming at favouring a net coral growth.

WP8 Ecosystem-based fisheries and marine reserve design

Two new objectives were added to the WP8 during the course of the project. These include 1.) investigating climate change and fishing activity and 2.) planning for a Marine Protected Area in the Miskito Cays. We used detailed information on weather conditions and fishing locations to model the behaviour of fishermen in the Bay Islands (Honduras) and assess how climatic and economic changes were likely to affect this behaviour. These results suggest that credible adaptation strategies in the area require the intervention of the market chain to make the sale price of fish more responsive to fuel price fluctuations and changes in fishing behaviour to improve fuel efficiency, including the revival of traditional ways of fishing.

Global coastline datasets and nautical charts were inaccurate for the area. Using numerous mapping and remote sensing data, the Miskito area environment has been characterized in terms of bathymetry, hurricane incidence, wave exposure, turbidity, temperature and bleaching regimes. Marine habitats were characterized and mapped

using remote sensing data. High-resolution (0.5-2.4 m) imagery for the area was produced which was then used to map the shallow marine habitats in the region. A rapid assessment of the reef was conducted for in situ characterization of the region and validation of the satellite imagery. While the best global coastline dataset available indicates the region includes 54 cays, covering 1,170.60 hectares, our mapping exercise indicated that the region includes 49 emerged Cays covering only 28.97 hectares. Additionally for the planning of the network of no-take reserves, the current uses were also mapped. As the area currently is used only for industrial fishing, we obtained Vessel Monitoring System (VMS) data for three fishing seasons and mapped the effort of each industrial fishery in the Honduran EEZ.

WP9 Evaluation of restoration methods for Caribbean corals

Recruitment Rate and Survivorship of Naturally-settled Corals on Curacao

Although coral cover on Caribbean reefs has declined significantly in the past 30 years, on Curaçao a similar but less dramatic decline has occurred. The maintenance and recovery of coral communities depends on the successful establishment, early survival and subsequent growth of coral recruits, and overall recruitment success differs between species experiencing the same environmental conditions. Variation in local coral recruitment rates is caused by variation in the composition of the local benthic habitat as well as the size of the adult source population. In addition, the total number of coral recruits, juveniles and adults in a given location will decrease during episodic disturbance events such as storms. Recruitment failure can halt, delay or even prevent coral community maintenance and recovery. A comparison of the community structure of juvenile stony corals between 2 to 37 m depth at the fringing reefs of Curaçao between 1975 and 2005 showed a decline of 54.7% in juvenile coral abundance and a shift in species composition. *Agaricia* species and *Helioseris cucullata,* the most common juveniles in 1975, showed the largest decline in juvenile abundance (a 9 and 120 fold decrease in density respectively) with *Helioseris cucullata* being nearly extirpated locally. In 2005, *Porites astreoides* contributed most colonies to the juvenile coral community, increasing from 8.2% (in 1975) to 19.9% of the total juvenile community. Between 1975 and 2005, juveniles of brooding species decreased in relative abundance while the abundance of juveniles of broadcast spawning species increased or remained the same. These data illustrate the magnitude of the changes that have occurred in only three decades in the composition of juvenile coral communities.

Using sexually produced recruits to restore critically endangered elkhorn coral (Acropora palmata) in Caribbean coral reef ecosystems

Until the late 1970s, *Acropora palmata* dominated coral communities on shallow reefs throughout the Caribbean and played an important role in ecological processes on coral

reefs. *A. palmata* populations have declined throughout the Caribbean over the past 30 years, foremost due to a region-wide outbreak of white-band disease (WBD) in the early 1980's and remnant populations of this species are now estimated to be 3% of their historic abundance. These population declines have prompted Caribbean-wide efforts to aid the rehabilitation of this keystone species. So far, such restoration activities have almost exclusively relied on asexual propagation of corals through fragmentation. However, sexually produced off-spring can be generated in far greater numbers and are genetically more diverse compared to asexually produced offspring. While coral gardening techniques using asexual fragments have been extensively studied and are well established worldwide, reef restoration using sexually produced recruits is a new, but rapidly developing field. To develop such techniques specifically to assist the recovery *A. palmata* populations, we launched a restoration program in Curaçao in 2010. While previous studies have shown that *A. palmata* larvae can be reared, settled and outplanted on the reef, reintroducing these lab-raised recruits back to the field remains extremely expensive.

We investigated the feasibility of using sexually produced recruits to restore degraded *Acropora palmata* populations and how to optimize existing coral reef restoration methods. Our results demonstrated that it is technically possible to rear *Acropora palmata* offspring from spawn and achieve post-settlement survival rates high enough so that these techniques can be used for restoration purposes. Settlement rates were high and almost one third of the reared larvae settled and completed metamorphosis within 5 days. We succeeded in introducing these settled *A. palmata* offspring to the reef where they were left to grow for extended periods of time. Of all the settlers introduced to the reef at the age of two weeks, 5.4% reached 18 months which greatly exceeds natural recruitment rates. Contrary to our expectations, coral settlers introduced to the reef survived better than settlers nursed under controlled conditions in a land based facility. After 18 months, 5.4% of all settlers placed on the reef were alive while only 1% of the settlers kept in the nursery had survived. Rearing *Acropora palmata* settlers in aquaria over extended periods of time did not only reduce their survival but also their growth rates. One year old recruits that were grown on the reef for 2.5 yrs grew approximately 6 fold larger and 4 times higher than settlers nursed in aquaria. Rearing *A, palmata* recruits in aquaria therefore does not necessarily contribute to higher survival or growth. Our cost-benefit calculation demonstrated that nursing corals in aquarium over extended periods of time prior to introduction to the reef renders large scale restoration efforts financially impossible. The costs per settler in this study varied considerably depending on the amount of time they were kept in the land-based nursery, increasing exponentially through time such that after one year, each settler remaining in the nursery cost $219 or $88, including or excluding facility construction expenses, respectively. In contrast, when *Acropora palmata* offspring are returned to the reef shortly after settlement (2 week old primary polyps), the costs

associated with restoration efforts decline dramatically. The value of each remaining settler was as low as $1.05 when facility construction expenses were not included. As far as we are aware this is the lowest rate achieved for rearing 1½ year old sexual recruits for reef rehabilitation purposes to date.

WP10 Evaluation of the efficacy and constraints to management tools

WP10 is a synthesis of information and research from WP1. To explore the relationship between good marine governance and reef management effectiveness, considered important for sustainable use of healthy coral reef ecosystems, the aim was to identify the governance constraints to implementation of management tools. We focussed on assessing from a wide range of stakeholders from different levels of governance (community and national levels) the perceived effectiveness of management tools or improving coral reef health, assessing the impact of management tools on peoples' livelihoods and identifying the governance constraints to management tools.

Governance constraints to effective management

Much of the research on marine management has focused on the identification of management measures such as marine protected areas (MPAs) to control human activity, yet such measures are often advocated with little consideration of the context-specific constraints to their implementation. A current gap existed in our understanding of how to identify the most appropriate management tools in recognition of the constraints pertaining to the existing governance system. The FORCE project aimed to identify the governance constraints to the implementation of management tools.

Five broad categories of constraints to reef management were identified by key informants: 1) Governability, 2) Influencing factors, 3) Governance structure, 4) Governance process, 5) Management implementation. The most commonly mentioned issues (stated by over 60% of respondents in all countries), were non-compliance and a lack of effective enforcement; lack of education and awareness among resource users; lack of resources and capacity for reef management; a lack of political prioritisation of reef management issues; lack of engagement of reef users in reef governance; and weaknesses in policy, legislation and regulations.

While the majority of categories of constraints to reef management were identified in all countries studied, the frequency with which different constraints were identified varied by country, key informant level (local versus wider), and sector (e.g. fisheries, tourism, conservation). Differences reported in the number and type of constraints identified among the four countries may be related to country-specific differences, such as the historical context of reef management, the nature of the governance system in each country, and the level of societal dependence on reef resources.

The analysis of perceived constraints highlighted specific challenges to different forms of reef management and points to possible governance reforms to assist the improved

efficacy of reef management. Understanding the current governance constraints faced by reef managers can help improve reef management in two ways: 1). Help managers identify particular management tools that may be more successful under the current management constraints (e.g., in cases where effective enforcement is a constraint, management approaches that aim to increase stakeholder engagement, stewardship and voluntary compliance may be more effective than those that rely on enforcement of regulations. 2). Help identify appropriate, targeted interventions needed to improve governance to support more effective coral reef management. For example, where a lack of cooperation and integration among reef managers is identified as a problem, efforts can be made to identify mechanisms to improve communication flows among different groups and organisations.

Community perceptions of governance

Good governance is widely seen as a prerequisite for effective natural resources management in the context of environmental decline and increasing anthropogenic pressures, including climate change. Few studies empirically and quantitatively examine governance principles, or explore links between perceptions of community members and the governance structures that influence their behaviour. Based on household interviews, community members' perceptions of governance processes were measured in twelve coral reef-dependent communities across four Caribbean countries, in relation to established principles of 'good governance'.

Perceptions of coral reef governance process can be reliably described using two themes, institutional acceptance and engagement. These measurable themes provide an indicator of governance quality, which can be used to explore relationships between good governance and its expected outcomes, including support for management and compliance with regulations. Cluster analysis provides unique empirical evidence linking structural characteristics of governance arrangements to community perceptions; four of five characteristics expected to facilitate good governance were present in communities with positive perceptions.

Results suggest a combination of supportive structures and processes are necessary to achieve governance systems positively perceived by community members. Findings are relevant to managers and policy makers seeking to design management systems and governance structures that are appropriate to local circumstances and that will engender stakeholder support.

Potential impact and main dissemination activities and exploitation of results

Overview

During the four years of the project, FORCE has produced a variety of resources to disseminate information about the project, important results from the project and important reef conservation ideas for the Caribbean. These ongoing activities range from a blog on the project's website to management and policy briefs on marine reserve design, yellowtail snapper fishery, the physical environments of the Caribbean, country reports on the social and ecological surveys to T-shirts on the importance of ecosystems services and can coolers on the importance of parrotfish for reef resilience. In the end we have expanded on those dissemination resources to include a coral reef managers' handbook, a webGIS with original data layers, the unique Reef Health Simulator which is a special interface to the modelling program and a significant number of scientific manuscripts in high profile journals. Throughout the project the field research conducted on governance and livelihoods and the ecological surveys ensured that project researchers have been engaged with policy makers, practitioners, stakeholders and the general public from the start. The nature of the governance and livelihoods research meant that that community meetings and feedback sessions were integral and these meetings, together with the regular interactions with field researchers created the opportunity to discuss information on the project and its results. The project's research activities culminated in the two separate workshops for practitioners and the production of the reef managers' handbook which based on the results and recommendation from the research provides managers with tools, information necessary for management. The dissemination activities from the FORCE are by no means complete as addition papers continue to be produced and published (i.e., those in addition to the original deliverables), and researchers will continue to present on FORCE research at scientific conferences. To date forty-eight presentations at international scientific conferences have disseminated the results from the project and this will no doubt continue into the foreseeable future with at least eight conference presentations planned by the end of the year. Our six Caribbean partners actively participate in discussions with governments, exchanges with other research and scientific within the region will continue to disseminate the results and recommendations towards the management of Caribbean corals reefs in the face of climate change.

General communication of the project to the wider community

Website

In early 2010 the FORCE website (http://www.force-project.eu/) was launched at the start of the project and has provided a source of information not only on the project research, activities and results but also on related Caribbean coral reef issues and information. The website contains information about the project, the research, and researchers. It is also a resource point for publications created by the project and dissemination tools produced, along with links to other repositories of information on coral reefs including Reefbase and Reefvid and Marxan for reserve design. Bite-size video clips featuring English and Spanish-

speaking project personnel combine interviews with project personnel and underwater footage in order to highlight some of the key lessons and messages from the project. The FORCE website is also the gateway for FORCE WebGIS and the Reef Health Simulator. In order to maintain longevity of the project outputs, the FORCE website will be maintained for a minimum of 5 years after May 2014.

Impact and dissemination to Coral Reef Managers

Policy briefs

The project began producing short policy and management briefs very early in the project and widely disseminated them at GCFI conferences over three years. The briefs have been produced on managing herbivores for reef resilience, managing yellowtail snapper as a sustainable alternative fishery, valuating reef fish for fisheries versus tourism, managing for reef complexity, managing for bleaching vulnerability using maps of coral bleaching environments and advice on how to interpret these maps for reserve design, factoring marine environments of the Caribbean into planning and nutrification are available on FORCE website as PDFs. These accessible and compact briefs have proven to be very useful and engaging to a diverse audience from reef managers and researchers to students and fishers.

Manager's Handbook

Information from the FORCE research and recommendations for managers throughout the region has been collated into the publication of the book, "*Towards Coral Reef Resilience and Sustainable Livelihoods: a handbook for Caribbean reef managers*". Copies of the handbook have been distributed to coral reef managers, fisheries managers, protected area managers, regional and international non-government organisations involved in marine management and research institutions across the wider Caribbean. A PDF copy in English and Spanish is available on the project website.

Workshops

A workshop entitled, 'Coral Reef Science of Management: Tools and Practical Solutions', was held in Corpus Christi Texas in November 2013. The workshop attended by reef managers from around the Caribbean participated in a two-way exchange between the researchers and the managers whereby FORCE researchers shared the latest social and ecological research relevant to Caribbean reef management conducted during the four years of the project and for participants to guide the development of resources for Caribbean coral reef management. The recommendations from the workshop were incorporated into the Caribbean reef managers' handbook.

On advice from the Caribbean reef managers at the 'Coral Reef Science of Management: Tools and Practical Solutions' workshop we produced a targeted policy brief. One of the overarching key findings from the project research came from our updated models that have shown that global action to reduce greenhouse gas emissions had little impact on average

coral state unless it was accompanied by local controls of parrotfish fishing. This modelling study concluded that combined global and local actions are necessary to reduce the rate of reef degradation and loss of habitat structure and aide the recovery from climate change impacts. Although global action to reduce greenhouse gas emissions is important to ease the effects of climate change on reefs, such efforts are not sufficient on their own to ensure reefs continue to exhibit net growth. The Caribbean reef managers felt that this was a very important message to convey to their policy makers and advisors because the prevailing thinking in the Caribbean is that it is only global action on greenhouse gas emissions that will make a difference for Caribbean reefs. On the recommendation from the Caribbean reef managers it was decided to create a 2-page concise brief highlighting the study that local actions to buy time for coral reefs in the context of climate change. On the managers advice the brief is short, succinct and visually appealing as busy policy makers responded best to information of that manner. The managers also suggested that they themselves would find the brief useful to communicate this message to their own government officials and policy makers. The brief has been disseminated to Caribbean managers and policy makers and is also freely available from the project website.

Tools to aid coral reef monitoring

During the course of the project it was identified that a tool related to coral reef monitoring would be most useful to reef managers and practitioners. Many managers and the monitoring protocols they employ for reef surveys use Excel to calculate and query data but it is not an easy system nor does it offer nuanced insights into the state of reef ecosystems. The Access programme has been favoured by researchers particularly for monitoring data across spatial and temporal scales therefore An Access Toolkit for Monitoring is available on the FORCE website.

The research on fish population indicators has produced a valuable tool utilising parrotfish mean size for assessing the comparative status of Caribbean reef fish communities and providing a region-wide picture of the current status of reef fish populations. This will be powerful in highlighting the countries or reefs in greatest need of fishery management attention. Based on this simple fish metric, we also have a continuum of reef states against which coral reef and reef fish managers can judge their own sites and use to monitor the effectiveness of management measures put in place to prevent fishing or to control fishing within sustainable limits. Simple indicators like this will be extremely important in helping to implement the much needed ecosystem approach to reef fisheries management in the future. This research will also inform the direction of future research on developing site and gear-specific values to use for these indicators in lieu of in-water AGRRA survey values. The use of the fish community metric (mean fish size) and in particular the mean individual fish size of the parrotfish family will be promoted as a useful indicator of fishing pressure/reef health through the many channels in which the University of the West Indies, Barbados are involved, for example: the online FAO EAF toolbox to which CERMES is a contributor; through MPA managers' training courses and workshops run by CERMES and our partners;

through the University's taught Master of Science programme's fisheries course; through the Caribbean Regional Fisheries Mechanism (CRFM) Reef and Slope Scientific Working Group *inter alia*.

Adoption of FORCE results for national management planning

One notable area of impact has been the recent designation of legislation to proceed with the formation of one of largest marine reserves in the Caribbean based on work by our Honduran partner, Utila Centre for Marine Ecology. University of Exeter produced a dataset that most accurately indicates the characteristics of the Miskito area in Honduras. Originally no data existed for the areas. Nautical charts were outdated and even the best global coastline dataset available were slightly inaccurate for the area. The Utila Centre for Marine Studies utilised those maps to submit for the now successful proposal for the largest marine protected area in Central America in eastern Honduras.

The success of this effort is two-fold as the MPA will include a large area for exclusion of industrial fishing (called ZEPA for its Spanish acronym: *Zona Exclusiva de Pesca Artesanal*) which will encompass a network of no-take areas. At the time this report was being completed we can proudly say this effort has been highly successful. In June 2014 the Minister of Agriculture signed the decree declaring the ZEPA and its no-take network. This process has been participatory as during the planning of the network of no-take reserves the current uses were also mapped. As industrial fishing fleets currently use the area we mapped the effort of each fishery in the Honduran EEZ which was presented to the Honduran government and proved invaluable in the engagement and consultation with the fishing sectors during the MPA designation process.

The analysis of resilience in Belize strongly supports the government's decision to ban herbivore exploitation in 2009, predicting that this decision increased the resilience of coral reefs six-fold. The Belize government is currently undertaking a review and extension of marine protected areas (MPAs) and the maps we created under the project have been added as a critical data layer in the reserve selection algorithm (areas predicted to have resilience >50%). Specifically, some areas identified south of Belize City were assigned high priority for reserve designation because our models of resilience predicted that MPA enforcement could have a relatively strong impact on future resilience in this location. The draft reserve plan is now undergoing public consultation.

Web-GIS and integrative reef model

The FORCE Web-GIS or Geographic Information System (http://webgis.force-project.eu/forcewebgis.html) is another important output. It contains recently developed spatial data layers on the physical environments of Caribbean reefs, current reef state, and maps of governance structure. It has a user friendly interface allowing its use without special training. Data layers can be queried to extract information for particular reef locations around the Caribbean.

In order to make the coral reef simulation model, *ReefMod* available online for use by non-specialists modellers making it more accessible and appealing we created a unique product called the Reef Health Simulator. This simulator is driven by *ReefMod,* developed at the University of Exeter, allowing the user to experience the effect of different management interventions and climate change scenarios on the benthic dynamics of a particular reef environment. The intuitive graphical user interface for the simulator makes it easy to work through a selection of modelled scenarios, with the outcome displayed as plots of coral and algal cover against time. Particular attention has been given to user friendliness of the tools by tuning them to the needs of the users that are supposed to use them. Post-project we will continue to develop educational activities using the Simulator specifically geared for secondary Caribbean students.

Communication with scientists

Scientific publications

As FORCE was a research project, the production of important scientific publications that can inform and influence management was an important component. To date forty two papers have been published from within the project. A further thirty manuscripts are in the publication process. Under the investigations on ecological processes that affect coral reefs a variety of manuscripts have been and will be produced elevating the level of knowledge of some of these previously unknown processes, for example, the processes of natural coral recovery investigating coral larval fitness, larval survival and settlement has resulted in six manuscripts being produced. With the rich dataset collected on size, abundance and life phases of all species of fish, six publications are in progress addressing various aspects of fish species richness, habitat complexity and Caribbean mesopredators.

Mesocosm experiments on the effects of pH, temperature, nutrients, light and flow on coral growth have resulted in five manuscripts. Scientific papers generated by the Universidad Autonoma de Mexico and their novel research on coral physiology and coral species responses to thermal and light regimes shed new light on the physiological characterisations of the photobiology of four coral species. Two significant results reveal for the first time new insights in coral physiology with regards to seasonality for reef-building symbiotic corals. Four manuscripts which have been submitted to high-impact scientific journals as these original findings contribute greatly to increasing the knowledge base in the field of coral physiology and photobiology.

Under the governance research a manuscript on community level perceptions of good governance principles and a further four manuscripts on perceptions of ultimate drivers, social network analysis and efficacy of governance are in various stages of preparation and submission to internationally peer reviewed journal to disseminate the research outcomes to the wider academic community.

Communication with students / training

Teaching

In addition to the multitude of scientific papers and reports produced for the scientific community and the higher education sector insights from the FORCE project research contribute to research-led teaching in undergraduate and postgraduate teaching at Newcastle University and the University of the West Indies. The research and data generated by the varied ecological and social research has contributed in part or wholly to three undergraduate, thirty-three masters, and eleven PhD dissertations.

Communication with stakeholders

Engagement with fisheries sector through Gulf and Caribbean Fisheries Institute Conferences

Throughout the project the FORCE annual meetings were held alongside the annual Gulf and Caribbean Fisheries Institute conferences, the premier forum for discussion concerning science on Caribbean coral reefs and the management of coral reefs and fisheries in the Wider Caribbean region. FORCE exhibited during each meeting to communicate results of the project, and provide an informal forum to solicit feedback from managers, fishers, other researchers, students and other stakeholders who participated in the conference.

National stakeholder meetings

In each of the four Caribbean nations where the governance and livelihoods research was conducted, national level meetings were held to explain the research and discuss some of the key issues involved with a range of national-level stakeholders. Similarly, at the community level, researchers organised public meetings with representatives of the local community, civil society and local institutions where the research were presented and discussed extensively. Public presentations in the form of slideshows and videos where presented within the local communities wherever possible. Whilst in the field the FORCE ecological survey teams also held meetings with local managers and government personnel. The ecological survey teams prepared country reports, summarizing the findings of the reef surveys which were distributed to in-group organizations and institutions that with whom we had liaised in-country. These included fisheries and marine protected areas planners and managers, dive operators and tourism-related personnel. Providing feedback promptly in the form of these summaries has been useful to update stakeholders and policy makers on the relative state of their coral reefs. From the local feedback it was noted that these summaries helped enhance people's appreciation for their reefs, particularly those whose reefs are considered healthy in relation to the other surveyed sites.

Many of the partner research institutions are Caribbean-based so the dissemination of FORCE research results is ongoing. As part of existing outreach education and awareness activities by CARMABI on Curaçao, exhibitions and talks are held during the coral spawning season. It also holds a variety of regular public presentations about its experiments both on larval fitness and coral restoration as well as educational lectures on general coral reef ecology where many people and media were updated on FORCE activities. Press releases

were directly shared with regional and local media outlets throughout the Caribbean with interesting results from published manuscripts. The Universidad Autonoma de Mexico, El Colegio de la Frontera Sur and the University of Costa are all very active in providing information to their local and national governments and the general public. They will continue to disseminate the results and outputs, particularly the handbook for many years to come. The University of the West Indies, Barbados and the Centre for Resource Management and Environmental Studies (CERMES) is one the most influential English-speaking regional institutions in the management of Caribbean coral reef ecosystems. They will continue to be active in disseminating the project's outputs throughout the region through the CLME and other initiatives of which they are members as well as through their undergraduate and graduate programmes in coastal and marine management.

Key informants interviewed during the research expressed their plans to use the Country Reports in preparation to support both applications for funding and policy decisions. For example, the Red Cross in St Kitts and Nevis hope to use results from the FORCE project to support funding applications to continue their work with fishing communities vulnerable to climate change.

Contribution to United Nations initiatives

Dr. Leonard Nurse from the University of the West Indies who is a member of the Inter-governmental Panel on Climate Change (IPCC) scientific team presented project results on projected SST trends over the Caribbean Sea under IPCC scenarios to the IPCC.

FORCE results contributed directly to a submission by the European Commission to the UN Convention on Biological Diversity's call for contributions over the impacts of climate change on coral reefs (CBD Ref.: SCBD/SAM/DC/JL/JG/82124), January 2014. We reviewed the draft contribution prepared by the EC and then provide extensive comments and additions based on new research undertaken during the project. The final EU submission featured the FORCE project research on carbonate budgets (Kennedy et al 2013 Current Biology) and methods for factoring climate change into decision making (Mumby et al 2011 Ecology Letters).

The maps, methods and data layers generated during the project by the University of Exeter have been extended beyond the project partners and have contributed to other initiatives and institutions outside the consortium. Mapping and remote sensing datasets have contributed to the recent United Nations Environment Programme's Global Coral Reef Monitoring Network (GCRMN) report, *Status and Trends of Caribbean Coral Reefs: 1970-2012* an exhaustive review of reef health in the Caribbean, and utilised information from FORCE to identify its drivers. FORCE researchers from the University of Exeter were actively involved in this effort.

Contributions to other projects and adoption of FORCE results

The wealth of data collected under the governance research provides the opportunity to contribute new knowledge for which various publications and initiatives have begun. FORCE

future scenario work generated additional impact within Europe as methods were exchanged with the Training Network for Monitoring Mediterranean Marine Protected Areas (ITN-MMMPA), a Marie Curie Initial Training Network (FP7-PEOPLE-2011-ITN Grant Agreement no:290056.) held in 2013 in Murcia, Spain, funded by the European Commission. The Initial Training Network for Monitoring Mediterranean Marine Protected Areas (MMMPA) aimed to train the next generation of MPA scientists and managers for the Mediterranean, equipping them with a flexible set of skills essential within a wide range of professional environments, including public administration, local authorities, industry and academia. Within the three day training workshop 'The social economic and institutional perspectives in the co-management of MPAs' FORCE futures methods made a popular and considerable contribution.

On a regional scale there is a strong potential for incorporation of the governance research into regional initiatives. Project outputs will feed into implementation of the Caribbean Large Marine Ecosystem (CLME) Strategic Action Programme (SAP) which will be implemented 2015-2020 and supported by the Global Environment Facility. Results of this work will inform the project 'Improving the Outlook for Caribbean Coral Reefs - A Regional Plan of Action 2014–2019', funded by the Australian government and implemented by the Caribbean Regional Fisheries Mechanism (CRFM).

Newcastle University have already expanded on the FORCE research through a Department for Environment, Food and Rural Affairs (DEFRA) funded initiative which extended the governance research to the countries of Turks and Caicos, Cayman Islands and Anguilla within the Caribbean.

The Caribbean Reef Livelihoods Framework was developed to help reef managers, community workers, planners and decision-makers to understand better the complex relationships between people and reefs by raising awareness of the wide range of factors that need to be considered. It also provides a framework for the subsequent research in the field. The document *A Livelihoods Framework for the Caribbean* has been disseminated to relevant institutions as well as was presented and discussed during both FORCE workshop with practitioners. The field research involved in the Caribbean Livelihoods Framework gave rise to four case study reports that were produced both as individual country reports and also combined into a more regional report on the *Socio-Economic Dependency on Coral Reefs of Communities and their Vulnerability to Change in Reef Resources*. This report has been widely disseminated to government and nongovernment organisations and institutions from the Caribbean Regional Fisheries Mechanism (CRFM) and Caribbean Development Bank (CDB), to World Forum of Fisher Peoples (WFFP), International Collective in Support of Fishworkers, to James Cooke and Charles Darwin Universities in Australia.

The results of the research on coastal livelihood enhancement and diversification in the Wider Caribbean have been used to generate several key outputs. A report on the *Use of Livelihood Enhancement and Diversification Initiatives for Coral Reef Management in the Caribbean* analysed how livelihoods initiatives have been used in the context of reef management efforts in the region. The report on the *Effects of Management Measures on Livelihoods* reviewed evidence of how reef management has impacted the livelihoods of

people in reef-user communities around the Caribbean. These reports have been disseminated regionally and globally.

A workshop held in Barbados in May 2013 brought together people from across the region, including practitioners from government, non-government and civil society organisations to discuss their experience in supporting livelihood change. The outputs of this workshop, based on discussions with participants who support livelihood change in coastal communities, combined with the lessons from the field research, were used to develop a set of *Guidance on Sustainable Livelihoods Enhancement and Diversification* which has been published online and circulated widely to relevant individuals and institutions. This guidance is based on experience in the Caribbean region and provides those designing and implementing such programmes with a valid starting point for improving the quality of their interventions and ensuring that conservation efforts are better integrated into the needs and aspirations of local people in the region. The regional workshop on Sustainable Livelihoods Enhancement and Diversification held in Barbados in May 2013, and the session on Livelihoods and Reefs held during the FORCE Reef Manager's Workshop in Texas, U.S.A in November, 2013, both generated significant response from participants. Appreciation was expressed for the inclusion of livelihoods-related issues in the FORCE research programme and participants highlighted how understanding livelihoods and livelihood change is an essential part of the process of improving management of coral reefs in the Caribbean.

The field research carried out by FORCE social science researchers on livelihoods worked in close collaboration with researchers on governance. The research was carried out using participatory methodologies involving close interactions with local communities, key informants and local institutions, as well as with national institutions with an interest in reef management. After the research analyses were completed, revisits to each of the four countries studied were held to report key findings to both local and national level stakeholders and a series of short community reports produced for each of the study sites have been distributed back to the communities, circulated at GCFI conferences and on the project website. This approach, combined with the close interaction with communities during the course of the research, meant that the potential for raising the profile of coral-reef related issues, and the educational opportunities provide by the research for local people were maximised. In each study location, the research process generated significant discussions about coral reefs, the changes and threats people face, and the livelihoods of people who depend on them.

Some effects of the research as a result of dissemination efforts are beginning to be felt. Parallels can be seen between the FORCE livelihoods research and that being done in the Coral Triangle Initiative in South-East Asia where the coastal livelihoods framework developed previously by IMM is being used and has been incorporated into recent publications on Sustainable Livelihoods and the Ecosystem Approach to Fisheries Management. The Partnership for African Fisheries implemented by the African Union has

indicated that the findings from the research will provide lessons for reef-dependent African fisheries at a time when regional policies for the development of fisheries are being developed. The Caribbean Development Bank has expressed interest in receiving further documents from the research to inform its climate change work. The Commonwealth Foundation, on receiving the reports on livelihoods and reefs, expressed its interest in linking with stakeholder groups engaged in participatory management of coral reef systems through its grant making facility. IMM have been in discussion with CANARI in the Caribbean the potential of Commonwealth Foundation funding for their reef-related work.

The FAO SIDS (Small Island Developing States) programme in Rome is interested in incorporating lessons from the research into its evolving policy work in the lead up to the Third International Conference on Small Island Developing States (SIDS) in Samoa later in 2014. In particular it would like to explore the potential of including reefs in Payment for Ecosystem Services (PES) as part of support to SIDS. The results of the research on the valuation of coral reef fish resources for fisheries versus tourism provide economic justification for investment in the conservation of reef fish resources to avoid significant economic losses from stock declines and to even increase current gains in the region. To date, this is the first study to conduct market and non-market valuation across numerous sites in the Wider Caribbean, highlighting the importance and relative values of extractive (fishing) and non-extractive (dive tourism) uses of reef fish. The research is also amongst the few Caribbean studies to discuss potential avenues for achieving a sustainable balance between extractive and non-extractive uses of coral reefs where economic returns can be maximised without compromising the health of the ecosystem.

The data layers and maps produced have been shared with other researchers at the Instituto de Oceanologia de Cuba, Cuba, University of Maine, USA, and Universidad Simon Bolivar, Venezuela. The map of environmental provinces of the basin has been requested from at least 20 researchers, including Judy Lang, the Scientific Coordinator of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Project, the main reef monitoring program in the basin. The methodology developed by FORCE to produce the map of environmental provinces has been replicated in the Coral Triangle in order to conduct targeted conservation activities. The initiative was undertaken by the Marine Science Group within World Wildlife Fund's Conservation Science Program.

The collaborative study on dissolved organic matter and light will potentially contribute to the research in seaweed aquaculture at the new Seaweed Centre at the Royal Netherlands Institute for Sea Research. FORCE research on measuring bioerosion by coral excavating sponges will also be furthered by a new grant which was recently successfully awarded by the Netherlands Organization for Scientific Research.