Environmental regimes in the Caribbean and implications for the dynamics and distribution of its coral reefs

Submitted by **Iliana Carolina Chollett Ordaz** to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Acknowledgements

This has been a journey across three continents, with many pleasant finds along the way. The journey started in Venezuela, in bed, during hepatitis convalescence, when my Dad, my nurse at the time, gave me a push to get the PhD application ready. It was time to go. The trip started and it took me to England and then to Australia. It has been a long and winding journey. I am grateful to all that I have found (and kept) on the way.

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This journey would not have been possible without my family. Thanks so much for letting me go and supporting me all this time, y perdon por los momentos que me he perdido.

I.

Abstract

Over evolutionary time coral reefs have been exposed to the influence of diverse environmental forces which have determined their structure and function. However, the climate of the earth is changing, affecting many biological systems, including coral reefs. Through this thesis the static and dynamic environment of the Caribbean basin was characterized using remote sensing and *in situ* data sources. This information was used to understand how present environmental conditions have shaped reef ecosystems and how the changing climate might jeopardize them.

Focusing on physical constraints that drive many aspects of coastal ecology, a region-wide categorisation of the Physical Environments of the Caribbean Sea (PECS) was developed. The classification approach is hierarchical; including a first level of 16 physicochemical provinces based on sea surface temperature, turbidity and salinity data; and a second level considering mechanical disturbance from wave exposure and hurricanes. The PECS categorisation will facilitate comparative analyses and inform the stratification of studies across environmental provinces in the region.

Montastraea spp. forereef habitats have the highest biodiversity and support the largest number of ecosystem processes and services in the Caribbean. One of the aspects of the physical environment, wave exposure, was used to predict the distribution of these habitats in the Caribbean basin with high accuracy (79%). The distribution of the habitat is constrained in environments of high exposure, a pattern likely to be driven by high rates of chronic sediment scour that constrain recruitment. This approach constitutes a fast and inexpensive alternative to traditional habitat mapping and complements global efforts to map reef extent.

Recent changes in temperature have impacted ecosystem function across the globe. However, the nature of the responses has depended upon the rate of change of temperature and the season when the changes occur, which are spatially variable. In the Caribbean Sea, temperature trends are highly variable in space (ranging from -0.20 to 0.54°C decade^{-1}) and most of the warming

has been due to increases in summer temperatures. The highly detailed spatial and temporal patterns assessed can be used to elucidate observed ecological responses to climatic change in the region.

In the face of increased temperatures it has been suggested that reefs may become increasingly restricted to locations of naturally low thermal stress, such as upwelling areas. However, when analysing the degree to which seasonal upwelling reduces the local thermal stress experienced by corals, it is clear that upwelling areas do not always offer meaningful protection. Hypothesised areas need to be assessed individually in order to evaluate their capacity as a refuge against climate change.

In this thesis large progress has been made in assessing the ocean climate of the Caribbean basin by quantifying spatial patterns and their rate of change. Although some insight into the consequences of these seascape patterns to the function and distribution of marine systems has been provided, more can be done to fully exploit the datasets produced.

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Author’s declaration

This thesis is constituted by my original work, and is the result of efforts I have carried out since the start of my research degree candidature. This manuscript contains no material previously published or written by another person except where due reference has been made in the text. The contribution of others to my thesis as a whole, including data providing, interpretation of results and editorial advice is stated below.

Chapter 1 consists of a paper to be submitted to the journal Limnology and Oceanography co-authored with Peter J Mumby, Frank Müller-Karger and Chuanmin Hu (University of South Florida). Peter J Mumby contributed to develop the concept and provided editorial advice and guidance throughout the development of the paper. Frank Müller-Karger and Chuanmin Hu provided temperature and turbidity data and comments on the manuscript. I developed the concept, carried out the analyses and wrote the paper.

Chapter 2 consists of a paper submitted to the journal Coral Reefs, co-authored with Peter J Mumby. Peter J Mumby contributed to develop the concept and provided ground truth data, editorial advice and guidance throughout the development of the paper. I developed the concept, carried out the analyses and wrote the paper.

Chapter 3 consists of a paper submitted to the journal Marine Pollution Bulletin and co-authored with Peter J Mumby, Frank Müller-Karger (University of South Florida), Scott Heron and William Skirving (Coral Reef Watch). Peter J Mumby provided editorial advice and guidance throughout the development of the paper. Scott Heron provided sea surface temperature data and comments on the manuscript. Frank Müller-Karger contributed to the interpretation of the results and provided comments on the manuscript. Willian Skirving provided comments on the manuscript. I developed the concept, carried out the analyses and wrote the paper.

Chapter 4 consists of a paper published in the journal Marine Ecology Progress Series and co-authored with Peter J Mumby and Jorge Cortés (University of Costa Rica). Peter J Mumby provided editorial advice and guidance throughout the development of the paper. Jorge Cortés provided comments on the manuscript. I developed the concept, carried out the analyses and wrote the paper.

1

General Introduction

The Caribbean Sea

The Caribbean Sea is a semi-enclosed sea part of the Atlantic Ocean, bounded by Venezuela to the south, the Lesser Antilles to the east, the Greater Antilles to the north and Central America to the west (Figure 1.1). The Caribbean seafloor is divided into four basins: the Yucatan, Colombian, Venezuelan and Grenada Basin. These are separated by ridges and rises: the Cayman Ridge, The Nicaraguan Rise, the Beata Ridge and the Aves Ridge, respectively (Case et al. 1984). Water from the Atlantic Ocean enters the Caribbean through passages in the Lesser and Greater Antilles (Johns et al. 2002). Once Atlantic Ocean waters enter the basin they form the Caribbean Current, the main surface circulation feature in the Caribbean Sea. This current flows along the southern Caribbean and turns towards the north-west to exit through the Yucatan Channel and form the Loop Current, which joins the Florida Current and finally the Gulf Stream (Johns et al. 2002; Richardson 2005).

The meridional migration of the Inter-Tropical Convergence Zone (ITCZ) exerts the major control of climate in the region (Granger 1985). At the beginning of the year, the ITCZ is in its southernmost position, strong northeast trade winds influence the area, and rainfall is at its minimum. The ITCZ moves towards the north around May, winds decrease and rainfall increases over the region (Granger 1985). In some areas the wet season can be interrupted as a result of an increase in the strength of winds due to the influence of the Caribbean Low-Level

Jet (Wang 2007). Spatial variation in these general patterns is affected mainly by latitude and topography, which influence both radiation incidence and rainfall intensity (Granger 1985).

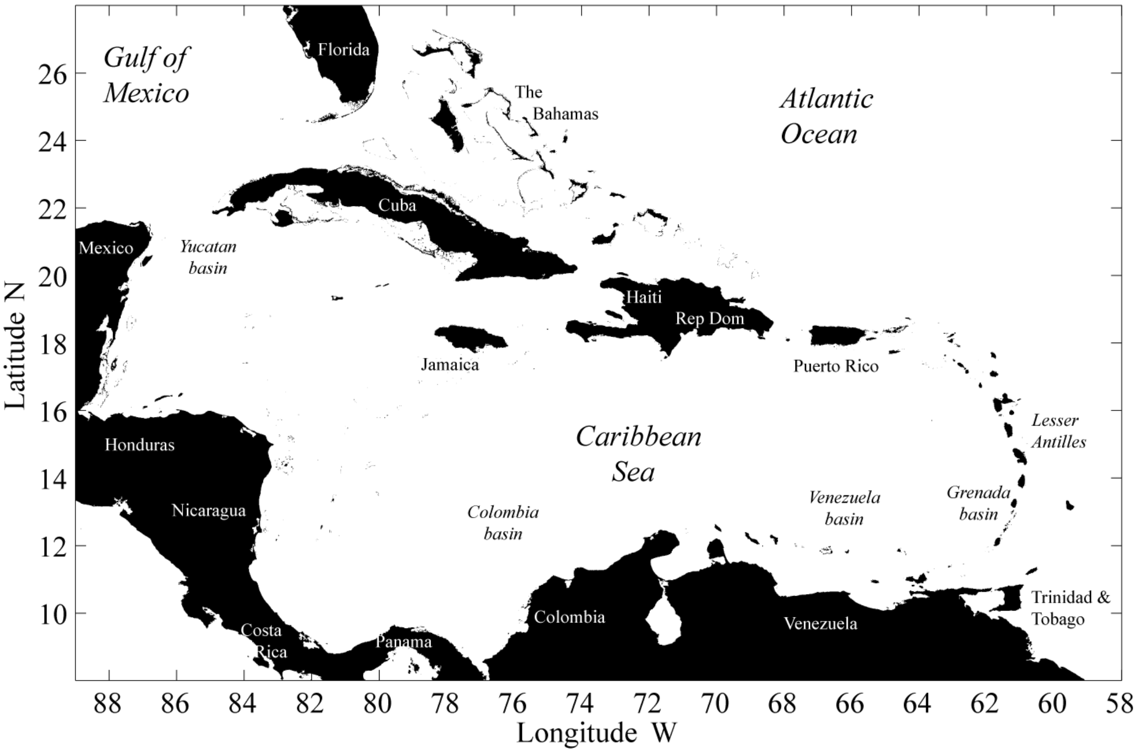

Figure 1.1. Caribbean basin (8-28°N, 58-89°W)

During the second part of the year, low pressure centres develop increasing the occurrence of hurricanes (Neumann et al. 1999). The Atlantic hurricane season runs from June to November. The area of hurricane genesis changes seasonally, moving from the western Caribbean at the beginning of the hurricane season to the east of the Atlantic basin and back. Once formed, storms move westward and north-westward and typically dissipate in about seven to eight days (Neumann et al. 1999).

Sea temperatures are relatively stable in the Caribbean. The annual temperature range lies between about 2ºC in Trinidad and 5.5°C in Cuba, and generally increases with distance from the equator. The warmest period occurs in boreal summer and coincides with the wet season (Granger 1985). The Caribbean Sea is influenced by the discharge of two of the world’s largest rivers (Amazon and Orinoco Rivers) and by seasonal upwelling along the southern margin (Müller-Karger et al. 1989). The riverine signal is noticeable during the wet season and can reach as far as Puerto Rico (Müller-Karger et al. 1989), while upwelling is active mainly during winter (Müller-Karger et al. 2004). River discharge from other sources and runoff also influences the oceanography of the area (e.g. Restrepo et al. 2006; Roder et al. 2009; Imbach et al. 2010). Although descriptions of the oceanography of particular areas of the Caribbean are available, a comprehensive assessment of the oceanography of the region has not yet been published, such as the assessment provided by Fiedler et al. (2006) for the Eastern Tropical Pacific.

Mangrove wetlands, seagrass beds and coral reefs are the dominant coastal ecosystems in the Caribbean. Approximately 10% of the world's coral reefs are found in the Atlantic, mainly located in the Caribbean Sea and the Bahamas banks (Burke et al. 2011). The region is very heterogeneous biogeographically and hosts at least 12,046 species of marine biota, including 116 species of zooxanthelate corals (Miloslavich et al. 2010). Reefs across the region have been declining for several decades (Gardner et al. 2003). This degradation has mainly been attributed to the widespread loss of a key herbivore, the sea urchin *Diadema antillarum*, due to disease (Lessios 1988), and the loss of two main reef builders, staghorn and elkhorn corals, also related to disease spread (Aronson and Precht 2001), overfishing (Jackson 1997) and other human impacts (Mora 2008) and climate change (Hoegh-Guldberg et al. 2007).

Oceanography from space

The ocean is a vast environment that varies greatly in space and time. Remote sensing instruments on board orbiting satellites allow the synoptic mapping of the oceans, which entails observing large areas simultaneously with a high frequency of observation (Srokosz 2006). Remote sensors, in spite of being restricted by the orbit, sample at a higher frequency and can reach a broader spatial coverage than *in situ* methods that sample in a scattered way (Green et al. 1996). Additionally, this tool provides a relatively favourable cost-effectiveness, allowing the sampling of large areas faster and at a lower cost than conventional methodologies (Mumby et al. 1999). Consequently, remote sensing is an optimal tool for the study of patterns and processes in the ocean at mesoscales, fulfilling a key role in measuring and understanding ocean variability.

Ocean-observing satellite sensors use electromagnetic radiation to assess the sea. Four broad classes of satellite sensors have been used to study the oceans: visible, infrared, microwave and radar instruments (Figure 1.2: Robinson 2010). Sensors that assess the visible part of the electromagnetic spectrum (between 400 and 700 nm) are used to measure ocean colour. The magnitude and spectral composition of the light leaving the water can be used to assess the presence of photosynthetic pigments, dissolved organic material or suspended sediments in the water. Infrared radiometers use wavelengths of 3.5-13 µm to estimate the temperature of the sea surface. At longer wavelengths (between one mm and one m) some sections have been reserved for microwave or radar instruments and are not used by television, radio or telecommunications. While microwave radiometers measure the radiation directly, radars emit pulses and measure the returned signal. All sea surface temperature, surface roughness and salinity contribute to microwave measurements, while surface roughness and slope can be measured by radar instruments (Robinson 2010).

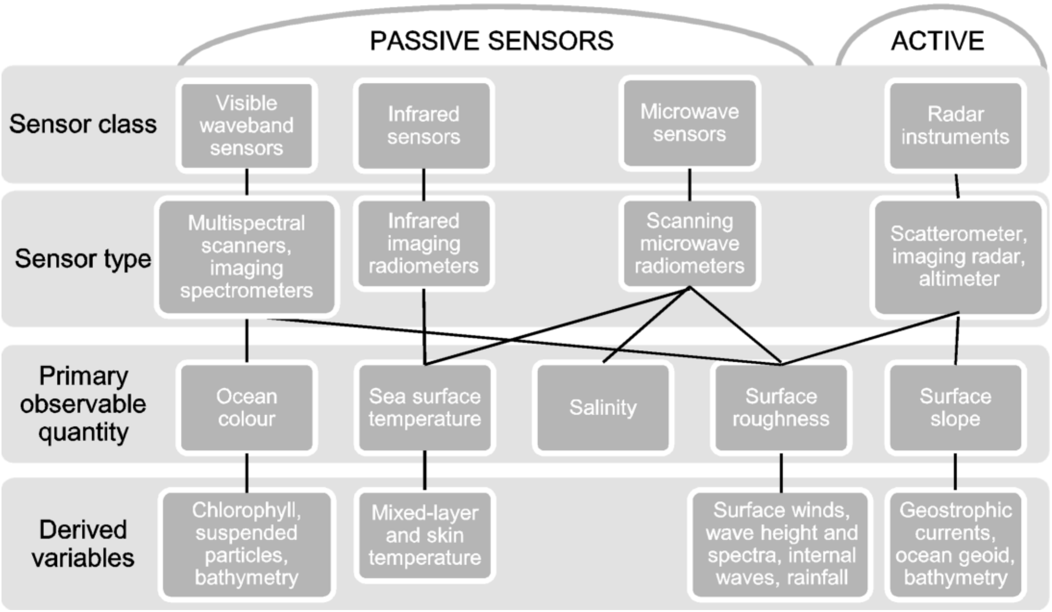

Figure 1.2. Different remote sensing methods and classes of sensors used in satellite oceanography along with their applications (redrawn from Robinson 2004).

Near-real-time remote sensing information enables monitoring present conditions, thereby raising awareness of changes occurring in marine systems. Additionally, stored historical data allow retrospective analysis and establishment of causative links through simultaneous evaluation of system responses together with several putative explanations. Furthermore, feeding of remote sensing data into predictive models enables scientists to forecast the future conditions of the system. Hence, remote sensing provides new ways of understanding the ocean and new insights in ocean science. Excellent reviews about remote sensing techniques used in oceanography and their applications can be found in Robinson (2004, 2010). I next consider the environmental processes that influence Caribbean coral reefs, many of which might be measurable using remote sensing.

Present climate as a determinant of reef function and distribution

Over evolutionary time coral reefs have been exposed to the influence of diverse environmental forces such as wave energy, extreme temperatures, upwelling, storms, river and runoff inputs, and these factors have been recognized as determinants of the structure and function of coral reef ecosystems (Grigg and Dollar 1990; Souter and Linden 2000; Knowlton and Jackson 2001). The environmental setting, the average conditions as well as anomalous events, modify coral reef ecosystem processes, such as recruitment, growth and mortality (Knowlton and Jackson 2001). These changes can drive the long-term dynamics of reef systems to different states and even shape their distribution (Kleypas et al. 1999; McManus and Polsenberg 2004). The main environmental drivers of reef function and distribution in the Caribbean are addressed below, together with a short description of methods commonly used for their regional assessment.

Hurricanes

Storms are acute disturbances that influence reef communities through direct effects such as increased mechanical stress, and indirect effects such as increased sedimentation, turbidity, and lowered salinity (Harmelin-Vivien 1995). The impact of storms can result in the mortality of corals, affecting adults, juveniles and recruits (Highsmith et al. 1980; Dollar and Tribble 1993; Mumby 1999; Bries et al. 2004). Hurricanes can also affect the fish communities (Bouchon et al. 1994) and reduce the cover of macroalgae in the short term (Mumby et al. 2005). Ultimately, hurricanes can shape the structure and function of the ecosystem (Connell 1978; Rogers 1993), coral reef morphology (Dollar and Tribble 1993; Madin and Connolly 2006) and distribution (Dollar and Tribble 1993). Hurricanes can also produce other unexpected indirect effects, such as increased connectivity among reef locations (Andréfouët et al. 2002; Soto et al. 2009), or decreased thermal stress during regional bleaching events (Manzello et al. 2007).

The National Hurricane Center from the National Oceanic and Atmospheric Administration offers detailed information regarding the position and strength of hurricanes in the Atlantic basin since 1851 (Neumann 1987). This information has been used by a variety of authors to study storm-related damage in reefs (e.g. Treml et al. 1997; Bries et al. 2004; Gardner et al. 2005). Storm-force winds may extend several kilometres from the hurricane track. In order to estimate the frequency of storms at a particular site, the effect of nearby storms that supply hurricane-force winds to the site should be considered. Several methods have been used to capture the impact of hurricanes around the tracks by using buffers large enough to ensure an adequate representation of the storms, yet small enough to preserve the climatological integrity of the site (Neumann 1987). Some authors have used buffers of fixed width such as 140 or 95 km (Neumann 1987; Treml et al. 1997). Gardner et al. (2005) went a step further and used three different buffers to capture the area of influence of hurricanes categories 1-2 (35 km), hurricanes category 3 (60 km), and hurricanes categories 4-5 (100 km). Keim et al. (2007) produced a further refinement of this method by incorporating the asymmetry of the storm on the resulting buffers, because in the northern hemisphere storms are more extensive on the right side (Shapiro 1983). Buffers were parameterized with observed sizes of hurricanes and have a maximum width of 160 km on the right side for storms of category 5. Wind speed fields can also be modelled using continuous models such as the Rankine vortex, SLOSH and Holland models (e.g. Phadke et al. 2003).

Wave exposure

Wave energy is one of the main attributes that characterizes a reef landscape (Sheppard 1982; Done 1983; Huston 1985; Graus and Macintyre 1989). Wave exposure has been related to the structure of coral and fish communities (Depczynski and Bellwood 2005), habitat complexity and beta diversity (Harborne et al. 2006). Exposure to waves drives key ecosystem processes in coral reefs. Water flux defines the dispersal and settlement of marine larvae (e.g. Abelson and Denny 1997), is critical for the supply of nutrients and food onto the reef (e.g. Hearn et al. 2001), increasing its productivity (e.g. Hurd 2000). Through mixing of the water column, wave energy also favours the decrease of thermal stress (Skirving et al. 2006) and promotes the flushing of metabolic wastes and toxins (Nakamura et al. 2003; Fabricius 2006), providing protection during bleaching events.

Despite the importance of hydrodynamic processes as structuring factors of reef communities, most studies do not measure wave exposure directly and they just classify locations as sheltered or exposed (e.g. Bellwood and Wainwright 2001; Depczynski and Bellwood 2005; Fulton et al. 2005; Vanderklift et al. 2009). The use of such qualitative approaches to assess wave exposure is largely due to the lack of availability of *in situ* wave data. However, wave exposure can be easily measured using cartographic indices. Many of these are based only on measurements of fetch lengths (distance of open water that the wind has blown over). These cartographic exposure indices are quantitative descriptions of the coastline configuration, likely to control the openness of a given area, under the reasoning that the longer the distance over which the wind can blow without encountering obstructions, the larger the waves can develop and the higher the exposure. The indices are usually calculated for several fetch directions, at evenly distributed radial bearings from a target location, and integrated into a single value (e.g. Tolvanen and Suominen 2005; Westerbom and Jattu 2006). Although simple to estimate, these indicators do not take into account the dominant wind direction and intensity that weighs the relative importance of the flux coming from different directions. As a result, other measures of exposure have included the influence of the wind in the calculations, either using wave theory (e.g. Ekebom et al. 2003; Lindegarth and Gamfeldt 2005) or simpler approaches (e.g. Fonseca et al. 2002; Tolvanen and Suominen 2005; Davies and Johnson 2006; Isæus 2004). Further refinements to the method include the influence of depth at the target location (Harborne et al. 2006; Bekkby et al. 2008), tidal fluctuations or changing bathymetry along the fetch (Malhotra and Fonseca 2007).

Detailed digital coastline can be derived from high resolution satellite imagery (e.g. Landsat TM, SPOT, IKONOS, or QuickBird) or from shoreline databases freely available online (e.g. Global Self-consistent, Hierarchical, High-resolution Shoreline Database at about 200 m resolution). Radiometer and scatterometer satellite wind sensors, or merged products (e.g. the Cross-Calibrated, MultiPlatform ocean surface wind or the blended sea winds products) provide maps of wind speed and direction over large areas.

Temperature

Ocean temperature controls species ranges, the strength of species interactions, the dispersal and survival of marine larvae and rates of metabolism (Sanford 1999; Thomas et al. 2004; Helmuth et al. 2006; O'Connor et al. 2007). The background temperature regime influences adaptation, acclimation and persistence of coral assemblages within regions (McClanahan et al. 2007). Anomalous temperatures can produce stress responses in corals, such as coral bleaching, the expulsion of symbiotic algae (Gates et al. 1992; Baker et al. 2008), and also influence the severity and dynamics of infectious diseases increasing host susceptibility and pathogen virulence (Harvell et al. 2002; Bruno et al. 2007).

Sea surface temperature has been measured from space using radiometers since 1982, providing global coverage and high accuracy (McClain et al. 1982). Satellites measure the temperature of the "skin" of the surface, in contrast to the "bulk" temperature measured by *in situ* devices. However, reprocessing efforts (e.g. Kilpatrick et al. 2001) have provided datasets that cover the entire globe and are consistent through time, supplying a unique alternative to the observation of the patterns and dynamics of temperatures in the oceans.

Turbidity

Sediments interfere with the photosynthetic and feeding activities of corals by reducing the light available for photosynthesis, and smothering (Rogers 1983; Rogers 1990). The removal of accumulated sediment represents an energetic cost to the coral, and this stress agent has been associated with reduced coral growth and accretion rates, and when excessive, with inhibited coral recruitment and increased coral mortality (Rogers 1990).

In general reefs are located in areas of low sedimentation. Mean sediment rates for reefs not subjected to stress from human activities are less than 10 mg cm^{-2} d^{-1} (Rogers 1990). Sediment accumulation and re-suspension can be altered by natural weather events (e.g. storms, see Andréfouët et al. 2002; Wolanski et al. 2005) and anthropogenic activities (e.g. dredging, coastal clearing and construction, see Fabricius et al. 2007; Ryan et al. 2008). Episodic high sedimentation events can stress coral reefs, with short-term sedimentation being more benign than long-term exposure (Philipp and Fabricius 2003). It is necessary to keep in mind, however, that coral communities can occur in a wide range of marginal locations (Perry and Larcombe 2003; Macdonald et al. 2005) and heavily turbid areas can encompass coral reef development (e.g. Perry 2003; Smithers and Larcombe 2003).

The colour of the sea varies when viewed from space. Satellite instruments perceive subtle changes in water colour and brightness that are related to the contents of the first few meters of the water column such as phytoplankton, suspended sediments and organic matter. Some of the most commonly used water quality parameters are the concentration of chlorophyll and the diffuse attenuation coefficient at 490 nm, which provide measures of phytoplankton abundance and water clarity respectively (Srokosz 2006). Most ocean colour algorithms have been developed for clear oceanic waters, and their use in coastal waters (where the optical properties are determined by various factors, such as yellow substance, suspended sediment, coloured dissolved organic matter phytoplankton concentration and bottom reflectance) is limited (Srokosz 2006).

Salinity

Salinity plays a vital role in the dynamics of coastal and marginal seas. Low salinity water from rivers and runoff can transport natural and anthropogenic contaminants into the sea, and directly stress marine ecosystems that are adapted to higher salinity levels. Direct effects of low salinity water on coral reefs include mortality (Goodbody 1961) and stress in coral adults and larvae (Vermeij et al. 2006). Stress symptoms after low salinity intrusions include increases in metabolic rates (Ferrier-Pagès et al. 1999) and bleaching (Goreau 1964; Kerswell and Jones 2003) in adult corals, as well as altered larval behaviour and substrate choice upon settlement (Vermeij et al. 2006). Salinity effects are, however, species-specific (Muthinga and Szmant 1987).

Although salinity is an important driver of marine ecosystem function, sea surface salinity has not been used much as an explanatory variable at large spatial scales largely because available *in situ* salinity measurements lack sufficient spatial and temporal coverage. To date, the World Ocean Atlas (Antonov et al. 2010) represents the best available compendium of salinity data in the world oceans. This is a set of objectively analysed climatological fields of *in situ* data gathered from several sources, with earlier observations recorded during the 17th century. Satellite-derived salinity from the National Aeronautics Space Agency's Aquarius mission is expected to fill this gap. The microwave instrument was launched in June 2011, and it is expected to produce monthly maps of sea surface salinity for the entire globe (Le Vine et al. 2010).

Climate change as a threat to reefs

The climate of the earth is changing: temperatures are getting warmer; ice and snow are melting and sea level is rising (Solomon et al. 2007). These changes are related to human industrial activity since the 18th century and the increased release of greenhouse gases (Solomon et al. 2007). Carbon dioxide, methane and nitrous oxide, the most important anthropogenic greenhouse gases, have increased to unprecedented values (Solomon et al. 2007). Global temperatures have increased in 0.74ºC during the last 100 years, and the rate has increased to 0.13 ºC/decade during the last 50 years. The ocean is absorbing 80% of the heat added to the climate system. Global average sea level has risen at a rate of 1.8 mm per year over 1961 to 2003. Additionally, at regional scales numerous changes in climate have been observed, such as changes in precipitation or wind patterns (Solomon et al. 2007). Increases in greenhouse gas concentrations and temperatures far exceed the natural range observed over the previous hundreds of years (Solomon et al. 2007).

These changes in climate have produced concomitant changes in many marine biological systems (Parmesan and Yohe 2003; Hoegh-Guldberg and Bruno 2010), including coral reefs (Hoegh-Guldberg et al. 2007). Temperature increases have been recognized as the major threat for reefs in a changing climate (Hoegh-Guldberg 1999; Hughes et al. 2003), probably because of the sensitivity of reef inhabitants to changes in temperature and the unequivocal evidence of increased temperatures on coral reef ecosystems. Thermal stress has been related to mass coral bleaching and subsequent mortality (Glynn 1996; Hoegh-Guldberg 1999; Baker et al. 2008), coral diseases (Bruno et al. 2007; Harvell et al. 2009), changes in reef fish (Munday et al. 2008) and reef invertebrate communities (Przeslawski et al. 2008).

Refuges from thermal stress

In the face of such a large menace it has been suggested that reefs may become increasingly restricted to locations of naturally low thermal and/or radiative stress (Glynn 1996; Salm and Coles 2001; Riegl and Piller 2003; West and Salm 2003). Some have speculated that areas that might be naturally protected from thermal stress should constitute priorities for conservation activities in order to increase the chance of survival of the ecosystem (Salm and Coles 2001; West and Salm 2003; Baker et al. 2008).

Factors that could decrease the effects of thermal stress include low light, high flow and lower temperatures (Salm and Coles 2001; Riegl and Piller 2003; West and Salm 2003). Based on these mitigating factors, different habitats have been suggested as refuges from thermal stress: (1) deeper reefs with low levels of light and temperature; (2) areas of strong vertical mixing that decrease the temperature of the water (Skirving et al. 2006) and flush harmful toxins (Nakamura and van Woesik 2001); (3) sites with high level of shading: high solar irradiance exacerbate the effects of high temperatures (Hoegh-Guldberg 1999), and therefore it has been hypothesised that shading of corals may moderate the effects of bleaching (Mumby et al. 2001); (4) upwelling areas that decrease temperatures (Glynn and D'Croz 1990). To test these hypotheses and determine to what extent these areas may act as a refuge against climate change, the regions need to be identified and the consistency of its effect needs to be quantified (Salm and Coles 2001). This has been done formally to assess the ‘deep reef refugia’ hypothesis (Bongaerts et al. 2010) but a formal assessment of the other hypotheses remains to be carried out.

Thesis overview

Through this thesis the environment of the Caribbean basin was characterized using remote sensing and *in situ* data sources. This information was used to understand how present environmental conditions have shaped reef ecosystems and how the changing climate might jeopardize them (Figure 1.3).

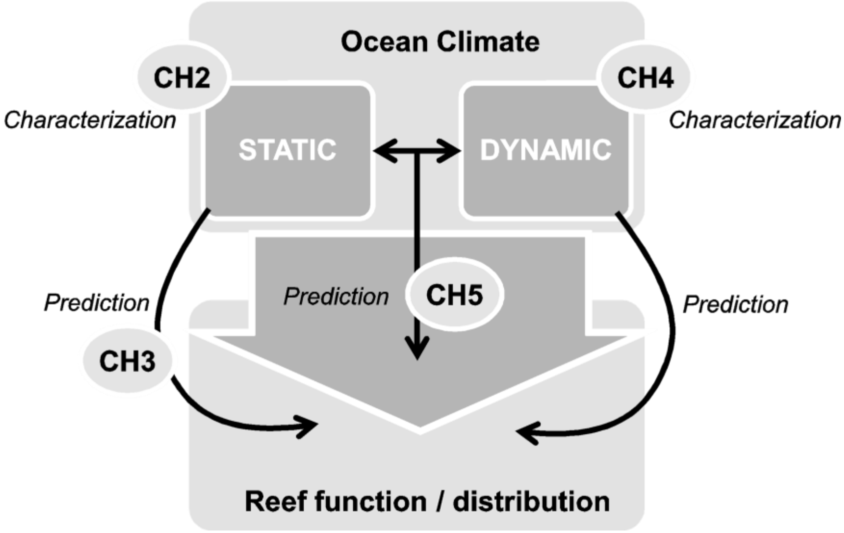

Figure 1.3. Conceptual diagram for the thesis chapters. CH2: Environmental provinces of the Caribbean, CH3: Static climate, characterized by wave exposure, as predictor of reef habitats, CH4: Recent temperature trends in the Caribbean, CH5: Upwelling as a refuge from warming.

Ocean climate characterizes the long-term oceanographic regime in a given location. For a particular time period, ocean climate can be represented by static features (e.g. average sea surface temperature). However, global and regional climates change over time and therefore there is also a dynamic component associated to climate (e.g. rate of change of sea surface temperature). In this thesis, the static ocean climate of the Caribbean is addressed in Chapter 2, where the basin is categorized according to its prevailing physical environment. The influence of ocean climate in the distribution of marine ecosystems is exemplified by Chapter 3, which uses wave exposure to predict the distribution of *Montastraea* reef habitats in the Caribbean basin. Chapter 4 addresses one aspect of the dynamic climate in the basin by quantifying recent changes in sea surface temperature. Finally, Chapter 5 examines characteristics of the static ocean climate (temperature anomalies) in order to explore the suitability of one hypothesised refuge for reefs (upwelling areas) to ensure reef function in the face of a changing climate.

Results are discussed within the context of the suitability of the tools used to fulfil the tasks and further applications of the generated products in order to obtain a more comprehensive understanding of environmentally-driven ecosystem function and distribution in the Caribbean.

Significance and innovation

During the development of this thesis a comprehensive compendium of datasets describing the environmental setting of the Caribbean was gathered. The best dataset available was used in order to fulfil each task, and most of the datasets have the additional value of being freely available. These data are being used by several research projects (e.g. FORCE, CARICOMP) in order to have a better understanding of environmental drivers of coastal marine communities in the basin.

Similarly, the best statistical approach was used in order to answer each question. The thesis presents an eclectic mixture of statistical methods, from simple statistical tests (Chapter 5), to mixed effect models (Chapters 3 and 4) and non-traditional approaches, such as neural networks (Chapter 2). Although the dataset is specific to the Caribbean, all the methodologies applied are fully transferable to other areas or other spatial scales. For example, the categorization of a region according to their physical environments (Chapter 2) could be done at more detailed spatial scales if relevant for local researchers. Likewise, spatial heterogeneity in warming rates (Chapter 4) could be studied using exactly the same methodology in a totally different area (i.e. the Great Barrier Reef).

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2

Physical environments of the Caribbean Sea

Chollett I, Mumby PJ, Müller-Karger FE, Hu C (submitted). Physical environments of the
Caribbean Sea. Limnology and Oceanography

Abstract

The Caribbean Sea encompasses a vast range of physical environmental conditions that have a profound influence on the organisms that live there. Here we utilise a range of satellite and *in situ* products to undertake a region-wide categorisation of the Physical Environments of the Caribbean Sea (PECS). The classification approach is hierarchical and focuses on physical constraints that drive many aspects of coastal ecology including species distributions, ecosystem function and disturbance. The first level represents physicochemical properties including metrics of satellite sea surface temperature (average, minimum and maximum monthly mean), turbidity (relative frequency of anomalies), and *in situ* salinity (average). The second level considers mechanical disturbance and includes both chronic disturbance from wave exposure and acute disturbance from hurricanes. The maps have a spatial resolution of one km^2. An unsupervised neural network classification produced 16 physicochemical provinces for the Caribbean Sea. Spatial patterns in province geography reflect well-known ocean processes. The provinces can be categorised into six broad groups: (1) areas of high turbidity and low salinity, such as the Orinoco River plume (Venezuela), Lake Maracaibo (Venezuela), Cienaga Grande de Santa Marta (Colombia) and Uraba Gulf (Colombia); (2) areas of high turbidity, broadly distributed in the basin; (3) areas of low salinity such as the high runoff region along Panama and Costa Rica; (4) upwelling areas in Yucatan (Mexico) and the southern Caribbean (Colombia and Venezuela); (5) high-latitude areas including the waters of the Gulf of Mexico and areas subjected to bathymetric effects, such as the Floridian (USA), Bahamian and Cuban shallow banks; (6) offshore waters of the inner Caribbean. Because physical environments underpin so much of coastal ecosystem structure and function, we anticipate that the PECS classification will facilitate comparative analyses and inform the stratification of studies across environmental provinces.

Keywords: self-organizing maps, oceanography, disturbance regime, mapping, marine biogeography.

Introduction

It has long been recognised that marine environments encompass vast environmental heterogeneity across a continuum of scales (Beer 1997). Setting boundaries to the ocean is the first step towards its quantitative study (Longhurst 2007). In principle, a categorization of the physical marine environment might help explain patterns of the structure and function of marine systems and account for commonalities or contradictions in the results of experiments or monitoring studies carried out at different locations (e.g. Santamaría-Del-Angel et al. 1994; Schils and Wilson 2006; Alemany et al. 2009; Iken et al. 2010). Environmental classifications should also provide a logical mean of stratifying field measurements so that outcomes can be scaled up appropriately.

Several attempts have been made to categorise the world’s oceans into regions. The US National Oceanic and Atmospheric Administration (NOAA) identified 64 large marine ecosystems: large areas with distinct bathymetry, hydrography and productivity (Sherman and Hempel 2009). Longhurst (2007) classified the world ocean into 57 biogeochemical provinces after examining imagery of sea surface chlorophyll concentration and reviewing physical oceanographic literature for each ocean basin. Spalding et al. (2007) produced an expert-derived classification of the marine environment into 12 marine realms, 62 provinces and 232 ecoregions, which are expected to support a relatively homogeneous species composition. These categorizations partition the Caribbean Sea into either two (Longhurst 2007; Sherman and Hempel 2009) or nine units (Spalding et al. 2007: Figure 2.1). Neither scheme was intended to categorize the physical environment or reflect patterns of species composition at an intra-Caribbean scale. This point is made clear by considering regional variability of sea surface temperature, an important environmental variable in determining pattern and function in marine systems (Clarke and Gaston 2006; Tittensor et al. 2010). There is great thermal variability (Figure 2.1) within even the most detailed classification available for the Caribbean (Spalding et al. 2007). For example, the southern Caribbean ecoregion (ecoregion 66 in Figure 2.1) encloses areas influenced by upwelling as well as offshore oligotrophic areas (Müller-Karger et al. 1989). Furthermore, similar physical environments have been arbitrarily separated into different ecoregions, as highlighted by the division of the Colombian upwelling areas (Andrade and Barton 2005) into ecoregions 66 and 67 (Figure 2.1).

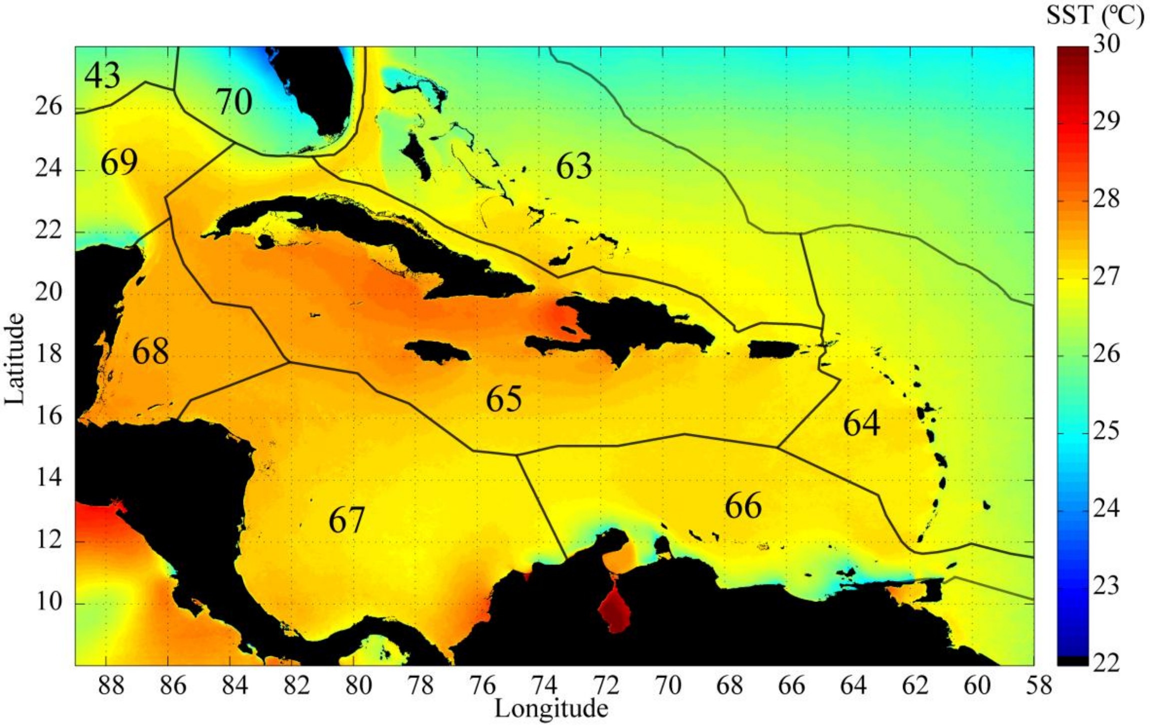


Figure 2.1. Average sea surface temperature map (AVHRR 1993-2008) and marine ecoregions in the Caribbean Sea (8-28ºN, 89-58ºW) according to Spalding et al. (2007): (43) Northern Gulf of Mexico; (63) Bahamian; (64) Eastern Caribbean; (65) Greater Antilles; (66) Southern Caribbean; (67) South-western Caribbean; (68) Western Caribbean; (69) Southern Gulf of Mexico; (70) Floridian.

The physical environment of the Caribbean Sea is spatially heterogeneous and such variations are likely to affect the function and distribution of marine organisms in the basin (Bailey 1998). Major sources of heterogeneity include river plumes (Müller-Karger et al. 1989; Restrepo et al. 2006), runoff (D'croz et al. 2005; Imbach et al. 2010), upwelling (e.g. Astor et al. 2003; Andrade and Barton 2005; Cerdeira-Estrada et al. 2005) and bathymetric effects (Cerdeira-Estrada et al. 2005; Wall et al. 2008). These mechanisms principally alter the physicochemical environment experienced by marine organisms (i.e. temperature, light, salinity), which influence fundamental biological processes including metabolism and photosynthesis. Here, we begin by creating a classification of the physicochemical environments of the Caribbean. This classification defines major physicochemical boundaries, but many organisms, particularly those living in shallow coastal habitats (less than 20 meters) area also strongly influenced by the mechanical disturbance regime (Short and Wyllie-Echeverria 1996; Madin and Connolly 2006). Two principal types of mechanical disturbance can be distinguished: chronic exposure to waves and acute, episodic physical disturbance from tropical cyclones (Connell 1978; Good 2004; Tewfik et al. 2007). We therefore created a hierarchical classification scheme of the Physical Environments of the Caribbean Sea (PECS) that encompasses the fundamental physicochemical regime at the top level and includes two forms of physical disturbance at lower levels. The PECS classification was developed directly from observed data rather than being imposed upon data, and was implemented at a high spatial resolution of one km^2. We anticipate that the classification scheme will benefit the systematic quantitative study of biological oceanography in the Caribbean in addition to that of coastal habitats including intertidal rocky shores and mangroves, and subtidal seagrass beds and coral reefs. Moreover, a detailed classification of physical environments will help inform conservation planning activities of the likely stratification of biodiversity in the area.

Methods

The dataset

The environment of the Caribbean Sea (8-28ºN, 89-58ºW) was defined in terms of sea surface temperature, turbidity, salinity, wave exposure and hurricane incidence. A short description of the source data and the methodology followed to obtain each data layer is given below.

Sea surface temperature (SST) data were derived from infrared observations collected by the Advanced Very High Resolution Radiometer (AVHRR) sensors flown on the NOAA’s Polar Orbiting Environmental Satellite Series. AVHRR data from 1993 to 2008 at one km^2 spatial resolution were gathered, navigated, processed and archived by the Institute for Marine Remote Sensing (IMaRS) at the University of South Florida. Nightly data were subjected to the cloud-filtering procedure described by Hu et al. (2009). From this dataset, we calculated the climatological average, the climatological minimum monthly mean (mMM) and the climatological maximum monthly mean (MMM).

Turbidity was assessed using the diffuse attenuation coefficient at 490 nm (k490: Mueller 2000). Time series data from 1997 to 2008 at one km^2 spatial resolution were derived from ocean colour observations collected by the Sea-viewing Wide Field of view Sensor (SeaWiFS) on board of GeoEye's SeaStar satellite. SeaWiFS data were collected, navigated, processed (using SeaDAS v4 software) and archived by IMaRS. Saturated values (k490=6.3998 m^{-1}, the maximum attainable value for this variable) were removed from the dataset. Spatial variability in the relative composition and nature of in-water constituents in coastal waters makes their quantification problematic in large regions (Babin et al. 2003; Blondeau et al. 2009). Additionally the Caribbean Sea contains optically shallow areas (e.g. the clear Bahamas banks: Cannizzaro and Carder 2006) with apparent high turbidity (k490 values up to 0.4 m^{-}1) that complicate regional assessments. Therefore we calculated the relative frequency of anomalies (percentage of times that k490 values were above 0.5 m^{-1}) as a proxy to identify high turbidity areas throughout the Caribbean Sea. While the 0.5 m^{-1} threshold accounts for the effects of optically shallow waters, the use of relative frequencies allows the comparison of areas with different observation frequency because of heterogeneous cloud coverage in this large region.

Salinity data from the World Ocean Atlas 2009 were obtained from the NOAA Data Center. The original data were collected from several sources, including bottle samples, ship-deployed conductivity-temperature-depth package, profiling float, moored and drifting buoys, gliders, and undulating oceanographic recorder profiles (Antonov et al. 2010). The earliest observations were recorded during the 17th century, and the last observations during 2008. The dataset was analysed in a consistent, objective manner on a 0.25° latitude-longitude grid at standard depth levels (Antonov et al. 2010). Here we used climatological monthly composites of salinity at the surface. From this source data we calculated average surface salinity which was then rescaled to one km^2 using bicubic interpolation in order to match the spatial resolution of the other layers.

Wave exposure, the degree of wave action on an open shore, is governed by the fetch (distance of open sea that the wind has crossed to generate waves) and the strength and direction of the winds. Here we measured fetch using the Global, Self-consistent, Hierarchical, High-resolution Shoreline database (GSHHS v1.5) and wind speed and direction were acquired from the QuickSCAT satellite scatterometer from 1999 to 2008. Wind data, originally at approximately 25 km spatial resolution, was rescaled to one km^2 using bicubic interpolation prior to the analyses. Wave exposure was calculated using the method described by Ekebom et al. (2003), where the exposure of a location is a function of the shape of the basin, wind speed and direction. However, Ekebom et al.'s method was developed in small archipelago environments (dozens of kilometres) with uniform wind conditions and fetch-limited exposure (Ekebom et al. 2003). For this study we are assessing a large region (thousands of kilometres) with high variability in wind distribution (Andrade 1993), and many open, fetch-unlimited areas. For that reason we made two modifications to the original method: (1) by specifying the shift between equations for “fetch-limited” and “fully-developed” seas, because for a given wind speed and a long fetch there is a fixed height to which a wave can grow (the threshold for a non-dimensional fetch, which depends on the fetch and the wind speed, 38,590 m, was given by the approach followed by Harborne et al. 2006); (2) by including spatial variability in wind fields using gridded wind data. Additionally, we calculated daily wave exposure and then produced an average for the entire time period, instead of using the average wind speed in each of the main directions (e.g. Ekebom et al. 2003). This approach allows inclusion of strong, sporadic winds which have a disproportionate influence on resulting wave patterns and would be missed otherwise.

Hurricane incidence was measured using the Atlantic Hurricane dataset (1851-2008), which tracks the location and intensity of the eye of tropical cyclones every six hours (Jarvinen et al. 1984). We confined the analyses to storms that reached hurricane intensity (wind speeds higher than 166 km h^{-1}). Hurricane-force winds may extend several kilometres from the hurricane track. We calculated the frequency of hurricanes in any given location using the approach described by Edwards et al. (2011). Essentially, the area of influence of each hurricane is captured in buffers (up to 160 km wide) that take into account the intensity of the storm, its asymmetry (because of the Coriolis force) and the reduction in wind speed with distance from the hurricane track (Keim et al. 2007). Using this approach, we mapped the total frequency of hurricanes for each Saffir-Simpson intensity class for the entire record at one km^2 spatial resolution.

Classification

The Caribbean basin was classified into physicochemical regions using Self Organizing Maps (SOM: Kohonen 1995), an unsupervised clustering approach. Other unsupervised classification methods were attempted (e.g. k-means, isodata, spatial conditional fuzzy c means); however, SOMs provided the best results (clearly separable, homogeneous groups), handled better turbidity and salinity data with skewed distributions, and required the shortest processing time.

The input variables for the classification were average SST, mMM SST, MMM SST, relative frequency of turbidity anomalies and average surface salinity, which are expected to depict the most relevant physicochemical features of the area. All variables were first standardized to allow meaningful comparisons. Standardization was achieved by dividing each variable, *x*, by its range (Legendre and Legendre 1998: Equation 1).

$$x_i' = \frac{x_i - x_{min}}{x_{max} - x_{min}} \quad \text{(Equation 1)}$$

The classification method (SOM) is a type of neural network based on competitive learning that both reduces the dimensionality of the data and displays similarities among data. SOM was preferred over more traditional clustering approaches, such as hierarchical clustering or k-means, because of its ability to deal with large datasets and non-linear problems. SOM does not make a priori assumptions about the distribution of the data, making it more appropriate for turbidity and salinity data, which have leptokurtic and skewed distributions. Other strengths of SOM are its ease of implementation, adaptation (the ability to change its structure based on external or internal information), parallelization (performing small operations in parallel), flexibility and speed (Xu and Wunsch 2009). A brief overview of the SOM algorithm is given below, but the reader is referred to Kohonen (1995) for a more technical discussion and to Sheridan and Lee (2011), Liu and Weisberg (2011) and Chon (2011) for reviews on its application in climatology, oceanography and ecology. Although the SOM has been used previously to extract patterns in satellite imagery (Richardson et al. 2003), most applications have used it to extract temporal patterns, and few applications have tried to use it for the extraction of spatial patterns and the identification of regions (but see Saraceno et al. 2006).

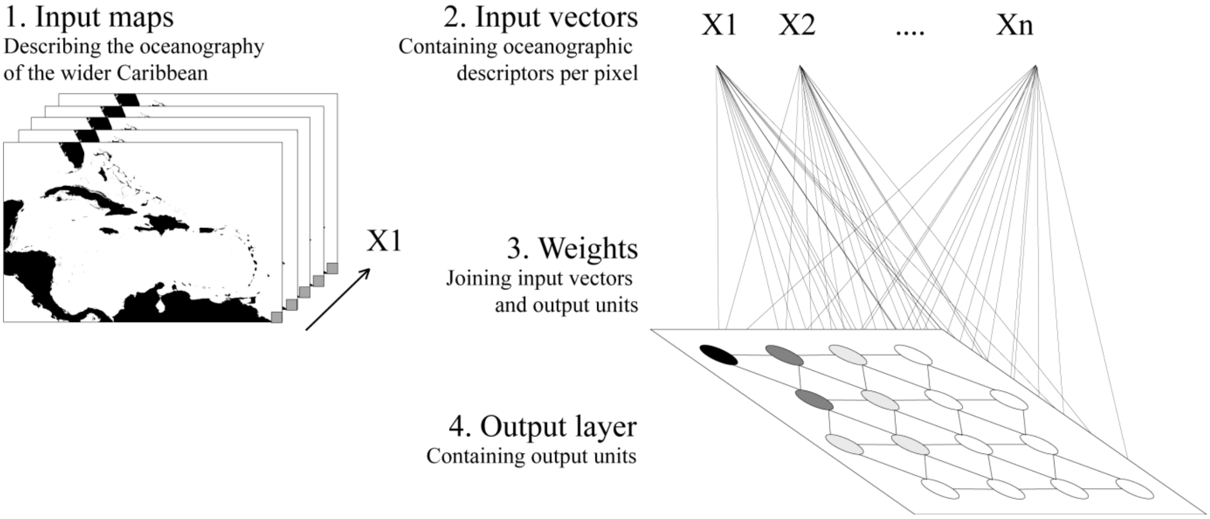


Figure 2.2. Overview of the SOM algorithm: each pixel within the temperature (average, mMM, MMM), turbidity and salinity input maps (1) is taken as an input vector (2), the input for the SOM algorithm. *N* input vectors (where *N* is equal to the number of pixels in the image) are linked to the output layer through weighted links (3). The output layer (4) is, in this case, a matrix composed by 16 (4x4) units in a hexagonal grid, where lines indicate the connections among units, and the update neighbourhood of the first (black) unit is defined by the grey gradient, with lighter colours highlighting farther units.

SOM is a nonlinear classification analysis in which high-dimensional data are mapped onto a two-dimensional output space while preserving the topological relationships among input data (Kohonen 1995). The input data for the analysis are *N* vectors (one for each pixel in the study area, more than three million in total) with five dimensions, corresponding to the descriptors of the physicochemical environments of the Caribbean. The SOM (Figure 2.2) consists of a set of units, nodes or neurons arranged in a two-dimensional grid. These units characterize the centre of the clusters. The number of units (and clusters) and the type of arrangement are defined by the user and are dependent upon the level of detail desired in the analysis. A weight vector of the same dimension as the input data is associated with each unit. This vector is initialized with random values or eigenvectors of the dataset. During the self-organizing process, input vectors are presented to the SOM and the distance of the weight vector of each unit to the input vector is calculated. The unit with the smallest distance is selected as the “winner”. At this point, the weights of both the winner and its neighbouring units are modified to more closely resemble the input vector. These changes depend on a learning rate which decrease with time (units change more at the beginning of the iterative process) and a neighbouring function that is spatially explicit (neighbour units farther away from the winner change less). The procedure is repeated until each input vector is presented to the network, and then the entire process is repeated many times, leading to a topologically ordered map. The inclusion of a neighbourhood function implies that similar patterns are mapped onto neighbouring regions on the map, while dissimilar patterns are mapped farther apart. Once the underlying patterns have been characterized with the output units, SOM results can be used to classify the input vectors into classes, where each vector is represented by the most similar unit.

The SOM requires the user to define the desired number of clusters a priori. To identify the optimum number of clusters we partitioned the dataset using 4-36 classes and compared the results using a validation criterion. While a few classes produce clusters that are well separated but internally very variable, too many clusters give more compact but overlapping clusters. To choose the optimal number of clusters (*k*), we evaluated the resulting classifications regarding their compactness or within-cluster variability, and isolation or between-cluster variability using the index described by Caliński and Harabasz (1974). The approach is analogous to the F-statistic in univariate analysis and has shown a superior performance when compared to other indices (Milligan and Cooper 1985). Within-cluster variability (*wSS*) was estimated by calculating the sum of squares of the Euclidean distances between each pixel (*N* pixels in total) and the centroid of its cluster, while between-cluster variability (*bSS*) was assessed as the sum of squares of the Euclidean distances between each cluster centroid and the centroid of the entire dataset. The Caliński and Harabasz (*CH*) index is given by the formula below (Equation 2). The number of clusters that maximizes *CH* suggests the best partition.

$$\mathrm{CH}_k = \frac{\frac{\mathrm{bSS}_k}{(k-1)}}{\frac{\mathrm{wSS}_k}{(N-k)}} \qquad \text{(Equation 2)}$$

The units of the SOM were arranged in a hexagonal grid, which allows a better visualization and more continuous transitions among the units. The learning rate was 0.9 during the initial phase and 0.02 during the refining phase. The initial neighbourhood size was set to 3, and the refining phase neighbourhood distance was set to 1. The initial phase consisted of 100 steps, while the refining phase 400; for 500 iterations in total. To calculate distances from a particular unit to its neighbours we used the link distance, which is simply the number of links that must be taken to reach the unit under consideration. The analyses were performed using the Neural Network toolbox in Matlab 7.10. GIS files with the PECS classification including both the physicochemical categorization and the physical disturbance regime can be requested from the author.

Results

SOM classification

The optimal partition of the input dataset was found when using 16 clusters (Figure 2.3). For this partition the Caliński and Harabasz index attained the second maximum value (Figure 2.3a). This classification scheme represents the best trade-off in minimizing the within cluster variability (*wSS*) and maximizing the between cluster variability (*bSS*, Figure 2.3b) while providing a number of clusters that is small enough to be easily visualized and interpreted.

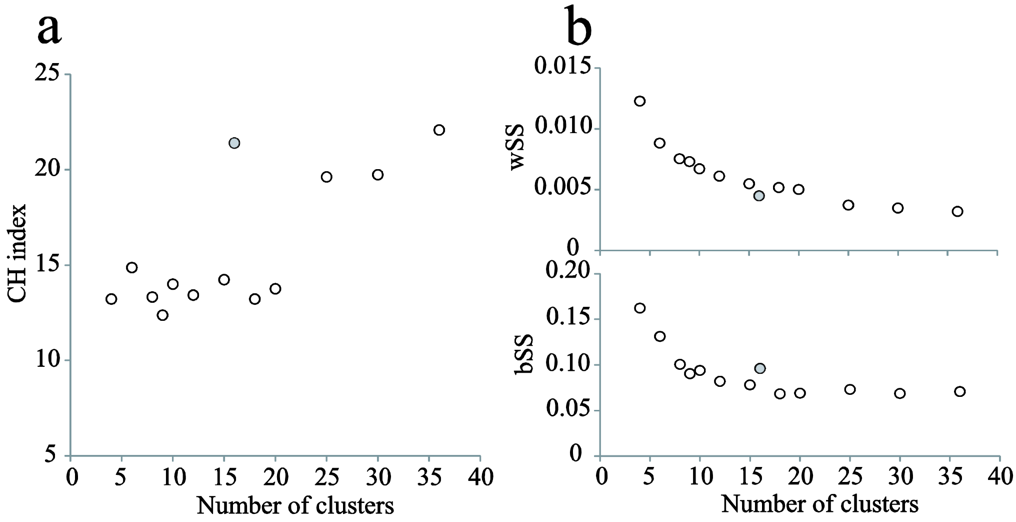


Figure 2.3. Metrics used to identify the optimum number of clusters (a) Caliński and Harabasz index (*CH*); (b) within cluster sum of squares (*wSS*) and between cluster sum of squares (*bSS*). In grey values corresponding to 16 clusters, the partition chosen.

The selected SOM classified the physicochemical environment of the Caribbean Sea into 16 clusters (Figure 2.4). Although no explicit geographic constraints were included, the clustering procedure mostly produced homogenous clusters with well-defined boundaries. Although maps obtained with higher numbers of clusters provide more detail, the distribution of the main physicochemical features remained stable when different partitions were applied to the dataset (not shown).

The number of pixels within each class was not evenly distributed and a few clusters (e.g. cluster 3, cluster 6) included most of the pixels, while others (e.g. cluster 13, cluster 14) enclosed a small subset of the region (Figure 2.5a). The SOM (Figure 2.5b) shows similar patterns adjacent of one another, dissimilar patterns at opposite ends of the SOM space, and a continuum of change across the array (Kohonen 1995). Clusters 13 and 14, on the top left corner, are very different to the rest, while clusters 2, 5, 6 and 10 are quite similar. These similar clusters represent offshore waters, with similar oceanographic characteristics, weak gradients and diffuse boundaries (Figure 2.4). When looking at the relative importance of the different variables in each cluster (Figure 2.6, Table 2.I) it can be seen that cluster 13 is characterized by the highest turbidity and the lowest salinity. Cluster 14 also shows high turbidity. Cluster 16 exhibits the lowest SST average and mMM and the highest MMM, while cluster 4 shows the highest average SST.

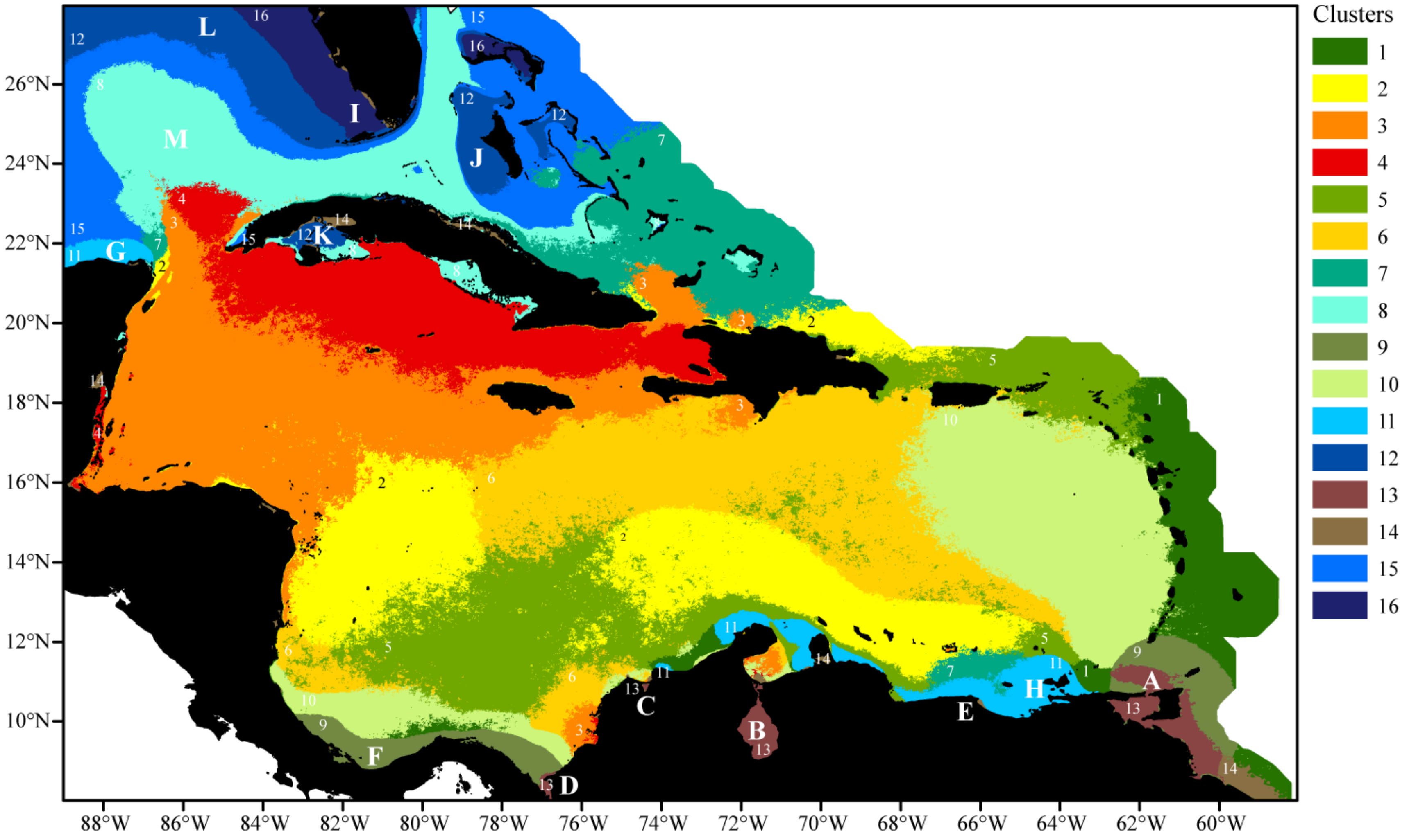


Figure 2.4. Spatial arrangement of the 16 physicochemical provinces in the Caribbean Sea and selected examples (A-N), described in Table 2.II. In order to enhance readability, numbers in the map indicate the cluster number.

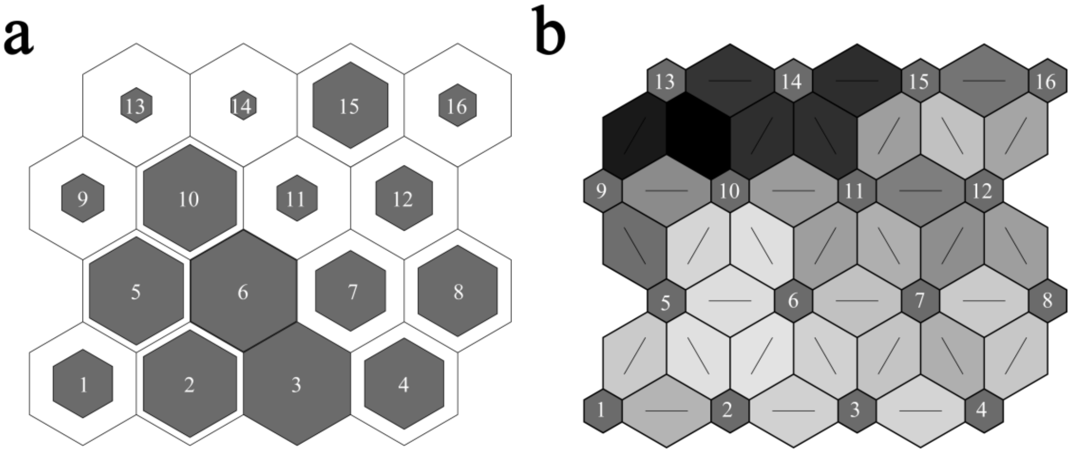
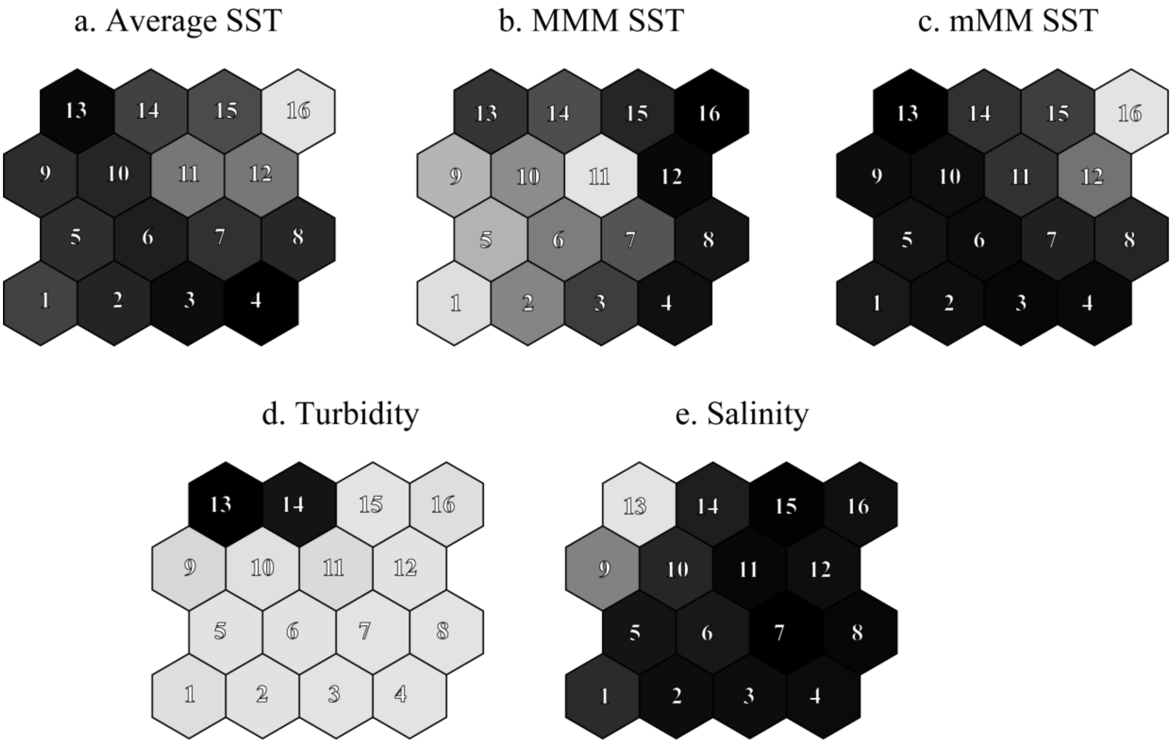


Figure 2.5. Topological arrangement of the SOM showing the relative location of the clusters. (a) The proportion of pixels associated with each numbered cluster is indicated by the size of each hexagon, where larger hexagons indicate a larger number of pixels represented by that cluster. (b) Euclidean distances between the centre of neighbouring clusters, where the hexagons represent the clusters, the lines connect neighbouring clusters, and the colour in the regions containing the lines indicate distances between clusters. Darker colours represent larger distances and lighter colours smaller distances.


a. Average SST

b. MMM SST

c. mMM SST

d. Turbidity

e. Salinity

Figure 2.6. Grid showing the location of the 16 clusters and the average value for each cluster for each environmental variable (darker colours represent larger values): (a) average SST; (b) maximum monthly mean of SST; (c) minimum monthly mean of SST; (d) turbidity; (e) salinity.

Table 2.I. Average and standard deviation of average SST, mMM, MMM, turbidity proxy and salinity for each of the 16 clusters

Cluster	Average SST (°C)	mMM SST (°C)	MMM SST (°C)	Turb (%)	Salinity (‰)
1	26.63±0.19	25.42±0.35	27.97±0.22	1.03±1.61	26.63±0.19
2	27.17±0.13	25.96±0.29	28.54±0.12	0.23±0.35	27.17±0.13
3	27.60±0.12	26.26±0.19	29.10±0.15	0.10±0.45	27.60±0.12
4	27.84±0.19	26.19±0.31	29.68±0.21	0.08±0.50	27.84±0.19
5	27.00±0.15	25.76±0.35	28.25±0.14	0.33±0.51	27.00±0.15
6	27.27±0.14	26.08±0.21	28.59±0.13	0.23±0.39	27.27±0.14
7	26.93±0.22	25.12±0.37	28.86±0.22	0.10±0.29	26.93±0.22
8	27.12±0.19	24.92±0.43	29.60±0.24	0.11±0.45	27.12±0.19
9	27.01±0.42	26.02±0.57	28.23±0.33	2.57±2.58	27.01±0.42
10	27.15±0.13	25.98±0.26	28.49±0.18	0.64±0.99	27.15±0.13
11	26.06±0.39	24.31±0.65	27.94±0.32	2.04±1.73	26.06±0.39
12	26.05±0.36	22.26±0.61	29.78±0.29	0.25±0.83	26.05±0.36
13	27.69±1.24	26.60±1.36	29.19±1.18	36.32±18.87	27.69±1.24
14	26.65±0.81	24.34±1.88	28.90±1.04	21.99±12.71	26.65±0.81
15	26.46±0.28	23.76±0.39	29.41±0.31	0.09±0.36	26.46±0.28
16	25.07±0.47	19.74±1.05	29.88±0.33	1.10±2.70	25.07±0.47

Physicochemical provinces of the Caribbean Sea

The physicochemical provinces of the Caribbean Sea can be broadly distributed into six groups, which are detailed below and in Table 2.II. (1) Areas characterized by high turbidity and low salinity were identified by the cluster 13. Examples are the Orinoco River plume (region A in Figure 2.4), an area under the direct influence of the Orinoco river, the Lake Maracaibo (region B); Cienaga Grande de Santa Marta (region C) and the Uraba Gulf (region D).

(2) Areas characterized by high turbidity, but not exceptionally low values of salinity (cluster 14) were broadly distributed in the Caribbean Sea. These conditions exist, for example, in the south, in the Golfete de Coro (Venezuela), and in areas under the influence of the Tuy (Venezuela, Region E in Figure 2.4) and Magdalena (Colombia) river plumes. In Central America turbid areas are located along the coast of Nicaragua and eastern Honduras, the Gulf of Honduras, Chetumal and Espiritu Santo Bays and in the Conil lagoon in the north of Quintana Roo, Mexico. In North America, turbid areas are located in Tampa Bay, Charlotte Harbour and Florida Bay. Finally, the Gulf of Batabano, eastern La Juventud Island and the Camagüey Archipelago in Cuba and Samana Bay in Dominican Republic have high turbid areas in the Greater Antilles.

(3) Areas characterized by low values of salinity (cluster 9) were located along the coast of Panama and Costa Rica (region F in Figure 2.4) and on the edge of the Orinoco River plume.

Table 2.II. Physicochemical provinces of the Caribbean Sea.

Main oceanographic features	Clusters	Example	Country	Description
High turbidity, low salinity	13	A. Orinoco River plume	Venezuela	Under the freshwater influence of the Orinoco River, the fourth of the world’s rivers in terms of discharge (Müller-Karger et al. 1989).
		B. Lake Maracaibo	Venezuela	The largest brackish lake in South America, influenced by the freshwater discharge of numerous rivers (Rodríguez 2000).
		C. Cienaga Grande de Santa Marta	Colombia	Large estuarine lagoon complex that forms part of the delta of the Magdalena River, the largest river discharging directly to the Caribbean Sea (Restrepo et al. 2006).
		D. Uraba Gulf	Colombia	The southernmost portion of the Caribbean Sea, with waters influenced by the freshwater discharges of the Atrato River and other small streams (Diaz et al. 2000).
High turbidity	14	E. River Tuy	Venezuela	The River Tuy concentrates the waste water effluents from the capital of Venezuela (Jaffe et al. 1995).
Low salinity	9	F. Panama-Costa Rica runoff region	Panama/ Costa Rica	Under the influence of river discharge and runoff (Roder et al. 2009; Imbach et al. 2010) driven by strong rainfall in the area (Portig 1965).
Upwelling	11	G. Yucatan upwelling	Mexico	Topographically and wind induced upwelling (Merino 1997; Melo-González et al. 2000).
		H. Southern Caribbean upwelling	Colombia/ Venezuela	Wind-driven upwelling occurs along eastern Colombia and most of the Venezuelan coastline, although the Guajira (Andrade and Barton 2005) and the south-eastern Venezuela (Astor et al. 2003) are the best known upwelling areas in the region.
High latitude areas	12,15,16	I. Florida banks	United States of America	Topographically induced fronts with colder waters in winter due to the action of sensible heat and evaporative losses in shallow areas (Beer 1997).
		J. Northern Bahamas banks	The Bahamas	Topographically induced fronts, with thermal contrasts enhanced at higher latitudes.
		K. Western Cuba banks	Cuba	These topographically induced fronts have been described by Cerdeira-Estrada et al. (2005).
		L. Gulf of Mexico	Mexico	The limits of the waters of the Gulf of Mexico are clearly delineated by the loop current. Within the Gulf waters exhibit higher seasonal variation in temperature (Müller-Karger et al. 1991).
Inner Caribbean	1-8,10	M. The Loop Current	USA/Cuba	Joining the Yucatan and Florida currents in a clockwise flow (Hofmann and Worley 1986)

(4) Areas with the lowest seasonal temperature maximum, also characterized by generally cold average and minimum SSTs (cluster 11) were located in the upwelling areas of Yucatan (region G in Figure 2.4) and the southern Caribbean (region H).

(5) High-latitude areas with low average and minimum temperature but high seasonal maxima were characterized by the clusters 12, 15 and 16. Shallower sections such as the Florida banks (region I in Figure 2.4), the northern Bahamas banks (region J) and the western Cuban banks (region K) were characterized by larger seasonal ranges when compared to surrounding areas, experiencing colder waters in winter and warmer waters in summer. Cold waters of the Gulf of Mexico (region L) also share a similar temperature signature with broad seasonal ranges.

(6) The inner Caribbean is characterized by several (1-8, 10) highly correlated clusters (Figure 2.5b). These classes are characterized by a mixture of relatively warm waters with high salinity and low turbidity. Most differences within this area are fuzzy, indicating smooth transitions between classes. The only exceptions are the waters of the loop current that identify a well-defined circulation path (region M).

Physical disturbance in the Caribbean Sea

To complement the oceanographic regime, the Caribbean Sea was characterized according to its chronic and acute physical disturbance regime (Figure 2.7). Chronic physical disturbance, represented by wave exposure patterns, changes predictably in the basin according to the prevailing direction of the wind and fetch (Figure 2.7a). The dominant effect of the north-easterly trade winds is clearly visible with land masses sheltering western regions. In general windward areas have higher wave exposure than leeward areas, unless they are sheltered by a land mass (e.g. westward cays of The Bahamas). 2,199 hurricanes have been observed in the Caribbean basin from 1851 to 2008. There is a clear spatial heterogeneity in the distribution of storms across the basin, with higher occurrence in the north and two centres of high activity in the passage between Yucatan and Cuba and east Puerto Rico (Figure 2.7b).

The chronic and acute disturbance regime can be used to refine the physicochemical provinces if relevant for the system under study. The northern Bahamas, for example, encompasses three physicochemical provinces characterized by bathymetry-driven temperature effects (Figure 2.7a) but this simple categorization can be enriched for shallow marine ecosystems by incorporating information on the chronic and acute disturbance regime. While chronic stress highlights spatial variability at the scale of a few kilometres (Figure 2.8b), the acute disturbance regime in the area shows a marked latitudinal gradient (Figure 2.8c).

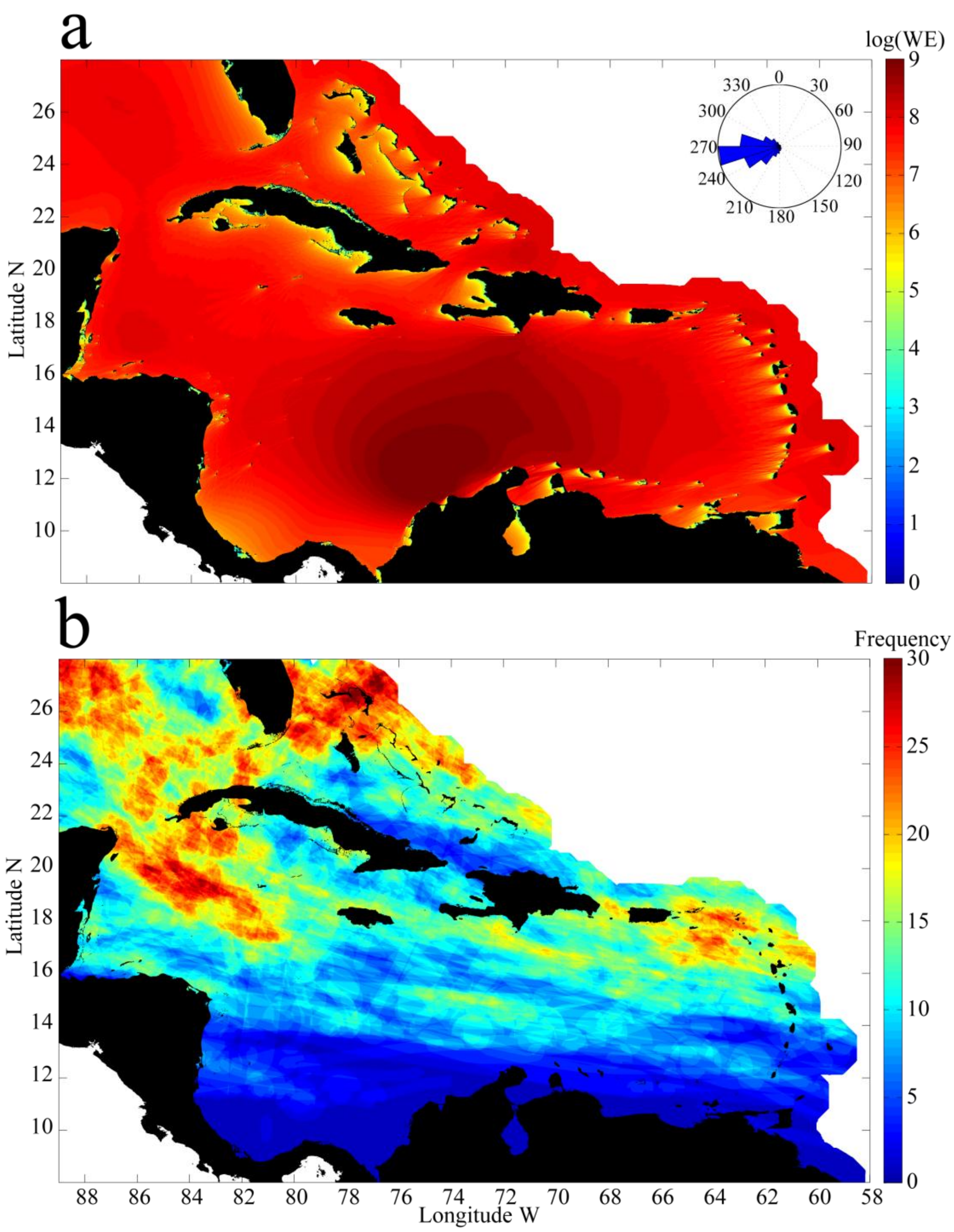


Figure 2.7. Chronic and acute physical disturbance regime. (A) Chronic stress given by wave exposure (Jm^{-3}). The wind rose in the top right corner shows the average wind conditions (1999-2008) for the entire basin; (B) Acute stress given by the frequency of occurrence of hurricanes category 1-5 in the last 157 years (1851-2008).

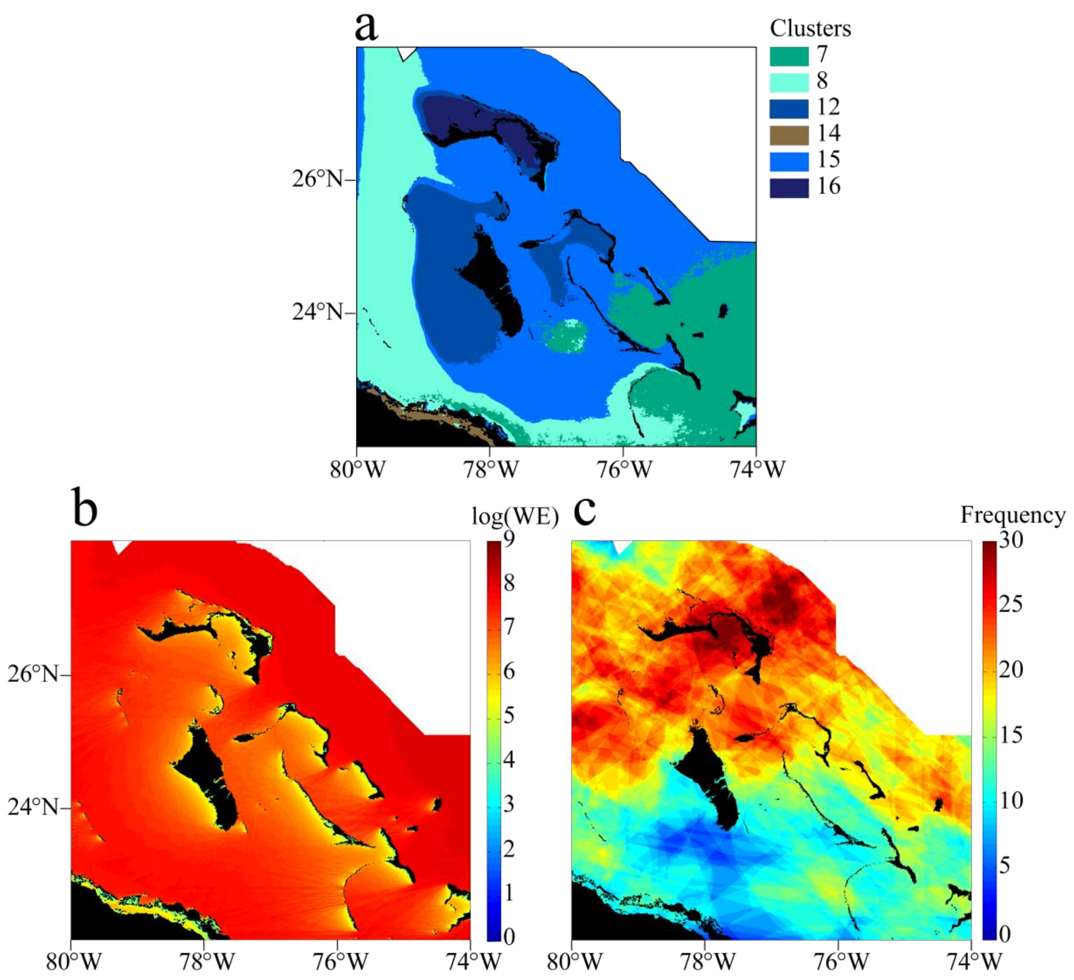


Figure 2.8. Case study of Northern Bahamas. (A) Physicochemical provinces, (B) chronic and (C) acute physical disturbance regime.

Discussion

Information on the physicochemical characteristics of the water masses and the physical disturbance regime was used to produce the hierarchical PECS classification. While the physicochemical classes are arranged in broad-scale spatial patterns, the physical disturbance impose additional pattern that operates over fine spatial scales. The PECS classification offers features that enhance its utility for research and conservation planning at regional scales: comprehensive coverage, a data-driven, objective classification approach, and high spatial detail, consistent with the scale of many research and conservation requirements in the area.

The Caribbean Sea was divided into 16 physicochemical classes, characterized by similar sea surface turbidity, salinity and temperature patterns. Although the input variables are measured at the ocean surface, SST and ocean colour are both strongly correlated to processes in the entire water column (Longhurst 2007; Oliver and Irwin 2008). Thus, the resulting classification has some value for the assessment of pelagic ecosystems in addition to its main focus of benthic systems. An important difference of this categorization compared to former schemes is that it allows regions with similar oceanography to be defined (e.g. broadly distributed turbid areas), enabling regional comparisons of patterns or processes in often distant, but comparable systems. While some regions have well-defined boundaries, indicating the presence of mesoscale features such as river and upwelling fronts, some regions have fuzzy edges indicating transition areas. The resulting classification is consistent with physical oceanographic literature for the basin (Table 2.II). However, precise boundaries should be interpreted cautiously because they indicate *average* locations of rapid change in oceanographic conditions. Many oceanographic features such as river plumes or upwelling fronts can exhibit strong interannual variability (Müller-Karger et al. 1989; Müller-Karger et al. 2004), and therefore have dynamic boundaries that are not captured by this static approach (Oliver and Irwin 2008).

The categorization proposed here does not replace global classification systems (e.g. Longhurst 2007; Spalding et al. 2007; Sherman and Hempel 2009) but provides a more detailed regional product that fulfils regional research and conservation needs. Previous categorizations aim to provide enough detail to support linkage to applied research and conservation (e.g. Spalding et al. 2007); however, several research (Cruz-Motta et al. 2010; Iken et al. 2010; Miloslavich et al. 2010) and management (Mills et al. 2010) assessments have observed a mismatch in spatial scales between these zones and practical applications. While more detailed environmental information has been suggested to better explain biodiversity and distribution patterns (Cruz-Motta et al. 2010; Iken et al. 2010), smaller regions have been highlighted as more suitable for conservation activities because they have more homogeneous natural attributes, human activities and aspects of governance that facilitate management (Mills et al. 2010).

The PECS classification, which is fully available through the author, has a number of research and conservation applications (Table 2.III). PECS is currently being used by researchers in the Caribbean (by the FORCE project) in order to explain basin-wide patterns of coral reef health. We expect the approach will provide an objective framework in which to plan, analyse and interpret research and/or conservation efforts within the basin.

Table 2.III. Issues that would benefit by referencing the PECS classification.

Approach	Issue	Action
A priori	Selection of locations to facilitate comparisons	Choose locations from physicochemical provinces that are similar / contrasting according to the aims of the study
A posteriori	Selection of locations to place results into context	Compare results with locations within the same environmental province
A posteriori	Modelling patterns of marine ecosystem attributes at regional scales	Use environmental province as an explanatory variable
A posteriori	Priority setting and planning	Use environmental province as ecological criteria within selection algorithms

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3

Predicting the distribution of *Montastraea* reefs using wave exposure

Chollett I, Mumby PJ (in review). Predicting the distribution of *Montastraea* reefs using
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Abstract

In the Caribbean region, forereef habitats dominated by *Montastraea* spp. have the highest biodiversity and support the largest number of ecosystem processes and services. Here we show that the distribution of this species-rich habitat can be explained by one environmental predictor: wave exposure. The relationship between wave exposure (easily obtained from wind and coastline data) and the occurrence of *Montastraea* reefs was modelled using logistic regression for reefs throughout the Belize Barrier Reef, one of the largest and most topographically complex systems in the region. The model was able to predict correctly the occurrence of *Montastraea* reefs with an accuracy of 81%. Consistent with historical qualitative patterns, the distribution of *Montastraea* reefs is constrained in environments of high exposure. This pattern is likely to be driven by high rates of chronic sediment scour that constrain recruitment. The wide range of wave exposure conditions used to parameterise the model in Belize suggest that it should be transferable throughout much of the Caribbean region, complementing traditional habitat mapping and global efforts to map reef extent.

Keywords: Millennium Coral Reef Mapping Project, habitat prediction, chronic disturbance regime.

Introduction

Shallow reef ecosystems play an important role in supporting biological diversity, ecosystem processes and ecosystem services (Moberg and Folke 1999). However, not all reef habitats are equal and some contribute disproportionately to certain ecosystem processes (Harborne et al. 2006b). An analysis of the value of Caribbean reef habitats, based on field survey data, qualitative reports and expert opinion, found that *Montastraea*-dominated forereef habitats (hereafter '*Montastraea* reefs') consistently had the highest abundance and richness of benthic and fish species, and were the greatest contributor to ecosystem processes and services, including tourism and fisheries (Mumby et al. 2008). *Montastraea* reefs were originally defined by Geister (1977) in his description of the zonation of Caribbean reef systems. They are typically dominated by two or more members of the *Montastraea* species complex (*M. annularis*, *M. faveolata*, and *M. franksi*) and have high structural complexity. The high ecological and societal value of *Montastraea* reefs raises their importance for conservation planning (Edwards et al. 2010) and because planning is a spatial process (Pressey 2004), it follows that maps of the distribution of *Montastraea* reef would be invaluable for reef management.

Mapping of reef habitats has traditionally been carried out using optical satellite products, which allow mapping geomorphological zones of reefs (e.g. forereef, reef crest, lagoon) with reasonable accuracy (Green et al. 1996; Mumby et al. 2004; Andréfouët et al. 2006). However, the discrimination of habitats within each geomorphological zone has proved challenging for optical satellite data (Green et al. 1996; Mumby et al. 1997), especially when the landscape is complex and includes several habitat types (Andréföuet et al. 2003). In order to accurately map coastal habitats, higher spectral resolution (number and width of spectral bands), which allow to detect subtle differences in reflectance between some habitats (e.g. seagrass vs. algal beds or coral reefs vs. gorgonian plains) is needed (Mumby et al. 2004). As a result, recent global mapping programs have confined themselves to geomorphological classification schemes (Andréfouët et al. 2006) rather than schemes based on the ecological habitat (Mumby and Harborne 1999). At local scales, some constraints of optical remote sensing have been overcome by complementing information provided by optical remote sensing with that provided by acoustic sensors that resolve water depth, together with the roughness and hardness of the seabed (e.g. White et al. 2003; Riegl and Purkis 2005; Walker et al. 2008; Bejarano et al. 2010). However, a satellite-based method for mapping reef habitats would likely be the most cost-effective option for mapping at scales that exceed tens of kilometres. In order to avoid the spectral limitations of optical satellite sensors, an entirely different approach is needed to map reef habitats; one that relates the distribution of the habitat to a metric that can be mapped from satellites. Predictive habitat models of this type are widely used to map species or communities (Guisan and Zimmermann 2000) and their efficacy will depend on the strength of the relationship between habitat distribution and independent predictors. Thus, the first challenge is choosing the most appropriate predictor variable.

Over millennial time scales the distribution of major reef habitats depends on the interaction between reef developmental processes and the oceanic physical environment (Stoddart 1969; Done 1983; Fagerstrom 1987). The role of wave exposure as a major control of reef distribution has long been acknowledged (Sheppard 1982; Done 1983; Graus and Macintyre 1989). Wave energy affects the organisms directly, by acting as a mechanical stress (e.g. Denny 1994), and indirectly, by affecting temperature (e.g. West and Salm 2003), sediment flux (e.g. Wolanski et al. 2005), nutrient intake (e.g. Hearn et al. 2001) and productivity (e.g. Dennison and Barnes 1988; Hurd 2000). Several studies have found a qualitative relationship between reef distribution and wave energy, loosely classifying the latter by indices of ranked severity (e.g. Geister 1977; Dollar 1982; Done 1983). The use of such qualitative approaches to account for wave exposure is largely due to the lack of availability of *in situ* wave data. However, wave exposure can be easily measured using cartographic indices (e.g. Ekebom et al. 2003; Tolvanen and Suominen 2005), and can be accurately estimated using simple physical models based on the configuration of the coastline and the regional meteorological conditions (Denny and Gaylord 2010). A few studies in coral reef ecology have used cartographic indices as proxies for wave exposure, such as a measure of the openness of the location (e.g. Wesseling et al. 1999), sometimes accounting for wind direction and intensity (e.g. Garcon et al. 2010) but to our knowledge this approach has only been used once in the Caribbean, in order to model beta diversity in the US Virgin Islands (Harborne et al. 2006a).

Montastraea reefs have typically been associated with “relatively sheltered” areas (Geister 1977,1980; Graus and Macintyre 1989). Here, we use a quantitative measure of wave exposure (merely driven by freely available satellite wind and coastline data) to quantify this relationship explicitly.

Methods

The study area includes the Belize Barrier Reef, the Ascension and Espiritu Santo bays and Banco Chinchorro in Mexico (Figure 3.1). The Belize Barrier Reef is the largest reef system in the Atlantic Ocean, and is composed of a 257 km-long barrier reef and three isolated atoll-like structures: Glovers Reef, Lighthouse Reef and Turneffe Islands. The lagoon between the barrier reef and the mainland is 20-40 km wide, shallow (~ five m depth) in the north and deeper (~ 50 m depth) in the south (Burke 1982). This area is ideally suited to quantify the effects of wave exposure as it is subjected to unidirectional trade winds (Koltes et al. 1998) and has a complex coastline. Wind-driven waves produce high wave exposure in unsheltered areas. Landmasses and surface-breaking barrier reef and atolls dissipate wave energy allowing for regions with low wave exposure. Consequently, the study area encompasses much of the wave energy spectrum and is not constrained to high or low energies.

The target habitat for this study was shallow to mid-depth forereefs dominated by colonies of the *Montastraea annularis* species complex (Knowlton et al. 1992). Data describing the presence or absence of the habitat in the forereef were collected during field campaigns between 1991 and 2009 (Figure 3.1). Field surveys were carried out by one of the authors (PJM) and involved detailed sampling along the reef (i.e., parallel to the reef crest) at intervals ranging from 500 m to three km. Each site measured approximately 100 m in the plane parallel to the crest and encompassed a depth range of approximately five to 30 m. The main alternative habitats were low-relief gorgonian hard bottom and sand (Mumby and Harborne 1999). A total of 386 sample sites were included in the analysis, 193 for habitat absence (where gorgonian plains and sand were dominant) and 193 for habitat presence (where *Montastraea* reefs were dominant). Although data were collected over a long time interval, no site would have shifted between habitat state seeing as this would involve geological time scales and even areas with mostly dead *Montastraea* colonies were still (functionally) categorised as *Montastraea* reef.

Wave exposure (i.e. the degree of wave action on an open shore), is governed by the distance of open sea that the wind has blown over to generate waves (fetch), and the strength and direction of the winds. . The quantification method is based on the reasoning that the longer the distance over which the wind blows without encountering obstructions (fetch) and the stronger the wind, the larger the waves can develop and the higher the exposure. We assessed fetch from maps produced by the Millennium Coral Reef Mapping Project (MCRMP: Andréfouët et al. 2006) and publicly available on the web at the Institute for Marine Remote Sensing (University of

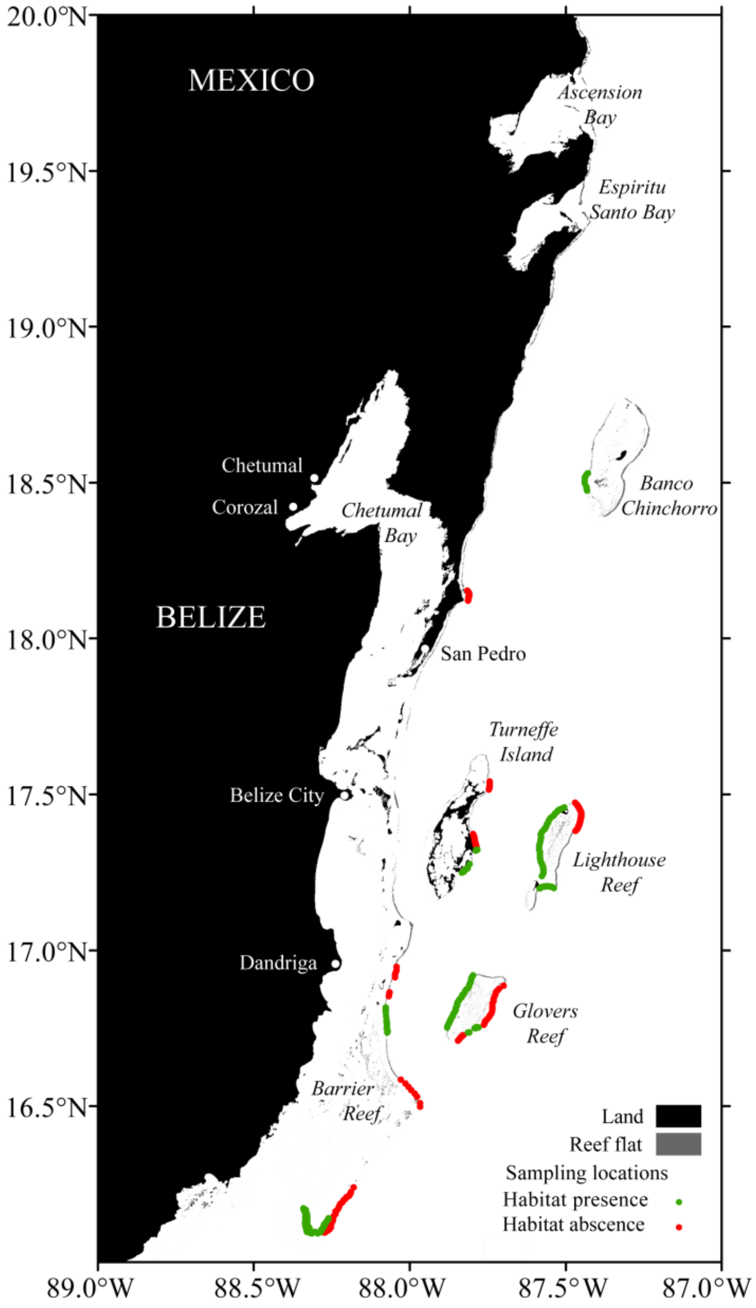

Figure 3.1. Study area (16-20°N, 87-89ºW) and ground truth locations.

South Florida) website (http://imars.usf.edu/MC/index.html). Both land masses and reef crests are capable of hindering the action of the waves, particularly in locations such as the Belize Barrier Reef System where offshore coral formations are common. Therefore, fetch was calculated by tracing a line from each marine location across the sea until either land or a reef crest was encountered. The fetch calculation proceeded as follows: first, a base map was produced from the MCRMP imagery by identifying land and reef crest locations. The map (in vector format) was converted to a raster where each pixel had a spatial resolution of 50 m. Finally, fetch in 32 compass directions (each with an angular width of 11.25º) was calculated with the aid of a Java program developed by David Finlayson and freely available online (http://sites.google.com/site/davidpfinlayson/Home/programming/fetch).

Wind speed and direction were obtained from QuikSCAT satellite scatterometer data (from 1999 to 2008), also publicly available on the internet through the company Remote Sensing Systems (http://www.ssmi.com/qscat/), among other sources. Wind data, originally at approximately 25 km spatial resolution, were rescaled to 50 m using bicubic interpolation prior to the analyses. By doing this, we are assuming the wind data is homogeneous within the 25 km area, a similar assumption to that taken by most researchers working with cartographic indices of wave exposure, which include data from one *in situ* climatological station in order to reflect the wave exposure patterns of large areas (e.g. Ekebom et al. 2003, Harborne et al. 2006a). Wave exposure (in Joules m^{-3}) was calculated using the method described by Ekebom et al. (2003), where the exposure of a location is a function of the shape of the basin, wind speed and direction (equations can be found in Appendix 3.1). This method based on wave theory includes equations for “fetch-limited” and “fully-developed” seas, because for a given wind speed and long fetch there is a fixed limit to which a wave can grow. The original method was modified to account for: (i) inclusion of reef crests into the calculation of fetch, because surface-breaking reef structures can obstruct waves; (ii) inclusion of spatial variability in wind fields using gridded wind data, because of the large size of the study area (previous studies analysed areas of dozens of kilometres and used a single source of wind velocity); (iii) calculation of daily wave exposure and then producing an average for the entire time period, instead of using the average wind speed in each of the main directions (e.g. Ekebom et al. 2003). This approach allows inclusion of strong, albeit sporadic, winds which have a disproportionate influence on wave energy yet their influence would be mostly lost if the analysis was confined to mean wind speed. (iv) Inclusion of “fully-developed” seas (see Harborne et al. 2006a) which were missing from previous studies carried out in areas that were always fetch-limited (e.g. Ekebom et al. 2003; Allen et al. 2007).

Statistical methods: The probability of encountering a *Montastraea* reef in the Belize Barrier Reef was modelled by fitting a logistic regression to the ground truth data (i.e. response variable, which indicates the presence or absence of the habitat), with the logarithm of wave exposure as the only explanatory variable. Performance of the model was evaluated using cross-validation: the dataset was split randomly in two groups, using 75% of the observations for model fitting and 25% for model evaluation, and repeating the procedure 1,000 times. The model calculates the probability of habitat occurrence based on the predictor and a threshold probability (the one that provides the best crossover of accuracy rates: Fielding and Bell 1997). Accuracy was represented using: (i) sensitivity (the proportion of correctly classified habitat locations); (ii) specificity (the proportion of correctly classified non-habitat locations); (iii) proportion of false positives; and (iv) proportion of false negatives. Averages are reported with their 95% confidence intervals.

Results from the modelling procedure were used to produce a map with the potential distribution of *Montastraea* reefs within the study area. In order to obtain probability values on the scale of the original response variable an inverse logistic transformation was applied:

$$p_i = \frac{e^{g(x_i)}}{1 + e^{g(x_i)}} \qquad (1)$$

Where $g(x_i)$ is the linear predictor fitted by the logistic regression.

Results

Wind in the region of the Belize Barrier Reef stem mainly from the north-east and dominate the patterns of wave exposure (Figure 3.2A). Windward areas have higher wave exposure than leeward areas, unless they are sheltered by an island or a reef crest.

By calculating wave exposure from daily wind estimates instead of climatological averages, the sporadic effect of strong winds that have a disproportionate influence on the instantaneous wave exposure (because of the geometric relationship between wind and wave height and wave height and wave energy, Appendix 3.1) was accounted for. Higher overall wave exposure estimates were obtained using daily exposure values than when the conventional climatological approach was taken (Figure 3.2B). Furthermore, differences between the two methods were heterogeneous across the study area. This highlights the significance of using the daily approach in regions with a complex coastline and temporal variability in wind speed and direction, where small changes in the direction of the wind can produce strong impacts in the overall wave exposure experienced at a given location. The logistic regression model was fitted using the more representative daily approach.

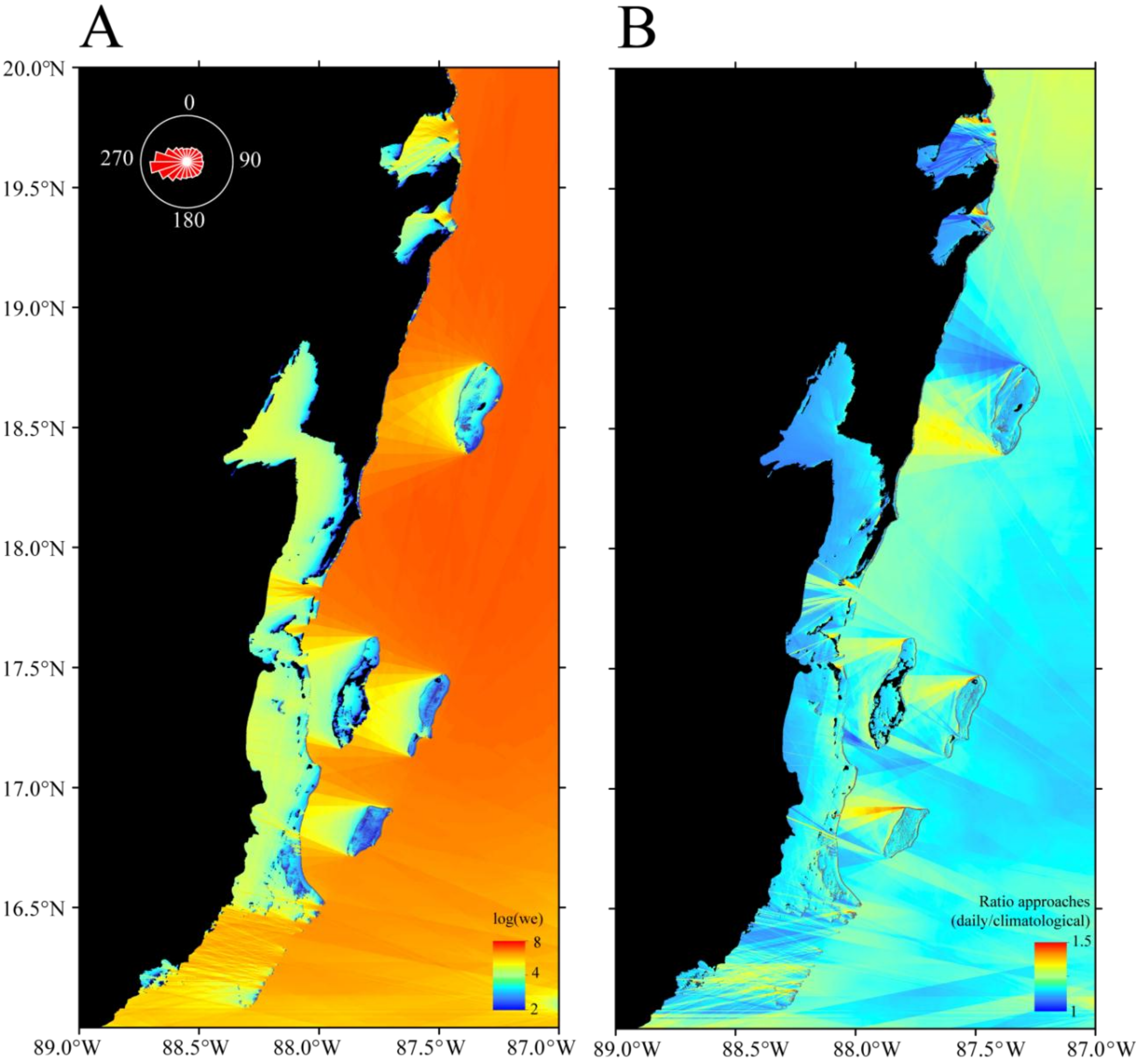

Figure 3.2. (A) Logarithm of average wave exposure (J m^{-3}) for the Belize Barrier Reef. Wind rose in top left corner shows the average wind distribution for the entire area (QuickSCAT data, 1999-2008). (B) Ratio between wave exposure calculated using the daily approach (Figure 3.2A) and the climatological approach commonly followed in the literature. Values of one indicate where estimates with both approaches are identical.

The logistic model (Table 3.I) explained almost half of the null deviance, and the linear predictor (see Equation 1) has the form:

$$g(x_i) = 12.34 - 2.00 * \log(WE_i) \quad (2)$$

Table 3.I. Regression coefficients, standard errors, t-values and p-values for the logistic model of prediction of *Montastraea* reefs.

Term	Regression Estimate	Standard error	t-value	p-value
Intercept	12.34	1.37	9.01	<2e-16
Log WE	-2.00	0.21	-9.42	<2e-16
Null deviance	535.11			
Residual deviance	290.82			

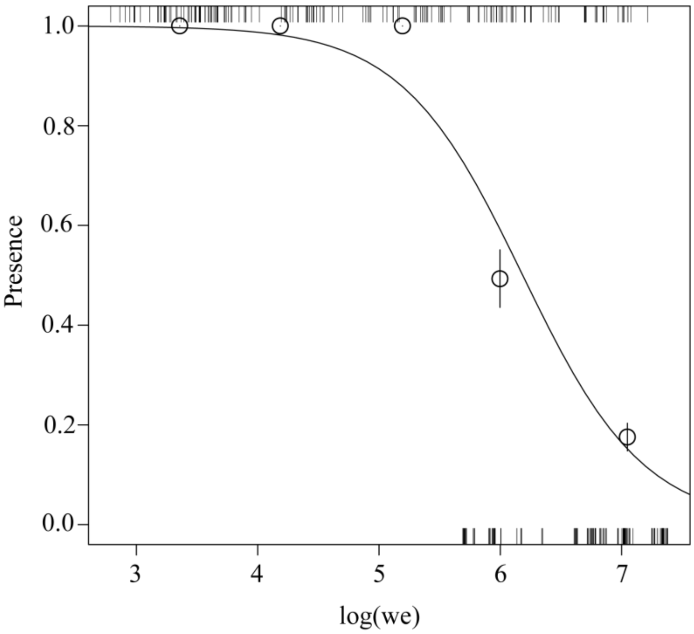

Figure 3.3. Predicted probability of presence of *Montastraea* reefs against the logarithm of wave exposure. Dents on the x axes show ground truth wave exposure values for presence (1) and absence (0) of habitats. On the plot area, the continuous line shows the fitted model, and the circles and whiskers show the average and standard error of presence/absence data for five categories of wave exposure.

The proportion of *Montastraea* reefs increases significantly with decreased wave exposure (Table 3.I, Figure 3.3). The logistic curve provides a good fit to the data when wave exposures was < 5.5 log(J m^{-3}), which is perhaps not surprising, given that there were no “absent” habitats sampled at that energy. The quality of the fitting decreases at higher wave exposures, when both the presence and absence of habitats is likely. At extreme values of the wave exposure gradient, the presence of forereef habitats is unlikely.

In order to carry out the validation of the model, a threshold criterion that allows contrasting the continuous probability generated by the classifier with the dichotomic ground truth data needs to be selected. If the threshold changes, the values in the error matrix (Table 3.II) would change. We chose a p-value of 0.4, which represents the value when the classification rates cross (Figure 3.4). This way, we are giving equal importance to false positive and false negative errors. This threshold can be revised according to the intended application of the classifier, if other user decides that sensitivity is more important than specificity or vice versa.

The model performed similarly for the prediction of habitat presence and absence, and sensitivity and specificity had the same value (81%: Table 3.II). Both false positives and false negatives were relatively uncommon, at rates of about 19%. In general the model achieved a good fit to data with an overall accuracy of 81%. These indices of classification performance have been calculated using models fitted with 75% of the data available, and therefore overestimate the actual error rates (Fielding and Bell 1997). The final model (Equation 2) using all the data is expected to have superior performance in predicting the distribution of *Montastraea* reefs.

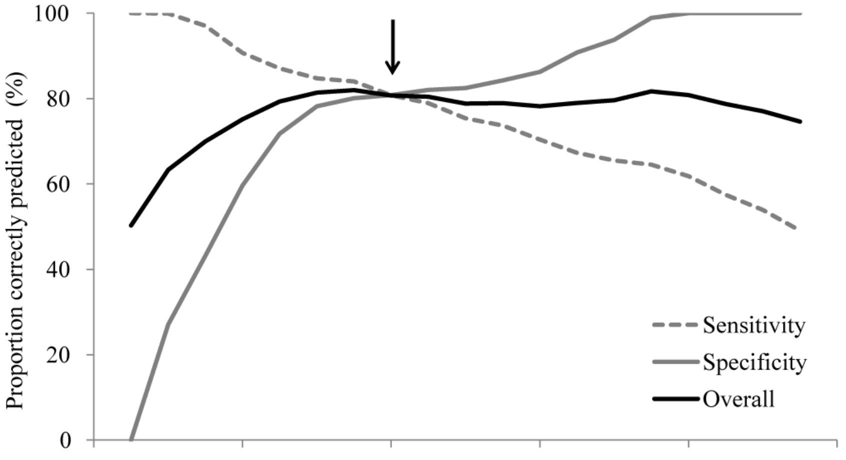

Figure 3.4. Effect of the selected p-value on the three error rates of the predictive model (overall accuracy, specificity and sensitivity). The cut-point selected, when the classification rates cross, was indicated with an arrow.

Table 3.II. Error matrix describing the agreement between the observed and predicted presence and absence of *Montastraea* reefs using a cut-off value of 0.4. Average and 95% confidence intervals of observed frequencies from 1,000 trials, where 75% of the observations were used for model fitting and 25% for evaluation.

	Predicted		
Observed	Presence	Absence	% Correct
Presence	38.69 [38.44 38.94]	9.25 [9.07 9.42]	80.77 [80.43 81.11]
Absence	9.25 [9.09 9.41]	38.82 [38.57 39.07]	80.77 [80.46 81.09]
Overall accuracy			80.73 [80.52 80.95]
False positive			19.24 [18.93 19.55]
False negative			19.16 [18.83 19.49]

The predicted habitat distribution map (Figure 3.5A) shows the probability of occurrence of *Montastraea* reefs across the Belize Barrier Reef. The likelihood follows the opposite trend that the wave exposure patterns (Figure 3.2A), with lower probabilities of occurrence of the target habitat in exposed areas. The map shows dramatic changes in probability across the scale of a few kilometres. Large scale changes occur at leeward and seaward sides of the atolls, however, small scale variations are associated to changes in aspect (when the coast suddenly changes direction) due to the presence of bays or capes, or along simple coastlines when the effect of the shadow of an island is no longer taking place. Note that it is more accurate to confine the map of predicted habitat to those areas of forereef (Figure 3.5B) although this is not so easy to read at the scale reproduced here (hence inclusion of Figure 3.5A for the entire seascape). A detail of Figure 3.5B showing the predicted habitat distribution map for Lighthouse reef is shown in Figure 3.6. This figure shows an interesting “pocket” of relatively low wave exposure and high probability of finding the habitat on the windward side of the atoll, highlighting the influence of wave exposure at detailed spatial scales.

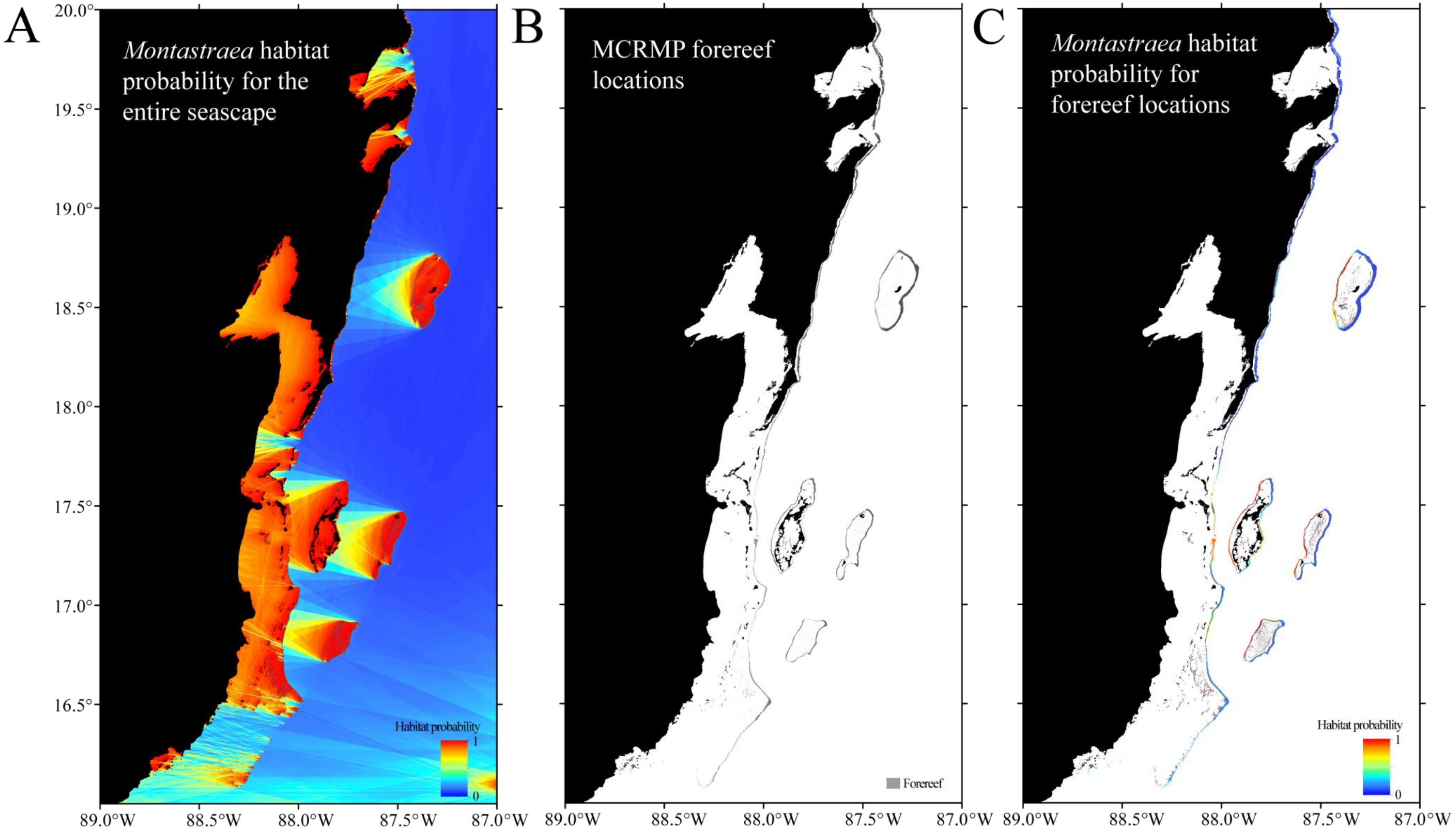

Figure 3.5. Predicted likelihood of *Montastraea* reefs in the Belize Barrier Reef. (A) Map for the entire seascape. (B) Forereef locations according to the MCRMP. (C) Map showing only predictions in forereef areas as identified by the MCRMP.

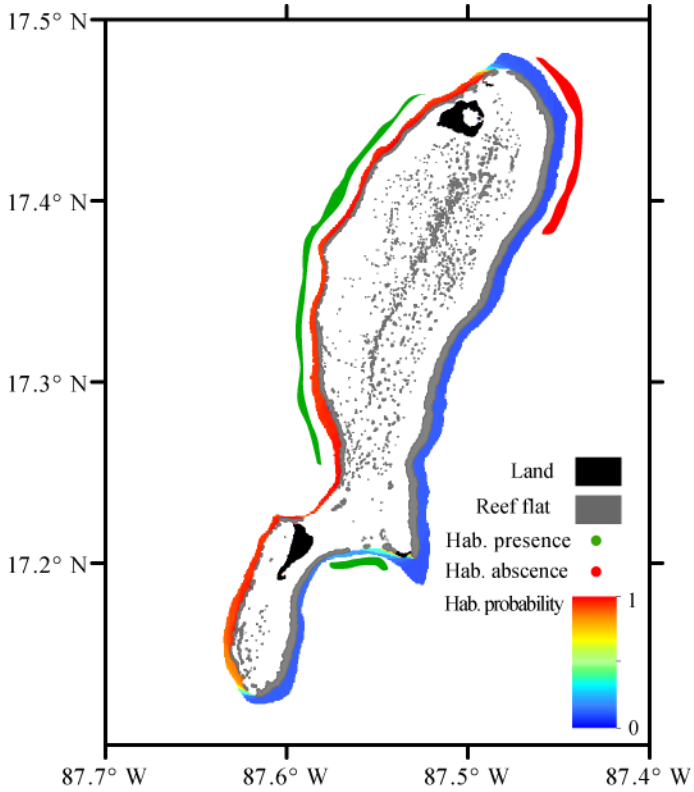

Figure 3.6. Predicted likelihood of *Montastraea* reefs in forereef areas (as identified by the MCRMP) of Lighthouse reef. Ground truth areas were represented outside the forereef in order to improve readability.

Discussion

Most structurally-complex Caribbean forereefs are dominated by colonies of massive corals from the *Montastraea annularis* species complex (Knowlton et al. 1992) and the role of *Montastraea* as a major reef framework builder is well established (Mesolella 1967; Jackson 1992). This group plays critical roles in reef accretion and community ecology, providing a framework that hosts a rich species assemblage (Goreau 1959). Across the Belize Barrier Reef system, the distribution of *Montastraea* reefs can be explained largely by patterns of wave exposure: the habitat is strongly associated with sheltered areas where wave exposure is less than 5.7 log(J m^{-3}). Conversely, the habitat is restricted at high values of wave exposure (above 7.2 log(J m^{-3})). Boundaries between these two states are fuzzy, and for intermediate values of exposure, habitats can be present or absent. Wave exposure, and therefore the probability of encountering *Montastraea* habitats, changes dramatically in a scale of a few kilometres (Figure

3.6). To our knowledge, wave exposure is the only environmental factor able to explain heterogeneity in habitat distribution at such detailed spatial scale. These results support historical qualitative patterns described in the Caribbean region (e.g. Geister 1977,1980; Burke 1982). Mixed membership at intermediate levels of wave exposure might be caused by other environmental factors that operate at local scales and preclude the occurrence of the habitat, such as depth, antecedent morphology, irregularities in underlying topography or differences in the type of substrate (Geister 1977). Additionally, classification errors can arise from inaccurate estimations of wave exposure given by limitations of the modelling approach (see below).

The method used here to estimate wave exposure incorporates information on the geomorphology, fetch (given by the configuration of the coastline) and the wind climate. All three elements are needed in order to predict where reefs are more likely. Wave exposure was calculated using wave theory. The method is a simple approximation of wave patterns in shallow areas, and does not include non-linear energy transfer due to wave interactions and energy dissipation due to wave breaking and bottom friction which also influence the resulting wave environment. Although further refinements to this method using wave generation models (e.g. Booji et al. 1999) could improve estimates of wave exposure, the implementation of those methods is computationally more demanding and would require the use of specialized 3-dimensional models. Even though they require caveats, simple methods based on the configuration of the coastline and wind patterns have repeatedly been shown to be sufficient predictors of spatial variation in coastal communities (e.g. Burrows et al. 2008, Hill et al. 2010, Harborne et al. 2006a) and has shown here to be an appropriate predictor of the distribution of *Montastraea* habitats. The method uses daily wind data. We recommend using this approach when daily data are available, because they better capture the wave environment in any given location when related to the climatological approach. Furthermore, the daily approach provides a more representative output with no overhead in processing time. By using daily data diurnal variations in wind speed and direction are overlooked; however, diurnal variations in wind are likely to be smaller than seasonal ones in the Mesoamerican reef. Differences in wave exposure between the climatological and the daily approach are spatially heterogeneous (Figure 2B). The differences are larger along areas with variable wind speed or in promontories where small differences in wind direction can have a major impact on fetch and therefore exposure. We anticipate that the use of the climatological approach might be more appropriate in areas where winds are less variable and the coastline is less complex.

Ecological drivers of distribution patterns

The distribution of *Montastraea* reefs in the Belize Barrier Reef follows a chronic perturbation pattern with wave exposure. There are at least three ecological scales at which causative mechanisms might operate and we consider each below: (i) the supply of larvae; (ii) the recruitment of larvae; and (iii) the mortality of adults.

The role of reefs and coastlines in modifying regional circulation has long been recognized (Hamner and Hauri 1981; Parnell 1988; Wolanski and Hamner 1988; Sammarco and Andrews 1989). The specific effects of wave exposure on retention or accumulation of larvae depends on the interaction of several factors, such as the direction and speed of the prevalent (mesoscale) currents, the tides, the speed of the winds, the size of the island or reef and the spacing between reef/land masses (Hamner and Hauri 1981; Black 1993). While it is feasible that patterns of larval supply and wave exposure are correlated in Belize, it seems highly unlikely that this could account for the distribution of *Montastraea* reefs. Individual *Montastraea* colonies grow for more than 100 years (Hudson 1981), meaning that the habitat develops over hundreds of years. Over this time frame, stochastic fluctuations in larval dispersal would be expected to supply larvae to more exposed areas and permit development of these long-lived corals. The problem with larval supply as a candidate mechanism is highlighted by the tight relationship between wave exposure and habitat distribution even at small scales, such as the southeast corner of Lighthouse reef (Figure 3.6). Here, the habitat distribution is patchy at a scale of only three km, which seems unlikely to be due to persistent patterns of larval supply.

We hypothesize that the mobile nature of sediment in highly exposed areas prevents successful settlement of larvae and subsequent survival, as it has been suggested by other studies (e.g. Jordán 1989). While the hypothesis requires experimental verification, indirect evidence in support of this mechanism stems from studies showing that adhesion of the larvae to the substrate can be hindered in turbulent environments through drag and lift forces (Denny and Shibata 1989; Jonsson et al. 2004); and that it is fairly well-established that mobile substrates, such as rubble, can prevent coral recruitment and induce the mortality of the few successful recruits (Fox and Caldwell 2006; Victor 2008). Conversely, the success of soft corals in exposed environments is mainly related to their rapid growth which allows them to avoid sand burial and scouring and enhance survival by attaining a size scape in a relatively short time when compared with scleractinian corals (Gotelli 1988; Jordán 1989).

Through dislodgment, breakage, scour and abrasion, wave force inflicts mechanical stress producing species-specific patterns of distribution based on the resistance of organisms to such disturbance (e.g. Denny 1994; Storlazzi et al. 2005; Madin and Connolly 2006). However, while colonies of adult *Montastraea* can be removed or exhibit fragmentation during hurricanes (Foster et al. 2007), there is no evidence that chronic forms of disturbance tied to wave exposure cause mortality of adult *Montastraea* that have a robust massive morphology (Bries et al. 2004). Moreover, the morphological plasticity of *Montastraea* allows them to cope with a fairly diverse range of environments (Todd 2008).

Geological context

In the present study we predict habitat distribution using the contemporary environmental setting. However, reef development is controlled by the interaction of the current environmental regime, changes in sea level and antecedent topography (Macintyre 1988). Fossil records have indicated high long-term stability in reef community composition prior to the 1980s (e.g. Mesolella 1967; Geister 1980; Pandolfi and Jackson 2001), when widespread degradation led to the collapse of some Caribbean coral populations (Gardner et al. 2003). During the Holocene, cores in Belize showed the replacement of coral assemblages following similar patterns to modern (pre-1980s) zonation, with turning points in reef development controlled by changes in sea level (Gischler and Hudson 1998,2004). Gischler and Hudson (1998) also showed changes in the dominance of corals in leeward and windward sides of isolated platforms in Belize. Holocene windward reefs were dominated by *Acropora palmata*, a robust shallow water coral, while *Montastraea annularis* was more abundant in leeward Holocene reefs. Differences in species distribution between windward and leeward areas have been also reported in other areas of the Caribbean region (Geister 1980; Pandolfi and Jackson 2001). While the replacement of species shows the persistence of species assemblages during periods of comparative environmental regimes, contrasts in windward and leeward sides of islands imply that the spatial distribution of wave energy has remained similar and that wave exposure has been a major control of reef distribution for the last dozens to hundreds of thousands of years. After each episode of sea level change, a new reef is formed, constituting an independent natural experiment on the role of wave exposure as the driver on the assembly of the new coral community (Jackson and Erwin 2006).

Model efficacy and transferability

To be useful as conservation and management tools, habitat models should be easy to apply, accurate and general (Guisan and Zimmermann 2000). Our model uses publicly available data sets, is computationally simple and correctly predicts the presence and absence of habitats with more than 81% of overall accuracy. The use of an environmental parameter with direct biological influence contributes to the generalization of the model and its transferability to other areas (Guisan and Zimmerman, 2000). When placing wave exposure values for Belize into a regional context (Figure 3.7) it is evident that the modal wave exposure of the Caribbean region coincides with that in Belize. It does, however, have lower values of wave energy than some parts of the Caribbean, because of low wind speeds (Koltes et al. 1998). Thus, Belize represents low to moderate levels of exposure well for the Caribbean but does not represent the highest exposures possible. Given that *Montastraea* reefs were mostly confined to that range of exposure that Belize captures well (from a Caribbean perspective, see Figure 3.3), it seems reasonable to expect the models to transfer widely throughout the Caribbean region.

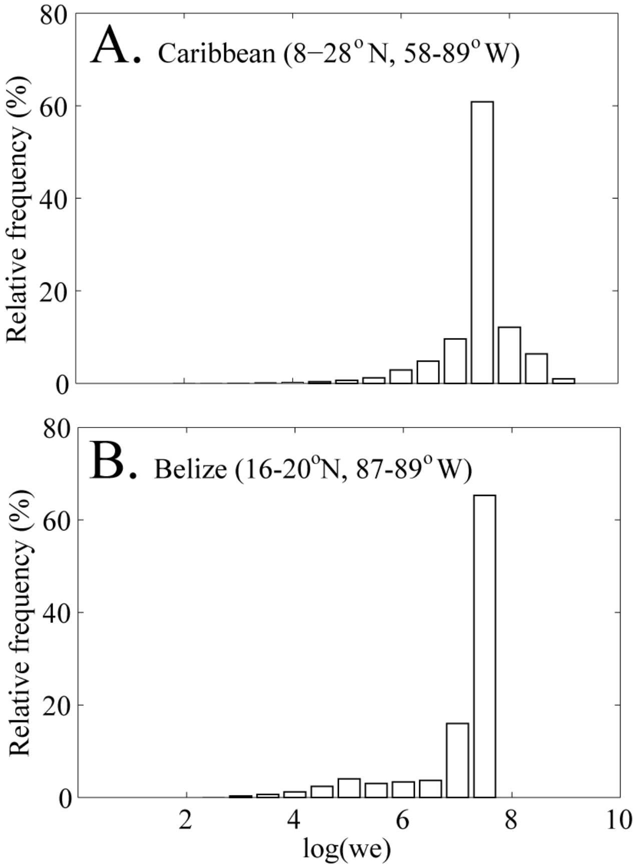

Figure 3.7. Histogram of wave exposure values for the entire Caribbean region (A) and Belize (B). Wave exposure for both regions was calculated using the same approach described in the Methods section but at a coarser spatial resolution (1 km) and using only coastlines provided by the freely available Global Self-consistent, Hierarchical, High-resolution Shoreline Database.

The method presented here allows predicting the location of species-rich reef assemblages found from low to moderate wave regimes. In the whole Caribbean area, this habitat has been dominated mainly by *Montastraea* spp. (Geister 1977). However, our method is equally applicable in comparable habitats where other species might dominate (e.g. Kjerfve 1998, Green et al. 2008).

Wave exposure is a strong correlate of the distribution of *Montastraea* reefs and can be measured relatively easily from satellite data on wind velocity and the locations of reefs and land. Utilisation of such methods to map this ecologically and economically important habitat throughout the wider Caribbean has the potential to improve implementation of a systematic approach to habitat conservation (Ferrier 2002; Possingham et al. 2002; Sarkar et al. 2005).

Appendix 3.1. Algorithm for wave energy calculation

Using the 32 fetch maps and the wind speed and direction for each day, the energy calculation proceeded on a pixel-by-pixel basis as follows (Ekebom et al. 2003):

1. A pixel is classed as fetch limited for this direction if the non-dimensional fetch ξ (Resio et al. 2003) is less than a threshold value of 38,590 m:

   $$\xi = \frac{gF}{U_{10}^2} < 38{,}590 \quad (3)$$

   where g is the acceleration due gravity (9.81 ms^{-2}), F is the fetch in metres and U_{10} the wind speed at an elevation of 10 m in ms^{-1}.

2. If the pixel is fetch-limited then significant wave height (H_{m0}) and period (T_m) can be calculated with:

   $$H_{m0} = 0.00082 \times U_{10}^{1.1} \times F^{0.45} \quad (4)$$

   $$T_m = 0.087 \times U_{10}^{0.46} \times F^{0.27} \quad (5)$$

   Otherwise, if wind and fetch agree with fully-developed sea conditions:

   $$H_{m0} = 0.034 \times U_{10}^2 \quad (6)$$

$$T_m = 0.81 \times U_{10} \quad (7)$$

3. The total energy of the wave system *WE* (J) is proportional to the wave height:

$$WE = \frac{1}{16} \rho g H_{m0}^2 \quad (8)$$

   where ρ is the density of sea water (1,030 kgm^{-3}).

4. When steps up to three have been performed for each of the *t* time periods (i.e. days) then the average energy, *E*, in joules can be calculated as the geometric mean of the individual energy estimates.

The transition between fetch-limited and fully-developed seas was identified using the concept of non-dimensional fetch (Resio et al. 2003) and following the approach of Harborne et al. (2006a). In order to find the transition point, equation (5) was written in terms of the non-dimensional fetch ξ (equation 3):

$$T_m = 0.047 \times U_{10} \times \xi^{0.27} \quad (9)$$

The transition occurs when the T_m values from equations (9) and (7) are equal: when the non-dimensional fetch = 38,590 m. Note that the distances beyond which there is no fetch limitation for wind speeds of 1, 5, 10 and 20 ms^{-1} are therefore four km, 98 km, 393 km and 1573 km.

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4 Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico

Chollett I, Müller-Karger FE, Heron S, Skirving W, Mumby PJ (submitted). Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico. Marine Pollution Bulletin

Abstract

Recent changes in temperature have affected the physiology and phenology of marine organisms and impacted ecosystem function across the globe. Nevertheless, the nature of the responses has depended upon the rate of change of temperature and the season when the changes occur, which are spatially variable. A rigorous statistical analysis of sea surface temperature observations collected using the Advanced Very High Resolution Radiometer satellite-based sensors over 25 years (1985-2009) was used to examine spatial variability in overall and seasonal temperature trends within the Caribbean Sea and the south-eastern Gulf of Mexico. The Caribbean has experienced high spatial variability in warming rates. Significant warming rates were, however, always positive, and ranged from 0.10 to 0.54°C decade^{-1}. The eastern Caribbean basin and the area dominated by the Loop Current in the Gulf of Mexico showed the highest warming trends. Higher latitude and upwelling areas showed no significant long-term changes in temperature. Most of the warming has been due to increases in summer (June-August) rather than winter (December-February) temperatures. However, warming was faster in winter in the Loop Current area and the south-eastern Caribbean, where the annual temperature ranges have contracted. Waters off Florida, Cuba and the Bahamas had a tendency towards greater cooling in winter, increasing the amplitude of annual temperature ranges. These highly detailed spatial and temporal patterns can be used to elucidate observed ecological responses to climatic change in the region.

Keywords: Remote Sensing, AVHRR Pathfinder, climate change

Introduction

Global sea surface temperatures (SSTs) are rising. Over the past 150 years global mean SSTs have increased by 0.04°C per decade (Trenberth et al. 2007). Recent temperatures are changing at a much faster rate than in the past: since 1979, the global rate of warming has increased to 0.13°C per decade, and is projected to continue to rise (Trenberth et al. 2007).

Changes in temperature are a general public concern (Patz et al. 2005; Solomon et al. 2007), but, from a biological perspective, consequences on the dynamics of marine organisms, brought about through changes to their physiology and phenology are of main significance. Temperature regulates a large number of physiological functions in all organisms (Gillooly et al. 2001; Gillooly et al. 2002; Brown et al. 2004). Increased temperatures can have either a positive or negative effect on physiological processes, depending on whether or not organisms are currently close to their thermal optimum for that particular function (Huey and Stevenson 1979). Effects of increased temperatures on the physiology of marine organisms include increased developmental and growth rates (e.g. Lough and Barnes 2000; Gillooly et al. 2002), decreased reproductive output (e.g. Philippart et al. 2003; Ruttenberg et al. 2005), increased prevalence of disease (e.g. Harvell et al. 2002; Sato et al. 2009), reduced planktonic life (e.g. O'Connor et al. 2007; Munday et al. 2009), and increased mortality (e.g. Gagliano et al. 2007; Rankin and Sponaugle 2011).

The rate of warming determines the response of the organisms and their ability to acclimatize (Peck et al. 2009; Rezende et al. 2011). Although warming is occurring at a global scale, rates of warming differ according to the location, with some places even showing long-term cooling (Trenberth et al. 2007). Spatial heterogeneity in temperature trends has been observed at basin scales (Andersen et al. 2002; Rayner et al. 2006; Good et al. 2007; Strong et al. 2008; Demarcq 2009) and also at regional scales (Peñaflor et al. 2009; Saulquin and Gohin 2010). This variability implies that temperature-induced changes in marine organisms will likely vary dramatically, and sometimes in contrasting directions, within a given study area.

Changing temperatures can also affect the phenology of marine organisms, that is, the timing of life-history events. Seasonal changes in the temperature of the water affect the migration of many species (e.g. Solow et al. 2002; MacLeod et al. 2006) as well as the timing of gametogenesis and therefore spawning or nesting time (e.g. Colin 1992; Olive 1995; Baird et al. 2009). Changes in phenology of marine species in response to recent changes in temperature have already been reported in different parts of the globe (e.g. Philippart et al. 2003; Weishampel et al. 2004). Global and regional analyses of SST data have found considerable spatial heterogeneity in temporal properties of SST warming: while some areas are warming evenly all year long, others are warming only in particular seasons (Trenberth et al. 2007; López García and Camarasa Belmonte 2011). Temporal (e.g. seasonal) differences in warming trends are likely to affect organisms differently. For example, the phenology of gametogenesis might be only weakly modified if warming occurs outside the main reproductive season. On the other hand, increases of temperature in summer might be more likely to tip organisms towards upper lethal levels than if warming occurred at cooler times of the year.

To fully appreciate the impact of rising temperatures on organisms and ecosystems, we must first understand the scales of change involved. Here we examined overall and seasonal SST trends throughout the Caribbean Sea and south-eastern Gulf of Mexico. We used satellite imagery for the period 1985-2009 and a statistical method that takes into consideration the complexities of environmental time series (Weatherhead et al. 1998). Although previous studies of satellite-based SST trends have included the Caribbean in their analyses (Strong et al. 2000; Strong et al. 2008; Demarcq 2009), our study is the first to resolve detailed spatial patterns within the Caribbean region. Further, previous studies have not assessed seasonal patterns in SST changes or employed statistical methods better suited for the detection of reliable trends in SSTs. Although our study is motivated by describing spatial and temporal patterns of changing SSTs, we anticipate that such trends will lead to the testing and generation of hypotheses across a wide range of fields because temperature has such a fundamental impact on biological function and ecosystem integrity.

Methods

Dataset

Satellites have supplied information about SST of the global oceans since the 1980s. To date, the National Oceanic and Atmospheric Administration (NOAA) Pathfinder Project (Kilpatrick et al. 2001) provides the longest consistent and continuous global SST dataset, with a very detailed spatial resolution (4 km). Trends in SST have been detected using Pathfinder data at global (e.g. Strong 1989; Lawrence et al. 2004; Good et al. 2007; Strong et al. 2008) and regional (e.g. Ginzburg et al. 2008; Peñaflor et al. 2009; Saulquin and Gohin 2010) spatial scales.

This study covers the Caribbean Sea, the south-eastern Gulf of Mexico, the Bahamas and Florida (8-28°N, 58-89°W, Figure 4.1). We used the Pathfinder v5.0 SST data derived from the NOAA Advanced Very High Resolution Radiometer (AVHRR: Kilpatrick et al. 2001; Casey et al. 2010). The spatial resolution was approximately four km for daily global images for 1985-2009. The Pathfinder SST accuracy is 0.1-0.5 ºC (Kilpatrick et al. 2001). Weekly composites were constructed and data gaps (i.e., no valid data of quality level four or greater; Kilpatrick et al. 2001) were filled by interpolating in time and then by interpolating spatially following the approach described by Heron et al. (2010).

Statistical methods

A number of studies have examined trends observed in satellite SST data using linear methods (e.g. Andersen et al. 2002; Strong et al. 2008; Peñaflor et al. 2009), which allows a simple approximation to the magnitude of SST changes. However, some variability in the time series ought to be considered during trend detection, such as seasonality and serial correlation, which influence the magnitude and significance of the calculated trends (Weatherhead et al. 1998). By incorporating temporal autocorrelation, we account for issues such as an abnormally hot month being usually followed by another particularly hot month, a simple fact that violates the assumption of independence of most regression analyses and influences the precision of the trend estimates (Weatherhead et al. 1998). This approach for the detection of trends has been commonly applied to detect trends in environmental data (e.g. Boers and van Meijgaard 2009; Zhang and Reid 2010), but to date, it has only been used by Good et al. (2007) to assess changes in satellite SSTs.

Monthly means were calculated from the 25 year-long time series of SST and these were used for regression analyses. We estimated linear trends in SSTs following the approach proposed by Weatherhead et al. (1998). Monthly SSTs were fit to a non-linear model with the form:

$$SST_t = \mu + S_t + \frac{\omega t}{12} + N_t \qquad (1)$$

Where *SST* at a given time *t* in months is a function of a constant term μ, a seasonal component S_t, a linear trend ω of rate °C $year^{-1}$ and residuals, N_t, assumed autoregressive of order one (AR-1 autocorrelation form). The seasonal component (S_t) is described by:

$$S_t = \sum_{j=1}^{4} \beta_{1,j} \sin\frac{2\pi jt}{12} + \beta_{2,j} \cos\frac{2\pi jt}{12} \qquad (2)$$

The residual variability (N_t) is described by:

$$N_t = \phi N_{t-1} + \epsilon_t \qquad (3)$$

This way, the residuals at time *t* are a function of the residuals at time *t-1* along with the noise (ϵ_t). The model used a generalized least squares fit and was fitted using the package nlme (linear and non-linear mixed effects) in R. Initial "guess" estimates for μ and ω were obtained through simple linear regression. We fixed an initial value of one for all β's.

The remaining variability ϵ_t was assumed to be random with standard deviation σ_ϵ. This variability, together with the parameter ϕ and the number of years of data, *n*, was used to calculate the error of the trend estimate (σ_ω):

$$\sigma_\omega = \frac{\sigma_\epsilon}{(1 - \phi)\, n^{3/2}} \qquad (4)$$

This implies that the precision of the trend is a function of the magnitude of the unexplained variability in the data, the autocorrelation of the noise, and the length of the time series (Weatherhead et al. 1998).

The number of years of data required to detect the trends described by Equation 1 at the 95% confidence level was also calculated following Weatherhead et al. (1998):

$$n = \left[\frac{3.3\, \sigma_\epsilon}{|\omega|\,(1 - \phi)}\right]^{2/3} \qquad (5)$$

To assess trends in different seasons we divided the year into calendar seasons. This way, we defined winter as December-February, spring as March-May, summer as June-August and autumn as September-November. SST was averaged over these periods for each of the 25 years and the SST trend for each of the seasons was estimated using Equation 6. This included similar parameters as Equation 1 but excluded seasonal effects:

$$SST_t = \mu + \omega t + N_t \qquad (6)$$

While temporal autocorrelation is likely higher in monthly data than in the series of seasonal means, we expect temporal dependency continues to be an important issue at this temporal scale (e.g. Hinkelman et al. 2009).

Finally, we calculated long-term trends in annual temperature range: by subtracting the winter from the summer SST average for each year and measuring how this amplitude changed over 25 years. To this end, we used the same approach described by Equation 6. Unless indicated, we report trends (ω) and associated errors (σ_ω: Equation 4) in °C per decade.

Results

Overall SST trends

The monthly time series of SSTs agrees well with the non-linear model used (Table 4.I, Figure 4.2). As might be expected, the constant term (μ) is higher for locations characterized by warmer SST regimes (e.g. Belize and Barbados). The model seems to accommodate time series of differing seasonal complexity, exhibiting annual (e.g. Northern Bahamas) or semi-annual (e.g. Barbados) components. Model residuals (not shown) do not display temporal patterns and, overall, the model is considered appropriate for the data.

The average trend in SST over the Caribbean Sea and the south-eastern Gulf of Mexico was 0.29°C decade^{-1} (including only significant values), with a range of -0.20 to 0.54°C decade^{-1} (Figure 4.1A). The study area showed spatially heterogeneous temperature trends (Figure 4.1A). The trend estimates exhibited modest (<0.005 °C decade^{-1}) standard deviations across the basin (Figure 4.1B). All significant trends were positive (Figure 4.1). Warming was greatest in the tropical Atlantic and eastern Caribbean Sea (e.g. Barbados, Figure 4.2A) and in the central Gulf of Mexico in the Loop Current region. However, temperature trends were moderate and significant throughout most of the centre and western Caribbean basin (e.g. Belize, Figure

4.2B). Long-term trends were small and non-significant in shelf waters off Florida, Cuba and the Bahamas (Figure 4.2C), in the upwelling area off the Yucatan Peninsula (Mexico, Figure 4.2D) and in the southern Caribbean Sea along the coastal upwelling areas (Figure 4.2E). Standard deviations of the trend estimates, which summarize the variability and autocorrelation of the noise (Equation 4), were higher in the upwelling areas of the southern Caribbean, as well as in the Loop Current region and the shelf waters off the western Florida shelf (Figure 4.1B). Both the size and the standard deviation of the trend estimate contribute to the lack of significance in different areas. When the effect size is small significance will not be achieved. The same occurs in locations with highly variable SST patterns where the noise is greater, or in areas where autocorrelation is large.

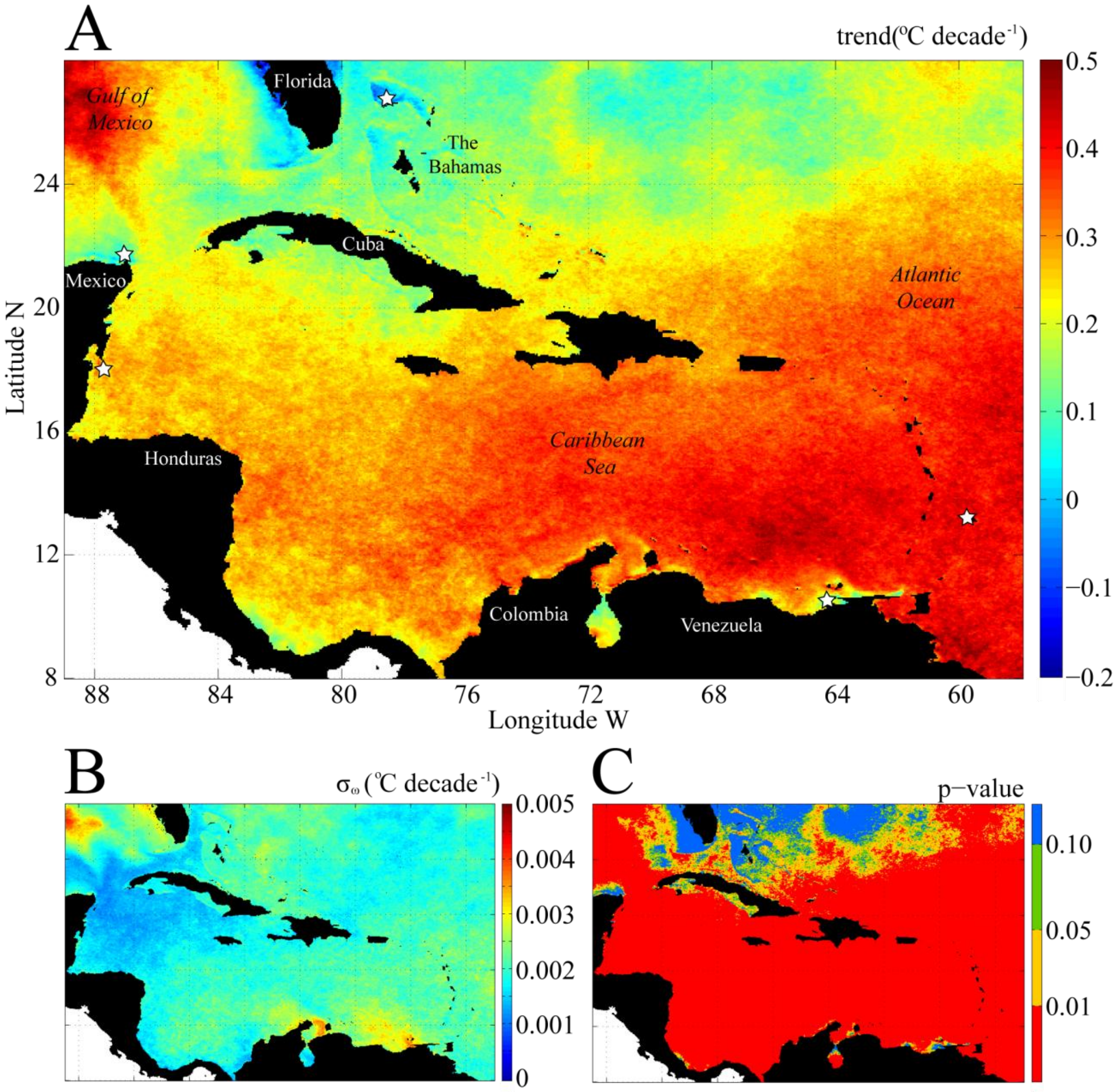

Figure 4.1. (A) Decadal SST trends in the Caribbean; (B) associated standard deviation (Equation 4); (C) significance of the trend. Stars indicate the locations for Table 4.I and Figure 4.2.

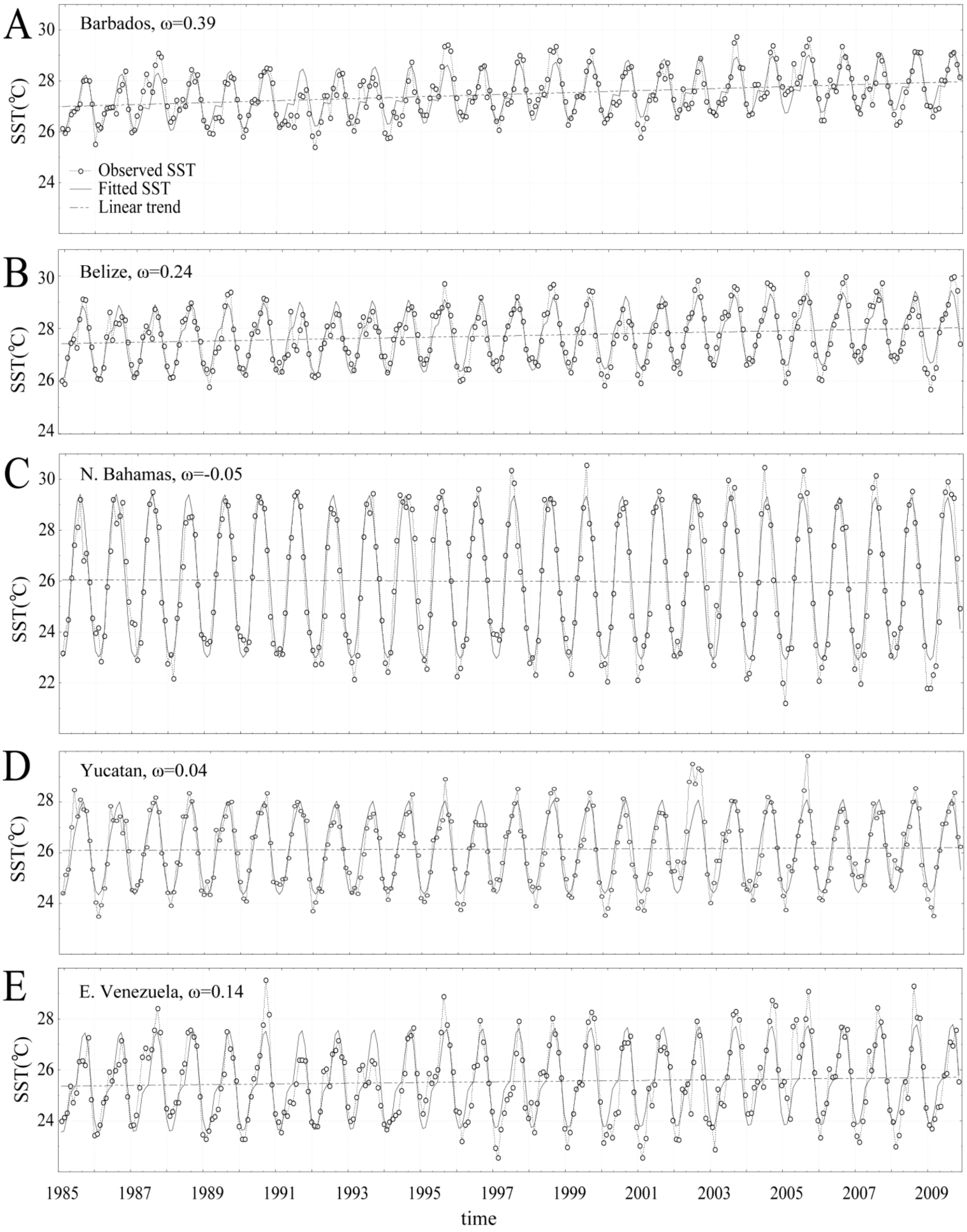

Figure 4.2. Observed monthly SST, model fitting and linear trend (ω) in ºC decade^{-1} in four locations of the wider Caribbean marked with stars in Figure 4.1: (A) Barbados (13.12°N, 59.65°W); (B) Belize (18.00°N, 87.50°W); (C) Northern Bahamas (26.65°N, 78.40°W); (D) Yucatan upwelling (21.68°N, 86.98°W); (E) Venezuelan eastern coastal upwelling (10.44°N, 64.35°W).

Table 4.I. Non-linear random effects parameter estimates (Equation 1) and significance for the five locations marked with stars in Figure 4.1 and plotted in Figure 4.2. Note that the units of ω are annual (not decadal) trends in $^{\circ}$C year^{-1}.

	Barbados		Belize		N. Bahamas		Yucatan		E. Venezuela	
Parameter	Value	p-value	Value	p-value	Value	p-value	Value	p-value	Value	p-value
μ	26.984	<0.001	27.422	<0.001	26.055	<0.001	26.092	<0.001	25.362	<0.001
ω	0.039	<0.001	0.024	<0.001	-0.005	0.567	0.004	0.559	0.014	0.198
$\beta11$	-0.908	<0.001	-0.905	<0.001	-1.595	<0.001	-1.154	<0.001	-1.596	<0.001
$\beta21$	-0.345	<0.001	-0.901	<0.001	-2.928	<0.001	-1.420	<0.001	-0.749	<0.001
$\beta12$	-0.184	<0.001	-0.092	0.007	0.027	0.662	0.055	0.243	-0.258	<0.001
$\beta22$	-0.365	<0.001	-0.255	<0.001	0.195	0.002	-0.193	<0.001	-0.543	<0.001
$\beta13$	0.003	0.897	0.089	0.007	0.141	0.005	0.094	0.011	0.051	0.230
$\beta23$	0.103	<0.001	0.115	<0.001	-0.025	0.610	0.048	0.201	0.085	0.047
$\beta14$	0.011	0.602	0.000	0.987	0.024	0.563	-0.003	0.925	0.031	0.388
$\beta24$	-0.064	0.003	-0.045	0.042	-0.047	0.263	-0.021	0.512	-0.110	0.002
ϕ	0.590		0.523		0.437		0.454		0.563	
σ_{ϵ}	0.441		0.416		0.721		0.550		0.710	

Seasonal SST trends

Seasonal SST trends were larger than trends observed in the overall time series of monthly means (Figure 4.1, 4.3). In general, warming of summer and autumn SSTs was more intense than warming of winter and spring SST in the region (Figure 4.3). Patterns in SST trends in spring and autumn show transition states between the summer and winter extremes. Positive SST trends in summer were significant in most of the study area (Figure 4.3F) with an average of 0.33 °C decade^{-1} (Figure 4.3E). A much decreased, non-significant summer warming was observed in the upwelling areas of Yucatan and the southern Caribbean Sea, as well as in the Lake Maracaibo (Venezuela) and the eastern Florida shelf.

Winter SST trends showed contrasting patterns in the Caribbean Sea and south-eastern Gulf of Mexico (Figure 4.3A). The regional average was 0.18 °C decade^{-1}. However, many pixels showed non-significant trends ($p>0.05$, Figure 4.3B). Very fast warming of winter temperatures occurred in the interior of the Gulf of Mexico in the area dominated by the Loop Current (about 0.7°C decade^{-1}), and in some areas of the south-eastern Caribbean. With these exceptions, warming in the region occurred at lower rates in winter than in summer. Near the coast, upwelling foci in the southern Caribbean showed non-significant warming in winter (Figure 4.3B). North of the Yucatan Peninsula SST trends in upwelling and neighbouring non-upwelling areas were similar and non-significant. In shelf waters off Florida, the Bahamas and Cuba trends were the lowest for the study region, with a slight tendency towards winter cooling (-0.2°C decade^{-1}, Figure 4.3A), although most of these trends were non-significant.

These changes in summer and winter temperatures result in variations to annual temperature ranges depicted in Figure 4.4. The seasonal temperature amplitude in the southern Caribbean Sea and in the Loop Current decreased over time, coincident with increases in winter temperatures (Figure 4.3B). These changes are mostly non-significant. In contrast, there was an increase in the annual range in the western Caribbean and shallow shelf regions of the northern areas of the study region, mostly related to decreases in winter temperatures in those areas (Figure 4.3B).

Discussion

SST trends in the Caribbean Sea and southeast Gulf of Mexico

The decadal warming rate calculated here for the wider Caribbean over the period 1985-2009 was 0.27 °C decade^{-1}. This rate is higher than that reported for the northern hemisphere for the period 1979-2005 by the Intergovernmental Panel on Climate Change in 2007 (0.19±0.13°C per decade from 1979 to 2005: Trenberth et al. 2007). Nevertheless, it lies within the range of values estimated by two analyses of recent satellite SST data at higher spatial resolution (Good et al. 2007; Strong et al. 2008). Using four km SST AVHRR data for the period 1985-2006, Strong et al. (2008) estimated rates of warming between 0.2 and 0.6°C decade^{-1} in a few selected locations within the Caribbean basin. Good et al. (2007) estimated rates of warming for the entire basin of about 0.3°C decade^{-1} for the period 1985-2004, based on AVHRR data at 2.5° spatial resolution.

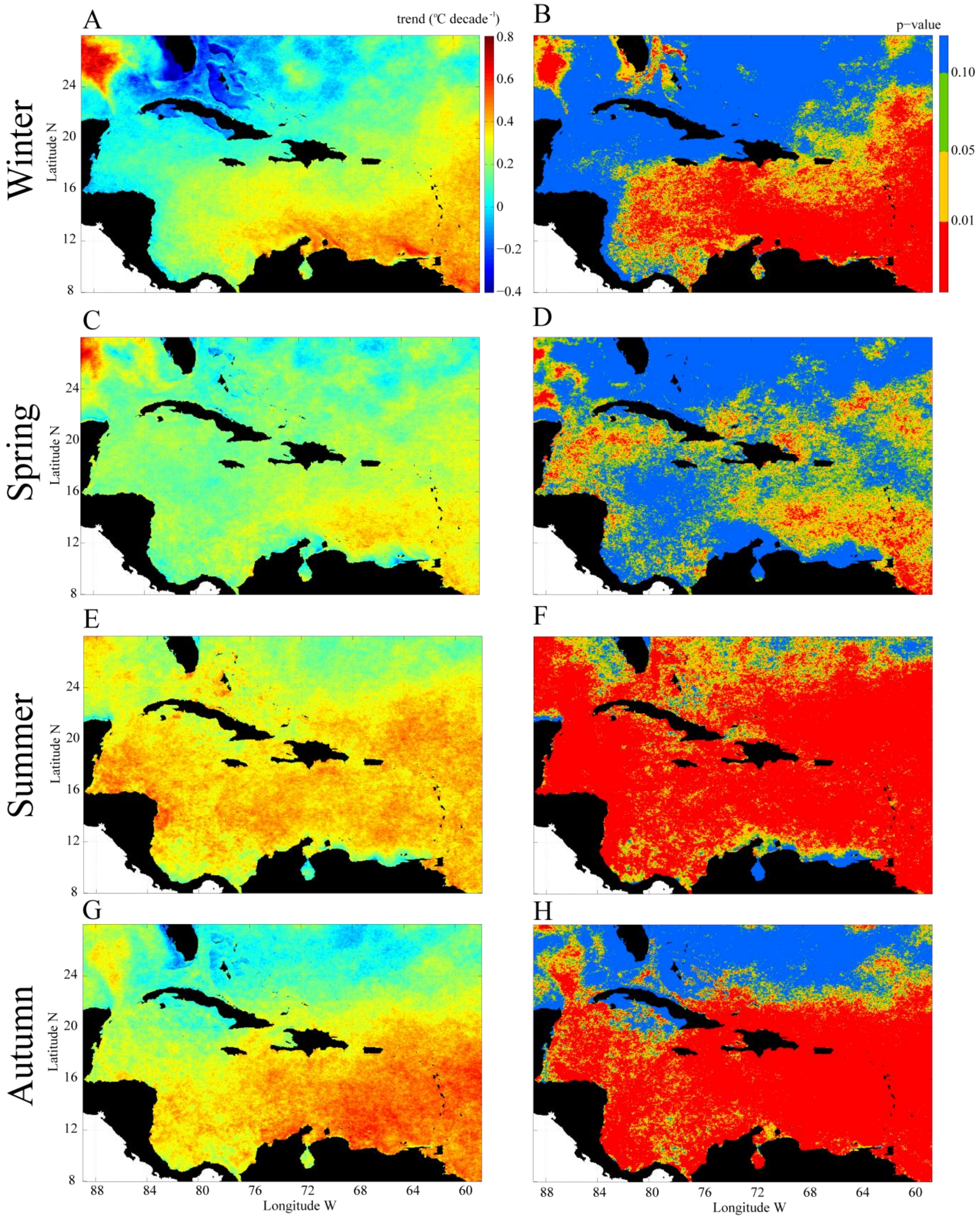

Figure 4.3. Seasonal temperature trends in the Caribbean and associated significance. (A) winter (December-February) trends; (B) significance of the trend in winter ; (C) spring (March-May) trends; (D) significance of the trend in spring; (E) summer (June-August) trends; (F) significance of the trend in summer; (G) autumn (September-October) trends; (H) significance of the trend in autumn.

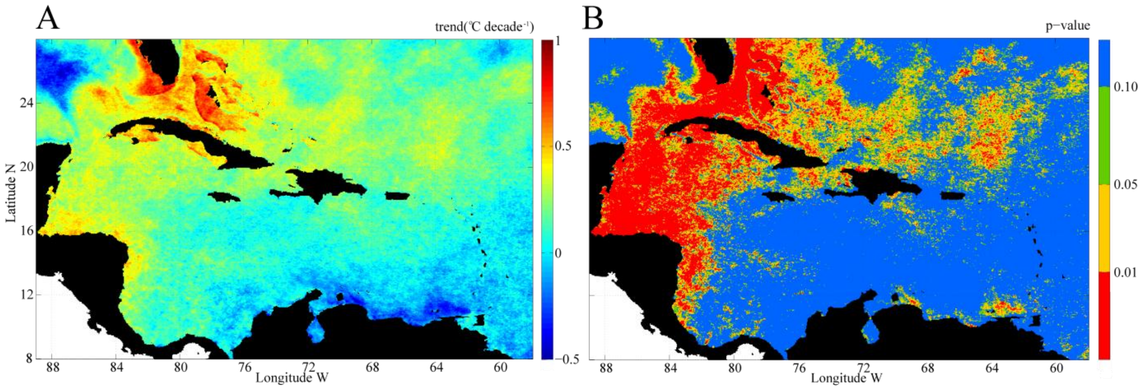

Figure 4.4. (A) Trends in annual ranges of temperature (summer-winter); (B) significance of the trend.

There is high spatial heterogeneity in SST trends within the Caribbean Sea and the south-eastern Gulf of Mexico (Figure 4.1). By examining the region using high spatial resolution data (related to previous studies such as Good et al. 2007 and Strong et al. 2008) the effects of oceanographic features within the Caribbean basin (e.g. loop current) that would otherwise be averaged out may be observed, providing a more accurate representation of the warming trends. Such detailed variability provides a portrait of disturbance incidence in the region, being more relevant in an ecological context. This information could be used to understand perturbation incidence and the likely response of marine ecosystems within the area (Parmesan and Yohe 2003; Root et al. 2003).

Summer warming has been more intense than winter warming in most of the Caribbean Sea and south-eastern Gulf of Mexico, which challenges some expectations (Parmesan and Yohe 2003; Trenberth et al. 2007). In light of these results, predictions regarding expected changes in the phenology and physiology of Caribbean marine species should be revisited, as for example has been done by Von Holle et al. (2010) when assessing (unexpected) recent delays in seasonal flowering of Floridian plants related to decreased winter temperatures.

The long-term patterns of winter cooling observed in high-latitude areas, specifically coastal and shelf waters off Florida, Cuba and the Bahamas, can be related to the more intense and frequent passing of cold-air fronts from the North American continent (Roberts et al. 1982; Melo-González et al. 2000). The southward advection of these artic air-masses has been related to the downward trend of the North Atlantic Oscillation since the early 1990s (Wang et al. 2010), which has already negatively impacted marine ecosystems in the region (e.g. Kemp et al. 2011). These cooling trends are in sharp contrast with the fast-warming trends observed in the

Loop Current, which transports warm waters from the Caribbean basin. The Loop Current is a surficial flow that joins the Yucatan and the Florida Currents, and it is active all year round (Johns et al. 2002). However, the SST signal of this current can only be detected during winter, when the thermal gradient of the Loop waters and the remaining waters of the Gulf of Mexico is pronounced enough to be seen at the surface (Bunge et al. 2002). *In situ* studies need to be carried out in this area to assess the temporal variability of sub-surface temperature trends of this important link between South Atlantic and North Atlantic waters.

There has been some speculation that climate change may lead to intensification of alongshore winds and thus wind-driven upwelling (Bakun 1990; Bakun et al. 2010). Although many observations sustain this hypothesis (e.g. Demarcq 2009), the weakening of upwelling in some areas has also been reported (Pérez et al. 2010). Satellite SST data showed no long-term trends in temperatures at any of the temporal scales assessed in the upwelling area on the northern coast of the Yucatan Peninsula (Merino 1997). This suggests that there has been no overall change in any of the driving forces of upwelling in this region. Non-significant SST trends in the upwelling system of the southern Caribbean (Astor et al. 2003; Andrade and Barton 2005) show that upwelling is also active in this area. However, the fast warming observed in winter in the area generally influenced by the upwelling plume, suggests that the magnitude of the upwelling is decreasing during this season. The weakening of upwelling could be related to a deepening of the thermocline or to a decrease in the intensity of the winds. Temperature observations collected *in situ* in this upwelling area as part of the CARIACO Ocean Time Series Program since 1995 (Müller-Karger et al. 2010) similarly show an increase in winter SST, related to a weakening of the strength of the winds observed between 2003 and at least 2011. These *in situ* observations suggest that a decrease in the winds may be the cause of the weakening of upwelling in the main upwelling season. On the other hand, the lack of warming of both the upwelling foci and the area influenced by the upwelling plume in summer suggest that the secondary upwelling event (Astor et al. 2003) is still active in this area. The lack of marked warming in the upwelling areas of the Caribbean and the southeast Gulf of Mexico does not imply that ecosystems that depend on the upwelling process will be unaffected by climate change (Mote and Mantua 2002). Although chronic stress due to long-term temperature increases may not be a major threat for these ecosystems in the near future, acute (short-term) thermal stress events due to higher variability in temperature may influence the dynamics of marine systems (Mumby et al. 2011), and constitute a stress factor also in upwelling areas, despite generally colder temperatures (Chollett et al. 2010).

Limitations of the analyses

Clearly, non-significant results shown here should be interpreted with caution. The number of years of data needed to detect a trend depends on the magnitude of the trend as well as the magnitude and autocorrelation of the noise (Weatherhead et al. 1998: Equation 5). The AVHRR Pathfinder dataset is the longest available to conduct detailed regional analyses. Yet is still insufficient to provide enough statistical power to assess decadal changes in temperature, especially where changes are small and/or the variability and memory of the SST patterns are high. For these cases, over forty years of data may be needed to detect significant trends, such as perhaps in the upwelling areas of the southern Caribbean Sea and shelf waters off Florida, the Bahamas and Cuba (Figure 4.5). Temporal autocorrelation and internal variability are intrinsic features of each location. Understanding these fundamental characteristics in SST patterns will help in determining reasonable expectations for trend detectability and aid in selecting better sites for climate studies, where the early detection of trends is more likely (Weatherhead et al. 1998; Karoly and Wu 2005).

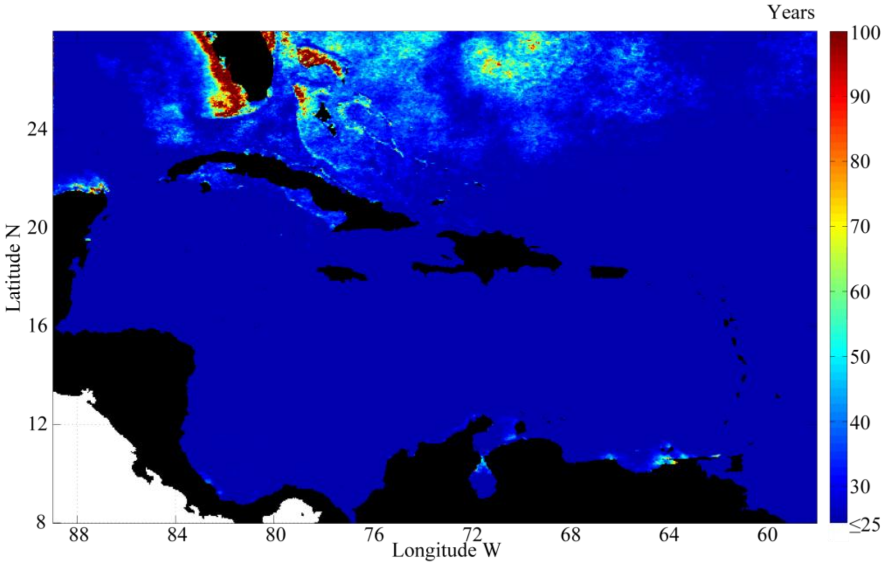

Figure 4.5. Number of years required to be able to detect the decadal linear trends described in Figure 4.1.A at 95% confidence level (Equation 5). Note this study used time series of 25 year length.

The analyses presented here represent the first detailed portrait of recent changes in SST for the wider Caribbean. However, the dataset and the analyses carried out have three potential limitations which we consider below: (1) biases in satellite temperature data; (2) length of the time series; (3) omission of the effects of climatic oscillations in the regression analysis. Many factors can affect satellite accuracy, including instrument bias (Reynolds 1993), instrument problems (Zhang et al. 2006), clouds (Kilpatrick et al. 2001) and atmospheric aerosols (Reynolds 1993). The Pathfinder project has made large efforts in minimizing biases and inconsistencies across the series of AVHRR instruments taking into account the lifetime of the instrument, the occurrence of rare events that could increase interannual variability (such as volcanic eruptions) and seasonal biases (Kilpatrick et al. 2001; Casey et al. 2010). The consistency of SST trends detected with different sources of satellite data (Lawrence et al. 2004; Good et al. 2007; Strong et al. 2008) suggests that temperature trends detected with satellites represent real patterns in recent ocean climate. The Pathfinder algorithm does not consider, however, the influence of spatial biases related to local seasonal weather phenomena, such as desert dust aerosols or cloud coverage that could affect the resulting SSTs (Zhang et al. 2004). Although these factors could contribute to the variability in SSTs and therefore decrease the level of confidence of the trend estimates, there is no evidence of decadal trends in total cloudiness or atmospheric aerosols in the Caribbean basin that could affect the overall patterns presented here.

Our analyses only examine 25 years of data and recent trends in temperature. On one hand, caution needs to be exercised when inferring long-term trends from relatively short records (Allen et al. 1994). However, the increased rate of warming reported during the last 30 years (Trenberth et al. 2007) suggests that the detection of trends in short, but recent datasets is reasonable. On the other hand, physiological and phenological responses of marine organisms are associated to this timescale, granting relevance to the study of recent changes in thermal patterns at detailed temporal and spatial scales.

The regression model used here does not incorporate the effects of climatic oscillations such as El Niño Southern Oscillation, the North Atlantic Oscillation (Giannini et al. 2001a; Czaja et al. 2002) and the Atlantic Multidecadal Oscillation (Knight et al. 2006) that are known to influence temperature patterns in the basin. However, their influence in sea surface temperatures occurs with some delay (Enfield and Mayer 1997; Giannini et al. 2001b) and the SST response is nonlinear (Hoerling et al. 1997) which makes their inclusion in spatially-explicit predictive models problematical.

The SST patterns observed in the Caribbean Sea and southeast Gulf of Mexico highlight the importance of regional assessments for determining the rate and timing of warming in particular locations, and the need for caution in extrapolating regional implications from global patterns. The regional changes in SST trends showed here have not been documented previously. While we still need to understand the ocean processes driving the spatial heterogeneity in temperature trends, it is certain that these patterns are having and will have significant consequences for marine organisms in the region. Although predicting the response of marine ecosystems to warming is difficult, data on SST trends are an important first step. Altogether with information on the thermal regime experienced at the location and the thermal performance for the process under study, the temperature patterns presented here would allow testing hypotheses of changes in biological systems using comprehensive ecological datasets. In this regard, more detailed information on the physiological and phenological responses of marine populations of the wider Caribbean to changes in temperature is urgently required as a baseline against which to test the effects of climate change (Baird et al. 2009). The ability of ecosystems to survive these changes in temperatures will depend on migration (e.g. Beaugrand et al. 2002) or adaptation potential (e.g. Császár et al. 2010), as well as the potential to undergo some re-assembly (e.g. Yakob and Mumby 2011).

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5

Upwelling areas do not guarantee refuge for coral reefs in a warming ocean

Chollett I, Mumby PJ, Cortés J (2010). Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. Marine Ecology Progress Series 416:47-56. doi:10.3354/meps08775

Abstract

Global warming is a severe threat to coral reefs. It has been proposed that upwelling areas could minimize the thermal stress caused by ocean warming, and therefore serve as a refuge for corals. Here, using 21 years of satellite sea surface temperature data, we analyse the degree to which upwelling reduces the thermal stress experienced by corals in four seasonal upwelling areas with reef development: Colombia in the southern Caribbean, Panama in the eastern tropical Pacific, Oman in the Arabian Sea and Madagascar in the Indian Ocean. Upwelling areas do not always offer protection from thermal stress. When compared with nearby non-upwelling areas, upwelling can only provide defence against warming events if: (1) the threat and the upwelling coincide; and (2) if this overlap produces a meaningful decrease of thermal stress in upwelling areas. These conditions were met in only two of the four upwelling areas analysed: Colombia and Oman. In Oman, upwelling decreases the magnitude, frequency and duration of thermal disturbances (identified when Coral Bleaching HotSpots, anomalies exceeding the average temperature of the warmest month, are larger than 1°C), while in Colombia upwelling only decreases their frequency. The protective role of upwelling seems to be limited geographically, therefore further upwelling areas need to be assessed individually in order to evaluate their capacity as a refuge from thermal stress.

Keywords: Coral reef, upwelling, bleaching, climate change, sea surface temperature, AVHRR

Introduction

In the last 100 years, global air temperature has increased 0.74°C (IPCC 2007) and the rate of temperature change is two to three times higher than has been observed over the past 420,000 years (Hoegh-Guldberg et al. 2007). Although land has warmed faster than the oceans, over 80% of the heat added to the climate system has been absorbed by the sea, the average temperature having increased by approximately 0.14-0.18°C per decade during the last twenty years (Casey & Cornillon 2001, Good et al. 2007, IPCC 2007). These facts have prompted concern that rising seawater temperatures could increase the frequency and severity of coral bleaching events and the irreversible decline of coral reef ecosystems (West & Salm 2003, McWilliams et al. 2005, Hoegh-Guldberg et al. 2007, Wilkinson & Souter 2008).

The rise of thermal stress on coral reefs has led to speculation that coral-dominated systems may become increasingly restricted to locations of naturally low thermal and/or radiative stress (Glynn 1996, Salm & Coles 2001, Riegl & Piller 2003, West & Salm 2003, Grimsditch & Salm 2005, Baker et al. 2008). These areas could provide “pockets of resistance” (sensu West and Salm 2003), not by increasing the physiological tolerance of the inhabiting corals, but by providing extrinsic environmental conditions that reduce the stressful conditions. Regions of relatively low thermal and radiative stress include upwelling systems (Riegl 2003), deep water areas of strong vertical mixing (Skirving et al. 2006), sites with high water flow (Nakamura & van Woesik 2001, Nakamura et al. 2003), or high levels of shading (Mumby et al. 2001, Fabricius et al. 2004). Although these areas could constitute a refuge from bleaching, they have other features that could dampen reef development. For example, upwelling areas can be subjected to cold thermal stress (Glynn et al. 1983), deep areas may host poorly connected reefs (Bongaerts et al. 2010), and high flow can dislodge corals (Madin and Connolly 2006).

This analysis focuses on just one of the potential sources of cool water on reefs: seasonal upwelling. Upwelling, the upward motion of subsurface water towards the surface, is an oceanographic phenomenon that decreases sea temperature and increases the nutrient concentration in coastal waters (Sverdrup et al. 1942). Lower incidences of coral bleaching and associated mortality have been related to the influence of upwelling in the Gulf of California

(Reyes-Bonilla 2001), Mexico (Glynn & Leyte-Morales 1997), Costa Rica (Jiménez et al. 2001), Panama (Glynn et al. 2001), Venezuela, Colombia (Rodríguez-Ramírez et al. 2008), South Africa (Riegl 2003) and northern Madagascar (McClanahan et al. 2007). Seasonal upwelling (as opposed to occasional upwelling) constitutes a persistent feature in time that has the potential to decrease the effects of thermal stress in a predictable manner (West and Salm 2003). Given the evidence listed above, seasonal upwelling areas have been proposed as possible refugia in a warming ocean, and therefore desirable locations for the establishment of marine protected areas (West & Salm 2003). However, some empirical evidence suggests that the ability of upwelling to prevent bleaching is not consistent over time: during the 1982-83 ENSO, upwelling was incapable of offsetting the warming of the water masses in the Pacific Panama. Sea surface temperatures (SSTs) in the upwelling area of the Gulf of Panama matched those found in the non-upwelling area of the Gulf of Chiriquí and coral mortality reached 84.7% in the former (Glynn et al. 1988).

Since upwelling and severe warming are seasonal and interannually variable phenomena (Astor et al. 2003, Philander & Fedorov 2003, Wang & Fiedler 2006, Wilkinson & Souter 2008, Bograd et al. 2009), their temporal variability needs to be considered in order to provide a more systematic analysis of the role of seasonal upwelling in preventing mass bleaching events. In this paper we assess the capability of upwelling to offset warming of the water masses using long-term temperature records. The use of long time series allows the evaluation of thermal patterns over continuous scales rather than confining the analysis to particular time periods that represent snapshots in time. Upwelling would offset bleaching only if (1) upwelling and severe warming events occur at the same time and (2) upwelling provides sufficient cooling to reduce the thermal stress experienced at the location. We examine the first prerequisite by determining the synchrony of upwelling and warming events in four regions of the globe. We then examine the second prerequisite, that upwelling reduces stress, by carefully examining the impacts of upwelling on the magnitude, frequency and duration of thermal anomalies within each region (i.e., comparing the stress in upwelling and nearby non-upwelling areas).

We stress that our analysis is confined to the effects of upwelling on the temperature experienced by corals and excludes other potentially beneficial impacts of upwelling associated with reduced light penetration or increased heterotrophic feeding by corals during plankton blooms that might be associated with upwelling events. Reduced light has the potential to decrease, or even prevent, bleaching (Lesser & Farrell 2004, Enriquez et al 2005), and enhanced heterotrophy has the potential to offset trophic stress associated with a paucity of symbionts (Grottoli et al. 2006, Houlbrèque & Ferrier-Pagès 2009). Unfortunately, it is currently not possible to generalise the potential impacts of these effects because of the lack of accurate models of the interactions between thermal stress, radiative stress, and heterotrophic plasticity.

Methods

Data source and study locations

Weekly sea surface temperature (SST) data for 1985–2005 were derived from the four km resolution Advanced Very High Resolution Radiometer (AVHRR) Pathfinder dataset (Case et al. 2010). The data were collected and processed by the National Oceanographic Data Center in cooperation with the University of Miami, and the weekly product used was provided by the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch program.

Using the 21-year dataset we examined the timing of upwelling and bleaching-like conditions in four regions of the world, with representation from all three tropical oceans. In each region, one upwelling area and a neighbouring non-upwelling area that contained coral communities were delineated. Reefs subjected to seasonal upwelling were first located based on previous research (Glynn 1993, Glynn et al. 2001, Díaz-Pulido and Garzón-Ferreira 2002, McClanahan et al. 2009). Subsequently the nearest non-upwelling reef, based on the UNEP-WCMC Biodiversity Map Library, was chosen for comparison. The regions, delineated in Figure 5.1 were (a) Colombian Caribbean at Tayrona National Park (NP) (an upwelling area, 11.5°N 74.2°W) and Rosario NP (a nearby non-upwelling area, 10.2°N 75.8°W), (b) Pacific Panama at the Gulf of Panama (upwelling, 7.5°N 79.0°W) and the Gulf of Chiriquí (non-upwelling, 8.0°N 82.0°W) (c) Oman at Sûr Maşirah Island (upwelling, 20.0°N 56.6°E) and Diymaaniyat Islands (non-upwelling, 23.9°N 58.1°E) and (d) northern Madagascar at Cap d'Ambre (upwelling, 12.0°S 49.0°E) and Nosy be Island (non-upwelling, 13.1°S 48.2°E). We briefly describe the upwelling and bleaching regime in each region below.

The Colombian Caribbean is characterized by strong upwelling along its north coast (Andrade and Barton 2005). Upwelling occurs at the beginning of the year because of the increase in the strength of the winds due to the latitudinal migration of the Intertropical Convergence Zone (Andrade and Barton 2005, Amador et al. 2006, Wang 2007). Additionally, the influence of the Caribbean Low-Level Jet produces a secondary intensification of winds, and thus upwelling, during summer (Wang 2007). On the other hand, bleaching in the Caribbean has been reported during summer months when incoming solar radiation is at its maximum (Wilkinson & Souter 2008).

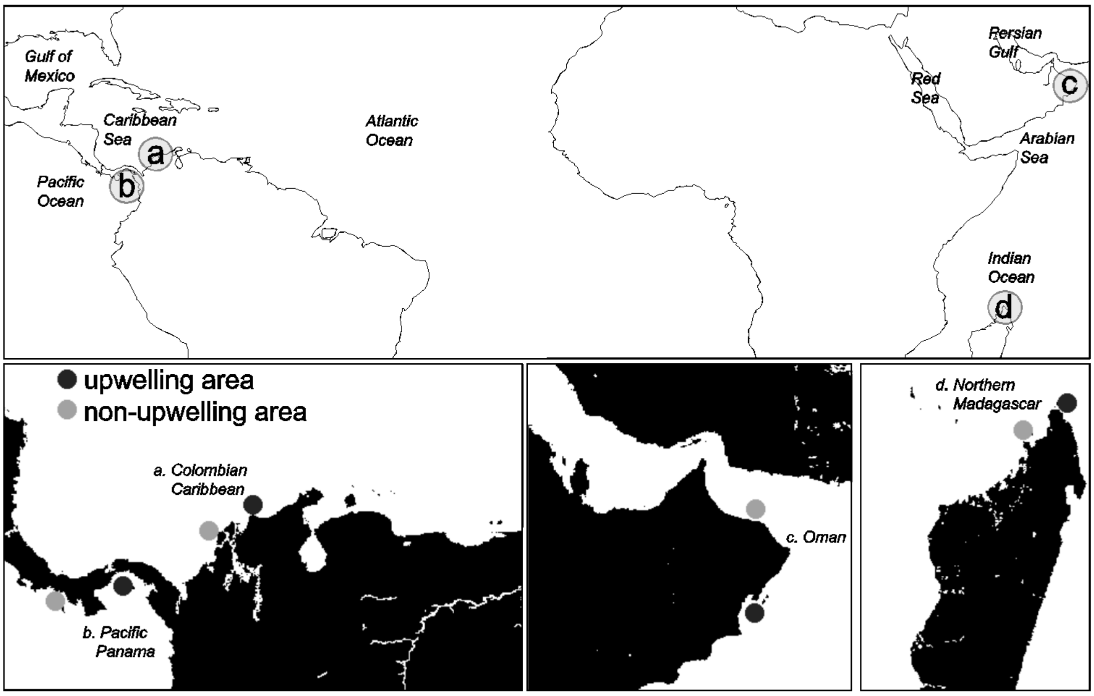

Figure. 5.1. Assessed regions in (a) Colombian Caribbean; (b) Pacific Panama; (c) Oman; and (d) Northern Madagascar. Upwelling areas showed in dark gray and non-upwelling areas in light gray.

Upwelling in the Gulf of Panama occurs also at the beginning of the year due to the migration of the Intertropical Convergence Zone (Amador et al. 2006). In the eastern tropical Pacific, warming disturbances are associated with ENSO events, with temperature anomalies typically lasting from March of one year to September of the following year, and with a mature phase of stronger anomalies from November to January (Wang & Fiedler 2006).

In Oman the southwest monsoon produces wind-driven upwelling off the east coast during summer (Shi et al. 2000). Anomalously high SSTs in this region have been attributed to unusual warming during the summer months, occasionally linked to El Niño-Southern Oscillation (ENSO) events (Wilkinson et al. 1999).

Unlike the other upwelling areas described, upwelling in Madagascar is not forced by winds, but by currents. The South Equatorial current produces upwelling at the northern and southern tips of Madagascar (McClanahan et al. 2009). This current shows no obvious seasonal variation, and exhibits high stability all year round (Sætre 1985). As in Oman, unusually warm conditions in Madagascar tend to occur in summer and have been linked to ENSO events (McClanahan et al. 2007).

Identifying upwelling and warming events

Using the weekly dataset, upwelling conditions were identified when temperatures in an upwelling area fell three standard deviations below the monthly average temperature experienced in the same month in a neighbouring, non-upwelling area. Temperatures below this threshold are likely to belong to a different statistical population (Zar 1999). This index provides a simple proxy to identify upwelling conditions, when waters are significantly colder that in the surrounding areas.

Conversely, HotSpot anomalies (Liu et al. 2006) were used to identify warming conditions that may produce bleaching. HotSpots measure the difference between the recorded temperature and the average temperature of the hottest month at that location. Only positive values are derived, since HotSpots were designed to measure positive thermal stress (Liu et al. 2006). In this study, only HotSpots larger than 1°C were used to indicate excessive thermal stress. Previous studies have found that corals are acclimated to local conditions (Coles et al. 1976, Coles and Jokiel 1977, Goreau and Hayes 1994, Brown et al. 1996, Castillo and Helmuth 2005, Ulstrup et al. 2006), and temperatures of 1°C above local seasonal maxima are enough to cause stress (Strong et al. 1997, Goreau et al. 2000, Liu et al. 2006). HotSpots were chosen over accumulated measures of stress such as Degree Heating Weeks (Liu et al. 2006) because the instantaneous coincidence of upwelling and warming needed to be assessed.

Data were collected within a region of 256 km^2 (16x16 pixels) around each location of upwelling or non-upwelling. This area is small enough to prevent contamination of upwelling and non-upwelling areas yet large enough to provide a good sample size for statistical analyses. Homogeneity of each 256 km^2 area was verified by computing the local mean and the variance using sliding windows of varying sizes (Fortin and Dale, 2005).

Prerequisite 1: Synchrony of upwelling and warming events

To estimate the temporal overlap of upwelling and warming conditions, the probability of occurrence of upwelling events was calculated and compared to the incidence of severe warming episodes in the region. For the entire weekly dataset, upwelling and warming events were identified using the metrics described above. Upwelling conditions were identified in each of the four upwelling areas. Severe warming conditions typically affect extensive areas (Baker et al. 2008, Wilkinson & Souter 2008), but the ability to detect their signal (HotSpots) in a given month changes among locations within a region. Because HotSpots are more likely when temperatures are close to the seasonal maximum, but given that the timing of the hot season changes among locations, areas with differing thermal regimes should be assessed to obtain a comprehensive estimate of the occurrence of severe warming. This is why in the present study, warming conditions were said to occur in a region if hotspots were found in either the upwelling or non-upwelling areas. Moreover, by allowing warming to be identified within upwelling areas, this approach is consistent with studies that have demonstrated local acclimation of corals to temperature and the occurrence of bleaching once temperature anomalies are experienced (e.g. Glynn and D'Croz 1990, D'Croz et al. 2001).

Each month of the time series was categorised as having an upwelling and/or hotspot event if at least one week of the month was positive for the respective event. Using this monthly information, the number of times upwelling (F_u) and warming (F_w) were present in a given month was calculated for the entire time period (over 21 years), in addition to the joint occurrence of the two events ($F_{u\cap w}$). This allowed independent monthly estimates of the frequency of each type of event to be obtained and their intersection in each region. The monthly incidence was then converted into the statistical likelihood of an event occurring in any given year using a binomial distribution. To allow clear comparisons to be drawn among regions, we standardized our results by dividing the joint probability of warming and upwelling ($P_{u\cap w}$) by the warming probability P_w (i.e., giving the proportion of warm periods for which upwelling also occurs). We will call this value ($P_{u\cap w}/P_w$) “standardized joint occurrence” throughout the text.

The timing of warming and upwelling events found in our work coincide with temporal patterns previously reported for the studied areas (Sætre 1985, Wilkinson et al. 1999, Shi et al. 2000, Andrade and Barton 2005, Amador et al. 2006, Wang & Fiedler 2006, Wilkinson & Souter 2008), which confirms the appropriateness of the metrics used to quantify these events.

Prerequisite 2: Reduction of thermal stress by upwelling

The co-occurrence of severe warming events and upwelling is not enough to identify an area as a meaningful refuge; upwelling should also translate into a milder thermal disturbance regime in that area. Three elements should be considered when assessing the impact of stressful events on biological systems: the intensity or magnitude of the disturbance, the duration of individual stress episodes and the temporal frequency of different episodic events (Connell 1978, Pickett &

White 1986). Following this categorization, if upwelling can provide refuge from warming, then upwelling areas would be characterised by smaller thermal anomalies, shorter anomalous periods and/or fewer anomalous episodes in the long term when related to nearby, non-upwelling reefs.

To gain some insight into the overall effect of upwelling on decreasing thermal stress in an area, the long term stress undergone in the last 21 years (1092 weeks) by the four regions assessed was quantified. Anomalous events were again identified when HotSpots were larger than 1°C. Using the weekly data, the magnitude of HotSpots, the duration of the anomalous episodes (when HotSpots were registered in contiguous weeks) and the total frequency of discrete anomalous events was calculated for the entire dataset in upwelling and non-upwelling areas in each of the regions (Figure 5.1). For each region, upwelling and non-upwelling disturbance estimates were then compared using one-tailed tests (t-tests and Z test for two proportions). To reduce a potential influence of spatial autocorrelation only random subsets of 30% of the delineated areas were used, and a bootstrap procedure (1000 iterations) was used to compute average statistics and their standard error.

Results

Prerequisite 1: Synchrony of upwelling and warming events

Warming events occur during the summer months in the Colombian Caribbean, Oman and Northern Madagascar (Figure 5.2a, 5.2c, 5.2d) but year-round in Pacific Panama (Figure 5.2b). In the southern Caribbean and the eastern tropical Pacific, upwelling occurs at the beginning of each year. The temperature decrease is acute in the eastern tropical Pacific, but the cooling lasts longer in the southern Caribbean (Figure 5.2a, 5.2b). This implies that the capability of upwelling to counteract bleaching conditions is greater in the Caribbean, where there is larger co-occurrence of seasonal cooling of water masses and episodic warming. In this region, the average of the standardized joint occurrence is 0.74. This implies that 74% of the time, when warming was present, upwelling was also present. In the Pacific, thermal anomalies can occur in any month, so upwelling would be able to offset warming only during the short cooling season. Thus, given the limited duration of upwelling, the average of the standardized joint occurrence of the two events in this area is only 0.41. Upwelling off the east coast of Oman is active during summer, which coincides with the occurrence of warm anomalies (Figure 5.2c). Upwelling therefore counteracts warming events during most of their duration, and the average of the standardized joint occurrence is 0.86. In Madagascar, upwelling occurs all year-round. Consequently, upwelling decreases the temperature of the water most of the year, and the average of the standardized joint occurrence is 73% (Figure 5.2d).

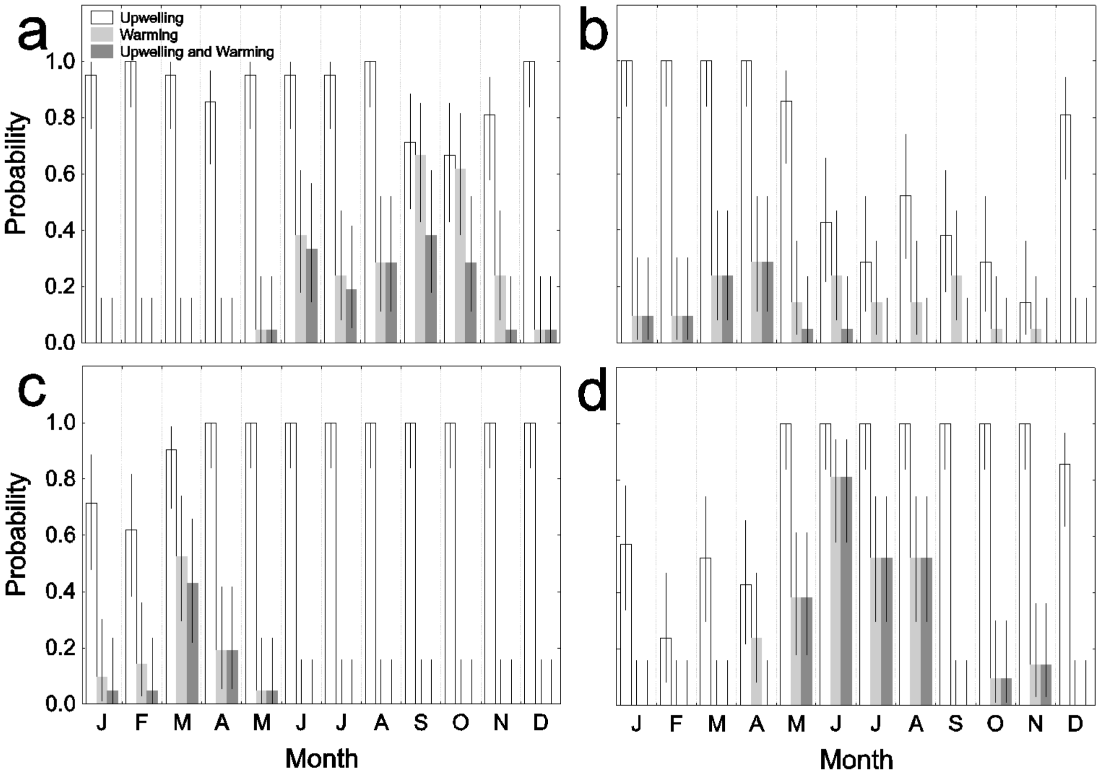

Figure. 5.2. Probability of occurrence of upwelling and warming events, as well as their joint incidence in (a) Colombian Caribbean; (b) Pacific Panama; (c) Oman; and (d) Northern Madagascar. Warming events were identified when HotSpots in the region (considering upwelling and adjacent non-upwelling areas) exceeded 1°C. Upwelling conditions were identified when temperatures in upwelling areas were three standard deviations below the monthly average temperature experienced in the same month in a neighbouring, non-upwelling area. Probabilities were calculated from monthly incidence of upwelling/warming conditions in 21 years; whiskers indicate 95% confidence intervals (1985-2005 AVHRR Pathfinder data).

In summary, the average of the standardized joint occurrence of warming and upwelling conditions is generally moderate to high ranging from 41% in Tropical Eastern Pacific, to 73%, 74% and 86% in Madagascar, the southern Caribbean and Oman respectively.

Prerequisite 2: Reduction of thermal stress by upwelling

When comparing the thermal disturbance regime in upwelling and nearby non-upwelling areas, upwelling does not decrease the magnitude of the thermal anomalies, the duration or the frequency of the anomalous periods in the eastern tropical Pacific or northern Madagascar (one-tailed Student's t-test, $p > 0.05$ for all contrasts). In contrast, upwelling in Colombia provides a significant reduction in the frequency of anomalous periods, decreasing the total occurrence of disturbance events by 12% (one tailed Z-test for two proportions, average and standard error: $z=-3.55\pm0.03$, $p < 0.05$).

Oman is the only case study analysed in which upwelling is able to reduce the three measures of thermal stress; decreasing the magnitude of the thermal anomalies (by 4%), the duration (by 24%) and frequency (by 55%) of disturbance events when compared to neighbouring non-upwelling areas (t-tests and one tailed z-test for two proportions, $t=-9.67\pm0.02$, $t=-10.39\pm0.03$, $z=-23.91\pm0.02$, $p < 0.05$).

Net outcomes of synchrony and impact on thermal stress

Our results lead to three distinct outcomes for the four upwelling areas analysed: (1) synchrony of upwelling and warming and significant reduction of stress in Colombia and Oman; (2) partial synchrony of upwelling and warming events and no reduction of thermal stress in the eastern tropical Pacific; and (3) synchrony but no reduction of stress in northern Madagascar.

To understand the net outcomes of variable synchrony and impact on thermal stress, the monthly frequencies of HotSpots were disaggregated for each area (upwelling and non-upwelling) within each of the regions assessed (Figure 5.3). In both upwelling and non-upwelling areas, warming conditions are more likely when water temperatures are closer to the maximum monthly climatological mean of the location.

In Colombia, the temporal overlap between upwelling and warming conditions at the beginning of summer due to the influence of the Caribbean Low-level Jet (Wang 2007), reduces the length of the warm season in upwelling areas by approximately four months in comparison to nearby non-upwelling areas (Figure 5.3a). The shortened warm season translates into a shorter period of vulnerability to thermal stress, and a lower frequency of thermal disturbance events (decrease of 10%). In this region of the southern Caribbean, upwelling may indeed provide a refuge from warming.

In the Gulf of Oman, upwelling occurs at the peak of the warm season and provides cooler conditions than in nearby non-upwelling areas. Upwelling decreases the maximum monthly mean by 2.3°C and punctuates the warm season, decreasing its total length by one month. In this way, upwelling weakens and shortens the warm period, reducing the incidence of thermal anomalies by 54%. In Oman, therefore, upwelling can provide effective protection against severe warming.

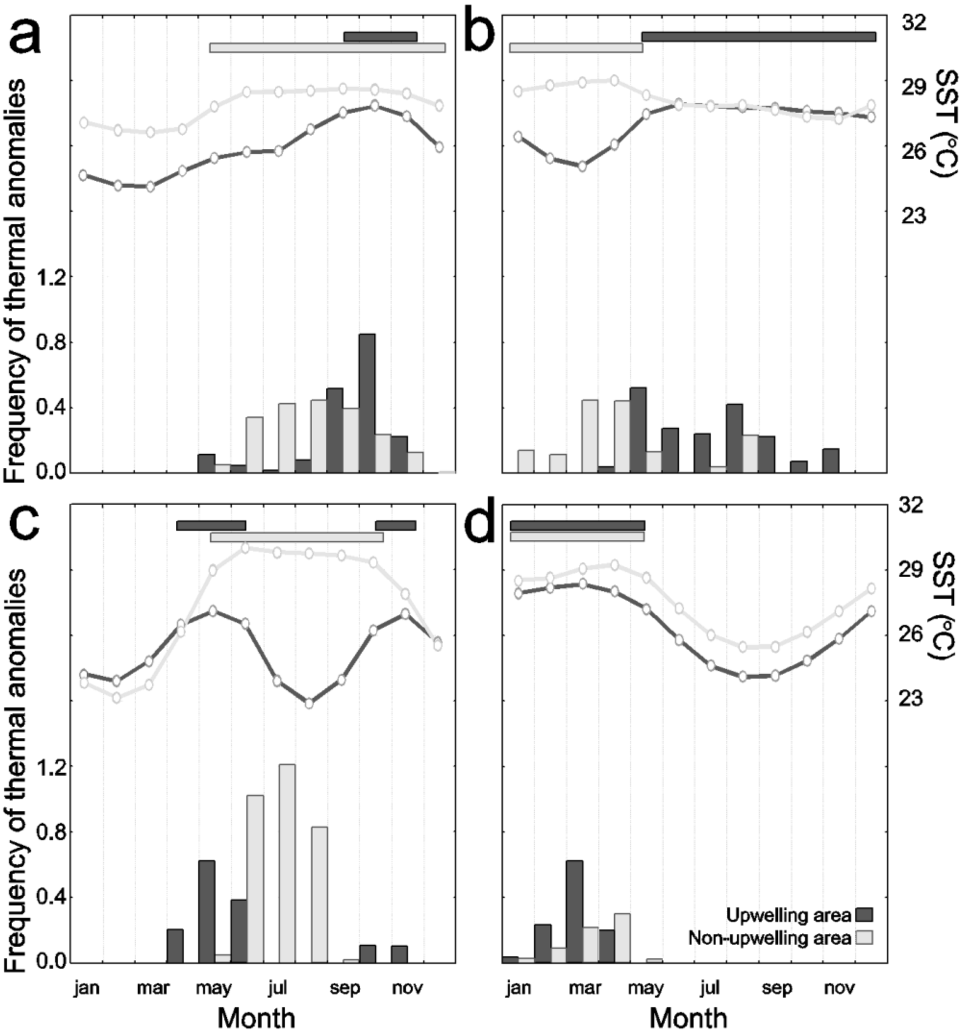

Figure. 5.3. Monthly distribution of temperature averages (lines) and frequency of thermal anomalous events (percentage of weeks when HS>1; bars) in upwelling and non-upwelling nearby areas in (a) Colombian Caribbean; (b) Pacific Panama; (c) Oman; and (d) Northern Madagascar. Horizontal lines highlight warm months in upwelling (dark gray) and non-upwelling (light gray) areas, when monthly temperatures were less than 1°C below the maximum monthly mean (1985-2005 AVHRR pathfinder data).

Warm seasons do not coincide in upwelling and non-upwelling areas of the eastern tropical Pacific (Figure 5.3b). Maximum incoming solar radiation occurs during the boreal winter in this region (Amador et al. 2006). This results in warmer waters in non-upwelling areas, but not in upwelling areas, where upwelling decreases the temperature of the waters and delays the onset of the warm season. As ENSO disturbances are possible all year, and upwelling does not decrease the length or weakens the warm season, both upwelling and non-upwelling locations are equally vulnerable to thermal disturbances. Additionally, sporadic ENSO events produce both a strengthening of the thermal anomalies and the weakening of the upwelling, further decreasing the significance of upwelling as a protection in the eastern tropical Pacific.

In Madagascar, the South Equatorial Current (McClanahan et al. 2009) reduces temperatures throughout the year. The seasonal temperature patterns in upwelling and non-upwelling areas are almost indistinguishable (Figure 5.3d): summers are equally long, the period of vulnerability to anomalies is similar, and consequently upwelling offers no significant protection from thermal stress.

Discussion

While there is evidence that upwelling has helped reduce the effects of bleaching at particular locations and times (Glynn & Leyte-Morales 1997, Glynn et al. 2001, Jiménez et al. 2001, Podestá & Glynn 2001, Reyes-Bonilla 2001, Reyes-Bonilla et al. 2002, Riegl 2003, Riegl & Piller 2003, McClanahan et al. 2007, Rodríguez-Ramírez et al. 2008), it does not necessarily follow that this oceanographic process will generally have such beneficial consequences. Although a number of upwelling regions remain to be analysed, our case studies reveal important differences in the potential of upwelling in the mitigation of warming. Upwelling is unable to counteract thermal stress if there is asynchrony between upwelling and warming (e.g. Panama). In contrast, if upwelling and warming are synchronous – as occurred in three of the four case studies – then upwelling will only provide a thermal refuge during warming if it also decreases the strength or the duration of the warm season and thus the period of vulnerability to thermal anomalies. This was found to be the case in Colombia and Oman but not in Madagascar.

In addition to the modification of the thermal stress regime, upwelling is likely to influence three other factors that might mediate the bleaching response of corals: incoming light, food supply and aragonite saturation state (Mumby et al. 2001, Lesser & Farrell 2004, Grottoli et al.

2006, Anthony et al. 2008, Baker et al. 2008). Upwelling draws nutrient-rich waters to the surface, promoting the growth of plankton and decreasing the penetration of light (D'Croz & Robertson 1997, Matthews et al. 2008). The reduction of light penetration leads to decreased radiative stress, potentially mitigating the negative synergistic effects of thermal and radiative stress in bleached corals (Lesser & Farrell 2004, Enríquez et al. 2005). Furthermore, it has been speculated that increases in plankton abundance and therefore food supply account for faster rates of recovery after bleaching episodes in some upwelling areas (Salm & Coles 2001, Wilkinson 2002). Upwelling, through the upward movement of deep water masses, is also likely to bring waters to the surface that have a reduced aragonite saturation state (Feely et al. 2008, Manzello et al. 2008), potentially aggravating the effects of coral bleaching (Anthony et al. 2008). This implies that the same deeper water masses that are beneficial for coral reefs, bringing cool and turbid waters as a defence against bleaching and nutrients to satisfy their heterotrophic needs, could also contain a chemical hazard. Additional research is required into the geographic and temporal likelihood of this mechanism to provide a clear assessment of the strategic value of upwelling areas as a refuge from climate change.

Although the extent to which upwelling may mitigate bleaching impacts through enhanced heterotrophy and reduced solar radiation are not yet clear, these benefits are only likely to accrue when upwelling and warming are synchronous. Such effects would therefore be less likely in the eastern Pacific than in the other regions studied which had higher synchrony. Moreover, these non-thermal benefits may be particularly important in locations like Madagascar where our analysis predicts the co-occurrence of upwelling and warming but no significant thermal protection.

The significance of upwelling regions as refuges for coral reefs will ultimately depend of their reliability in time. There is a large degree of uncertainty regarding the effects of climate change on upwelling intensity (Wang et al. 2010). While increases in wind stress and cooling have been observed in some of the main eastern boundary upwelling systems during the last few decades (Bakun 1990; Snyder et al. 2003; McGregor et al. 2007; Vargas et al. 2007), some evidence to the contrary also exists in which upwelling has decreased (Di Lorenzo et al. 2005). Such uncertainty in the future dynamics of upwelling should be borne in mind before any action is taken to stratify reef management activities on the basis of upwelling refugia from bleaching.

The structure of reef communities has not been studied along an upwelling gradient in terms of species composition, zonation and diversity patterns. We could expect to see some correlation between environmental variables and biotic patterns indicating that the effects of upwelling (nutrient enrichment, low temperatures) are affecting the structure of coral assemblages. To what extent these coral assemblages respond differently to thermal stress (i.e. exhibit different tolerance and/or resilience to bleaching), is yet unknown, and add uncertainty when comparing the response of communities from different environments to common stressors.

The incidence of upwelling and warming is variable on seasonal and interannual time scales. Our analysis of seasonal upwelling in four geographic locations concluded that synchrony between warming and upwelling is often high but does not necessarily confer a refuge from thermal stress. We recommend that management actions predicated on upwelling-based refugia consider both the synchrony and extent of the impact of upwelling on thermal stress. We also point out that while upwelling may confer benefits to reefs, in terms of reduced bleaching incidence, they have the potential to cause detrimental effects if aragonite saturation state is reduced and/or if elevated turbidity reduces rates of coral calcification to the extent that reef accretion ceases. In short, upwelling has the potential to benefit some reefs in the short-term but whether upwelling proves to be an “ace up the sleeve” for reef conservation in the long-term remains to be seen.

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6

General Discussion

Suitability of the tools

Limitations of remote sensing products to monitor coastal processes

Most of the datasets used in this thesis were collected from orbiting satellites. The broad view and short return time provided by satellite remote sensing makes it ideal for the study of dynamic, large-scale phenomena (Mumby et al. 1999). However, remote sensing has limitations, particularly in coastal areas. Robinson (2010) provides a detailed assessment to the limitations of existing sensors and platforms. Below we will go through the main limitations of the satellite products used during this work.

Ocean colour: In coastal areas, the colour of the water is determined by a mix of several constituents such as phytoplankton, suspended sediments, dissolved organic matter and bottom reflectance. This complex mixture obscures the optical signal received by the satellite, hampering the estimation of in-water constituents. The signal received by an ocean colour sensor comprises two components: scattered energy from the atmosphere, and energy reflected form the water body (Liu et al. 2003). Only 10-20% of the satellite measured signal originates from the water surface (Gordon 1997). Hence, the removal of atmospheric effects is crucial to obtain accurate estimates of water reflectance (Moore et al. 1999). In coastal waters, non-phytoplanktonic particulate material contributes significant amounts of the signal used to conduct atmospheric correction, making the removal of atmospheric effects much more difficult (Hu et al. 2000). Additionally, in shallow reef areas, light reflected from the bottom produces an optical signal that changes with the depth and nature of the seafloor (e.g. the clear and shallow Bahamas banks in Figure 6.1a). This contribution needs to be removed before the water constituents can be quantified, adding another level of complexity to the estimation procedure in those areas (IOCCG 2000; Ackleson 2003).

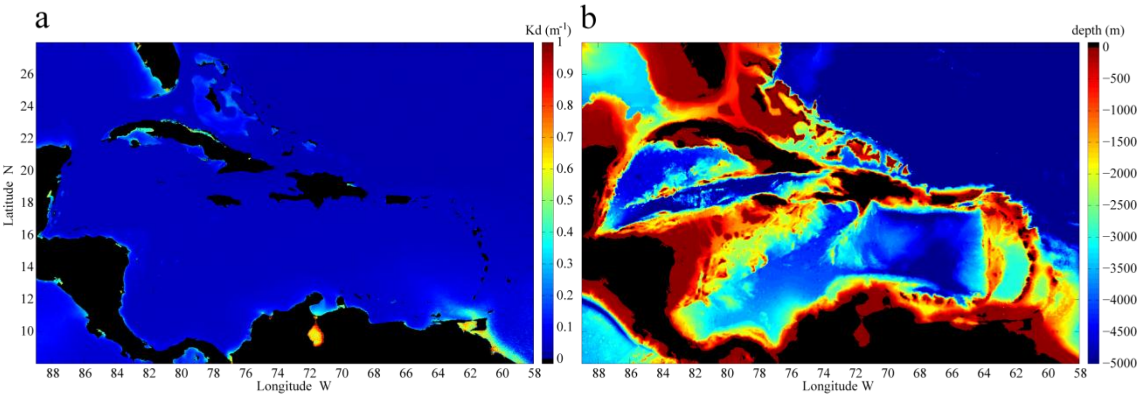

Figure 6.1. (a) Average turbidity (diffuse attenuation at band 3 or k490, SeaWiFS 1997-2008); (b) Bathymetry (GEBCO_08 grid v 20091120) for the wider Caribbean.

Due to these complexities, deriving water quality parameters with sufficient accuracy in coastal waters is still one of the main challenges in marine remote sensing. In small regions the quantification of in-water constituents has been possible through the development of specific algorithms for the area of interest, which are calibrated with *in situ* data (e.g. Chen et al. 2007). Yet, this type of approach is not possible when assessing large areas simultaneously. Therefore, remotely sensed data have been used for the monitoring of qualitative patterns in large areas (e.g. Andréfouët et al. 2002; Sheng et al. 2007; Paris and Chérubin 2008), as it has been done in the present work (Chapter 2). New sensors with improved capabilities (more and narrower spectral bands) will aid in atmospheric correction and bio-optical applications. However, further technological development is needed before this tool can be used to its full potential.

Sea surface temperature (SST): Infrared remote sensing faces two main challenges: minimizing the effects of cloud contamination on the measured radiance and minimizing the effects of spatio-temporal biases in infrared estimations. Only cloud-free pixels can be used for infrared estimations. Although a variety of tests are used to detect clouds and exclude these pixels while estimating SST, small clouds that do not cover the entire pixel, thin cirrus or sea fog are often not captured, which produces small underestimations of radiance and therefore SST. To overcome these issues, some secondary (post-processing) procedures have been implemented to identify remaining cloud contamination and remove it from the dataset. In Chapter 2, one of these procedures (Hu et al. 2009) was used to remove clouds from one km Advanced Very High Resolution Radiometer (AVHRR) satellite imagery. Recently, however, Barnes et al. (2011) showed that this method can miss real cold anomalies. Fortunately, the analyses of Chapter 2 were focused on climatological averages, and average monthly maximum and minimums; therefore the possible exclusion of short-term extreme cold events would have had little impact on the overall results. A better approach to maximize cloud filtering while retaining valid SST observations (still to be developed) needs to be used in the future for similar datasets.

Reprocessing efforts such as the AVHRR Pathfinder project (Kilpatrick et al. 2001) constitute one of the best alternatives to study climate variability and change. The AVHRR Pathfinder uses data from diverse satellites with consistent algorithms, calibrating for sensor change and sensor drift and making full use of a large *in situ* dataset for the estimation of the coefficients, which are seasonally-dependent (Kilpatrick et al. 2001). As mentioned in Chapter 4, the AVHRR Pathfinder minimizes many of the biases observed in satellite data (e.g. instrument bias, instrument problems, seasonal biases: Kilpatrick et al. 2001; Casey et al. 2010). However, the effects of spatiotemporal biases related to local seasonal phenomena that affect cloud cover or atmospheric aerosols remains a major problem, having the potential to skew SST estimates. Future releases of the Pathfinder project are expected to address this issue.

Other datasets based on interpolated SST from satellite and *in situ* data provide similar (Reynolds and Smith 1994) or longer temporal coverage (Rayner et al. 2003) than the AVHRR Pathfinder. Although some oceanographers strongly prefer the blended products, they have a much coarser spatial resolution (one degree) that does not resolve the detailed patterns observed with satellite imagery alone (Casey and Cornillon 1999). A new project, the Group for High Resolution SST (GHRSST), is attempting to produce a higher-resolution (about 10 km) merged satellite (including several sensors) and *in situ* dataset (Donlon et al. 2009). There are many expectations that this new generation of global SST products will be the best alternative for operational monitoring and forecasting of the ocean in the near future.

Ocean winds: The main two limitations of scatterometry is that the technique cannot approach resolutions better than 10 km and its performance is compromised close to the coast because of the occurrence of stray signals and brightness contrasts between land and sea (Tang et al. 2004; Robinson 2010). The accuracy of scatterometers is degraded in coastal regions. At near-shore buoys (14-80 km away from the coastline), root mean squared error estimates of wind speed and direction were 58 and 36% larger than at offshore buoys (Tang et al. 2004). To overcome this issue, dramatic measures such as the establishment of 30 km buffers for the removal of all possible land contaminated pixels have been suggested (e.g. Plagge et al. 2009). However, this approach is not under consideration for research in coastal areas, where the target winds are required precisely in the boundary between land and sea. A more desirable approach would include the use of higher spatial resolution products (between 2.5 and 12.5 km, e.g. Tang et al. 2004; Plagge et al. 2009) that are filtered using land contamination removal algorithms (Owen and Long 2009; Plagge et al. 2009). Currently these high resolution datasets are of experimental nature and not freely available, but their use would enable as much data as possible to be included, while avoiding inaccurate wind estimates along the coastline.

Scatterometer data may not resolve nearshore wind variability and the effects on the shear of the wind due to small islands, headlands, capes and friction with coastal topography; however, it have shown clear spatial variations across the Caribbean basin which coincide with patterns described for the area (Andrade 1993). This dataset has proved to be useful in depicting large scale meteorological features, like the ones described in Chapter 2 of this thesis.

Sensors more appropriate for the task of measuring small-scale features, such as the Synthetic Aperture Radar (SAR), could help improve spatial resolution. However, SAR is not appropriate for large-scale applications or to develop climatologies, because of its long revisit intervals (10-15 days) and small spatial coverage (tens to hundreds of meters: Robinson 2010). A more synoptic view using this tool would require a constellation of satellites that are not yet available.

Salinity: In this work, sea surface salinity (SSS) was assessed using an *in situ* database (the World Ocean Atlas, WOA, Chapter 2). However, there are now satellite instruments designed to provide global SSS data for climate studies, such as the Aquarius instrument on board of the NASA’s SAC-D spacecraft, which was launched in June 2011. The instrument includes a set of three radiometers to measure salinity, and a scatterometer to correct for ocean’s roughness. Although the spatial (150 km) and temporal (monthly) resolution of this resource is coarse, it is expected to provide SSS with high accuracy (0.2 psu) and a spatial coverage that has never been observed before (Le Vine et al. 2010). The comprehensive coverage is expected to overcome the problems of sparse sampling of the WOA (Figure 6.2: Antonov et al. 2010). To date, the WOA represents the best available compendium of salinity data in the world’s oceans, and it is invaluable for describing the climatology of an area. However, it lacks the detailed spatial resolution to resolve small scale differences, and the temporal resolution needed to identify seasonal or rare events that have the potential to produce large scale impacts in marine ecosystems.

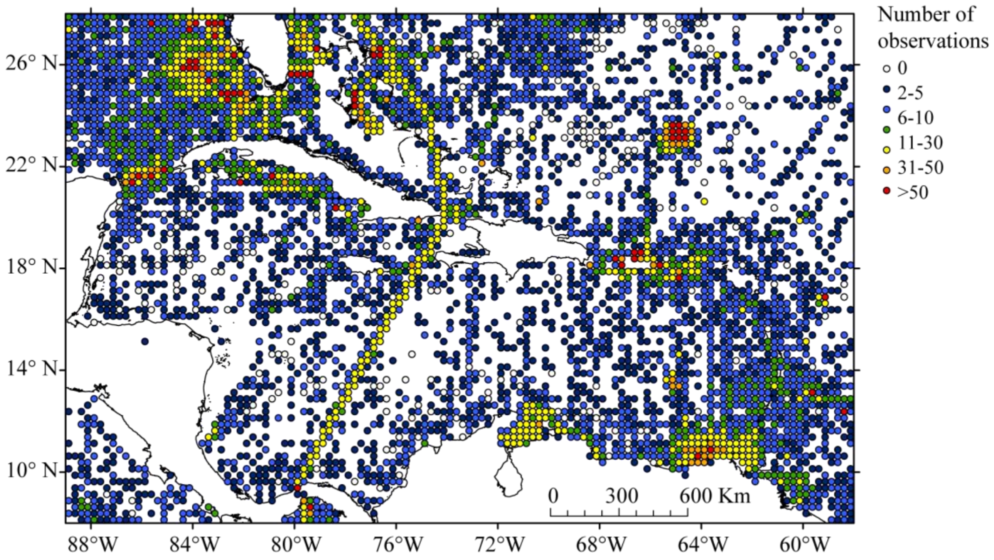

Figure 6.2. Number of surface *in situ* salinity observations in 0.25° grid areas included in the WOA database

The examples described above highlight situations where there is a clear need for satellite measurements of certain accuracy or resolution that cannot be provided because the remote sensing tool is not yet available. Although many of these issues have been addressed by regional studies (e.g. Chen et al. 2007) or through the production of experimental products (e.g. Plagge et al. 2009), the development of synoptic oceanography will be held back until these problems are solved and the solutions are available to a wide audience. To date, the only alternative for users of satellite imagery is to be aware of data limitations and match the application of interest with the best available dataset, of remote or *in situ* origin.

The issue of spatial scale: different scales for different questions

Physical and biological processes in the ocean encompass a wide range of temporal and spatial scales Figure 6.3). The physical circulation of water masses dominates all processes at a global scale. At regional scales (1-100 km), the variability is dominated by oceanographic fronts, eddies, tides and waves. Finally, at local scales, the variability is a function of the interaction of the behaviour of the organisms with local physical processes such as turbulence and mixing (Dickey 1990; Srokosz 2006).

The abiotic template is a powerful constraint on ecosystem function (Turner 2005). However, no single scale is appropriate to study all ecological problems. Because environmental and ecosystem patterns vary over multiple spatial scales, the critical factor is to identify the appropriate resolution at which to address the particular question. Only once the appropriate scale has been chosen, the appropriate remote sensing tool can then be selected (Figure 6.3).

When using methods of remote-sensing, it is always important to ensure that the sampling capabilities of the satellite in space and time are optimized to match the spatial and temporal variability of the ocean phenomenon under study (Robinson 2010). There are no tools that can provide both high temporal and spatial resolution, therefore, we should not expect to fully transfer applications of remote sensing in meso and global scales to local scales, or vice versa. In certain situations, the desired resolution cannot be provided because the remote sensing technology is not yet adequate. Once more, being aware of these limitations can help to use remote sensing tools in an appropriate and targeted way.

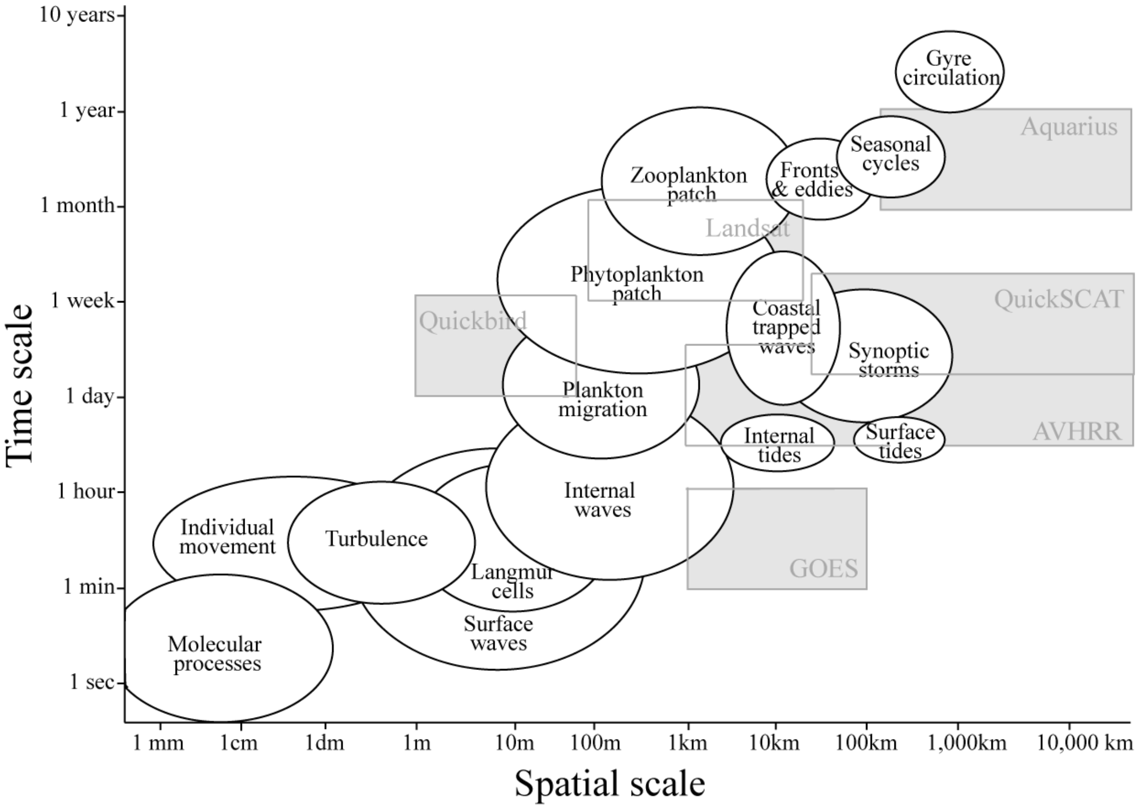

Figure 6.3. Diagram illustrating the relevant spatial and temporal scales of several oceanographic processes and the approximate resolution of some satellite/sensors (base diagram of ocean processes from Dickey 1990).

Further applications

Climate is the primary control in the distribution of organisms and ecosystems. In this thesis (Figure 6.4) large progress has been made in assessing the ocean climate of the Caribbean basin by quantifying spatial patterns (Chapter 2) and their rate of change (Chapter 4). Although some insight into the consequences of these seascape patterns to the function and distribution of marine systems has been provided (Chapter 3, Chapter 5), more can be done to fully exploit the datasets produced.

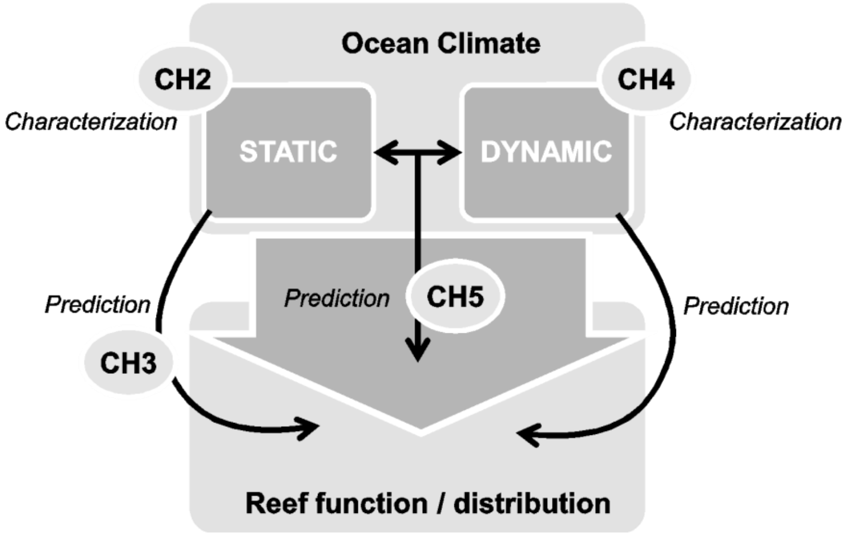

Figure 6.4. Conceptual diagram for thesis chapters (from Figure 1.3, Chapter 1). CH2: Environmental provinces of the Caribbean, CH3: Static climate, characterized by wave exposure, as a predictor of reef habitats, CH4: Recent temperature trends in the Caribbean, CH5: Upwelling as a refuge from warming.

Understanding the influence of different environments in marine systems

Maps that describe the environment of the Caribbean basin and its categorization in environmental provinces (Chapter 2) can be used to explain how biological function changes among regions, and why the attributes of marine systems differ or agree from one region to another. Reviewing previous research efforts, the categorization of the Physical Environments of the Caribbean Sea (PECS, Chapter 2) could be used to test hypotheses related to patterns of spatial variation of marine assemblages assessed by the Census of Marine Life program (Miloslavich et al. 2010). Recent research attempts have failed to find a relationship between existing oceanographic classifications, such as the Large Marine Ecosystems (Sherman and Hempel 2009) or Marine Ecoregions of the World (Spalding et al. 2007), and patterns of the distribution or diversity of organisms found in the Caribbean basin (Cruz-Motta et al. 2010; Iken et al. 2010; Miloslavich et al. 2010). According to Cruz-Mota et al. (2010) and Iken et al. (2010), much of the within-region variability observed in the Census of Marine Life database could be largely explained by differences in the environment not captured by existent classification systems. This remark suggests that an environmental-data driven categorization, such as PECS, could provide a better explanation for the spatial patterns found in this important dataset in the Caribbean basin.

When considering on-going research in the area, PECS would be ideal for the assessment of datasets collected by large monitoring efforts, such as REEF, ReefCheck, the Caribbean Coastal Marine Productivity (CARICOMP: CARICOMP 1999) and the Atlantic and Gulf Rapid Reef Assessment (AGRRA: Kramer 2003) programs. Region-wide analyses of CARICOMP data on seagrasses, mangroves and coral reefs have not yet been accomplished, but PECS is an ideal platform to assess patterns of ecosystem state or productivity within the region. On the other hand, AGRRA data on reef state, which is freely available online, have been used for regional-wide analyses by a few researchers to assess spatio-temporal trends in reef communities (Schutte et al. 2010) and identify drivers of reef degradation (Mora 2008). The use of the PECS categorization as covariates in these analyses would have improved the model fits by accounting for some of the spatial structure in the data.

The PECS categorization can also be used to refine models of ecosystem function for the basin. Two spatially-explicit simulation models of coral reefs exist for the Caribbean (Langmead and Sheppard 2004; Mumby 2006). These models vary in complexity, but include interacting species and simulate reef processes such as recruitment, growth, mortality, and natural disturbances, which are known to be influenced by oceanographic regimes (Hubbard 1997; Knowlton and Jackson 2001). Information on the physical environments of the Caribbean could be used to parameterize these models according to their environmental regimes, allowing the regional evaluation of their coral reef ecosystems. This information would clarify the role of the physical environment on reef dynamics and identify environments that promote reef resistance and resilience under diverse scenarios of local and regional change.

The use of PECS could have implications for local, national and regional marine management as it provides insight into how some coastal areas differ and require specific considerations, whilst similar areas may be able to share management approaches. On the whole, the PECS categorization could allow for the systematic, quantitative study of coastal communities, and contribute to more effective decision-making and planning through ecosystem-based management in the area.

Understanding the effects of differential warming rates in marine ecosystems

In a different line of thought, information on the dynamic ocean climate (Chapter 4) could also be used for many applications. Maps of recent changes in SSTs could provide insight into temporal modifications of physiological function in the basin, such as changes in coral growth rates during the last decades (e.g. Bak et al. 2009). Additionally, the observed trends could be used to compare previous and current spatial patterns in physiology or phenology, such as the spatial variability in the distribution and prevalence of coral and octocoral diseases (Cróquer and Weil 2009; Weil and Cróquer 2009), which has generally been attributed to increased temperatures (Harvell et al. 2009). In this regard, more detailed information on the physiological and phenological responses of marine populations of the Caribbean basin to changes in temperature is urgently required as a baseline against which to test the effects of climate change.

To fully understand the effects of increased temperatures on marine ecosystems, it is necessary to know the usual temperatures of a given area (Figure 6.5a, 6.5b) and where on the tolerance curve are the main inhabiting organisms sitting at. Some areas of the Caribbean, such as the Lesser Antilles, already have high average temperatures and are warming at relatively fast rates (27.56°C, 0.38°C dec^{-1} in St. Lucia). However, the warmest areas (e.g. western Jamaica, 28.22°C) are warming at intermediate speeds (0.24°C dec^{-1}). On the other hand, because of the weakening of the southern-Caribbean upwelling, La Blanquilla, an island off eastern Venezuela that previously experienced relatively low average and seasonal SST maxima (26.60°C and 28.17°C), is now experiencing rapid warming (0.39°C dec^{-1}, Figure 6.5). Quantifying such spatial differences in usual temperature conditions and trends is relatively straightforward. However, it is still unclear the extent that local acclimation serve to accommodate organisms' responses to increasing SSTs before they are tipped beyond their thermal optima.

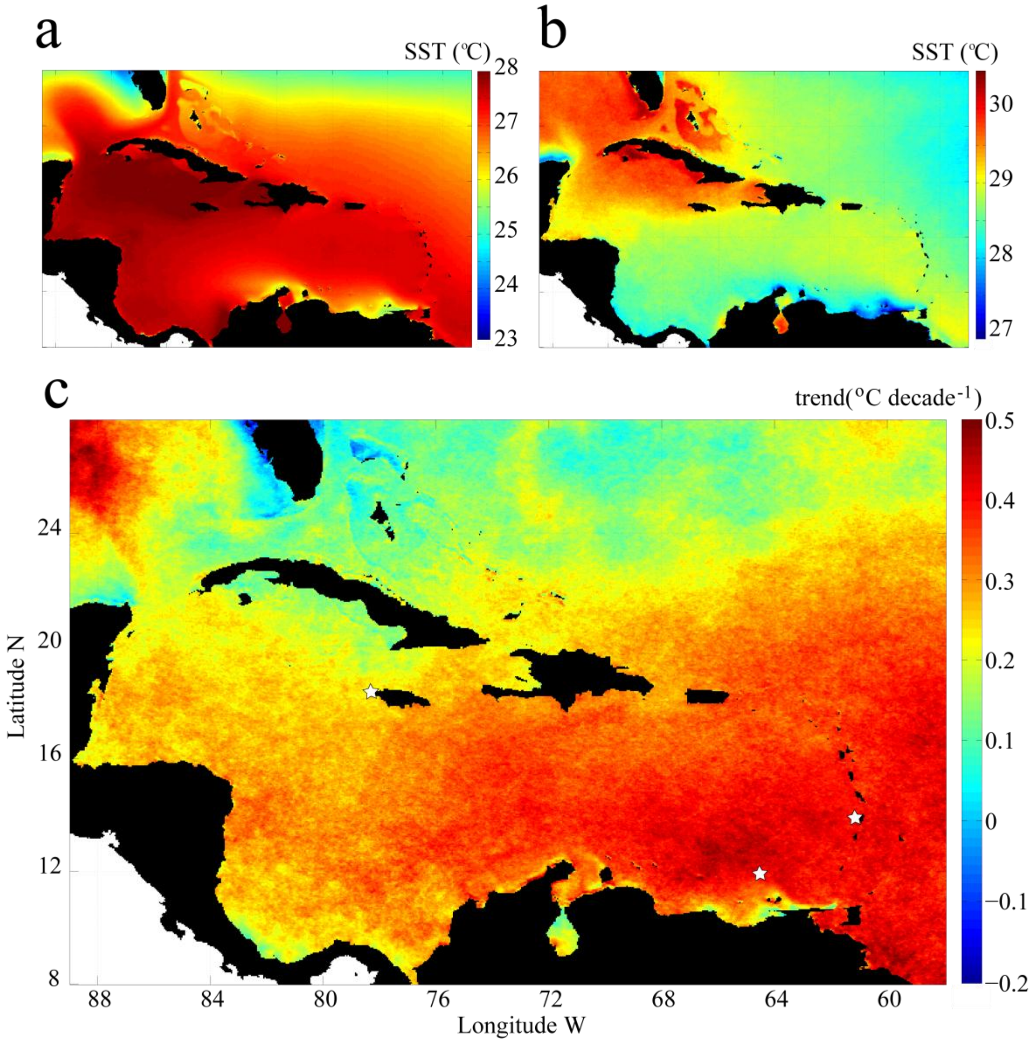

Figure 6.5. (a) Average SST; (b) SST maximum monthly mean and (c) SST trends in sea surface temperature in the wider Caribbean (AVHRR Pathfinder, 1985-2009). Stars show (from left to right) locations in Jamaica, La Blanquilla (Venezuela) and St. Lucia, mentioned in the text.

Making progress in seascape marine ecology in the Caribbean

The region-wide degradation of the wider Caribbean has motivated a wealth of studies incorporating meta-analyses that address regional questions about the status of coral reefs in the basin (Mora 2008), attempting to quantify their recent changes (Gardner et al. 2003; Schutte et al. 2010; Alvarez-Filip et al. 2011) and the potential drivers of their decline (Gardner et al. 2005; Mora 2008). Although it is well known that climate regulates many patterns and processes in marine ecosystems, and that the dynamics of reef communities vary substantially among regions (Hubbard 1997), many studies still overlook these issues when asking questions at a regional level (e.g. Gardner et al. 2003; Weil and Cróquer 2009; Schutte et al. 2010; Alvarez-Filip et al. 2011). By ignoring local climate, these studies assume that patterns and responses of organisms and ecosystems should be the same across the entire Caribbean, a naive assumption when considering the spatial variability of the basin (see Chapter 1; Chapter 2). Even if it is not the focus of the research question, information on the (relevant) environmental characteristics of the locations should be included in regional analyses. It is expected that two of the outputs of this thesis, the map of environments of the Caribbean (Chapter 2) and the map of recent SST trends (Chapter 4) would contribute in this respect. GIS files with the SST trends and the PECS classification, including both the physicochemical categorization and the physical disturbance regime, will initially be available to the scientific community through email, and then through a web-based Geographic Information System produced and maintained by the European Union's *Future of Reefs in a Changing Environment* (FORCE) project (http://www.force-project.eu/) later next year. It needs to be emphasized that different aspects of the physical environment may be needed when tackling particular research questions (see for example, the mismatch of temporal scales in the environmental predictors and biological responses used in Mora 2008). Nevertheless, the availability of this fundamental information in an accessible format will hopefully encourage the inclusion of environmental context in future regional analyses in the basin.

The climatological environmental regime defines the typical setting where organisms and ecosystems develop. The environmental disturbance regime, however, has also shaped marine ecosystems through their development (Knowlton and Jackson 2001). Although the statistical methods to characterize average conditions (based on the central limit theorem) are well understood and routinely applied by coral reef ecologists (e.g. Zar 1999), drawing generalizations from extreme conditions requires the use of a different approach. In this thesis and in most research done in coral reef ecology, standard statistics have been used to describe the patterns of rare disturbances such as bleaching events (e.g. Mumby et al. 2011; Chapter 5) or hurricanes (e.g. Edwards et al. 2011; Chapter 2). When extreme events are rare but not necessarily unprecedented (e.g. hurricanes in the north of the Caribbean basin), other better suited statistical approaches, such as extreme value theory (Katz et al. 2005), should be used to model the disturbance regime. Nevertheless, when events are too rare and they cannot be captured by the tails of the distribution (e.g. severe mass-bleaching events that have happened at best once or twice in record), their modelling is much more complicated (Easterling et al. 2000). Climate change is expected to not only modify the means of environmental parameters (as assessed in Chapter 4), but also increase the frequency of extreme events (Done 1999; Trenberth et al. 2007). The coarse spatial resolution of climate change models and their inability to incorporate some natural modes of climate variability (e.g. ENSO) make them poorly suited for assessing the spatial variability in the intensity and frequency of climate extremes (Donner et al. 2009). This is an avenue that needs to be addressed for the progress of ecological studies in the Caribbean and worldwide.

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