

Predicting the habitat distribution and grazing of coral reef fish

Submitted by **Sonia Bejarano Chavarro**,
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*To Devon, a small farewell
For my peace (your gift)
Deep gratitude from the middle of my heart.*

ABSTRACT

Although today coral reefs need to be managed to ensure their persistence in the challenging conditions imposed by a rapidly changing environment, practitioners worldwide often lack adequate tools to achieve this. Spatial patterns of the abundance of reef resources, but also of the processes that govern reef recovery after disturbance, need to be mapped at relevant scales to identify priority conservation measures. In this thesis I took important steps towards the construction of adequate tools for reef managers: towards creating maps of reef resilience. The first step comprised the accuracy enhancement of thematic maps to discriminate typical forereef habitats that differ in their structural complexity. The second step consisted of the creation of statistical models to predict spatial patterns of the density and biomass of several fish species including grazers. To date, fish species richness can be mapped but not the spatial patterns of abundance or biomass of key species of reef fish. Here, I demonstrate that it is possible to predict spatial patterns of the abundance of key species of grazers across large scales on Caribbean reefs by mapping their acoustic roughness. The third and fourth steps focused on improving our understanding of the process of parrotfish grazing on Pacific reefs. I created models to predict the grazing impact of populations of grazers from their abundance data incorporating sources of spatio-temporal variability in their grazing behaviour. Although grazing of Pacific parrotfish communities is a subject of growing concern and several aspects of its dynamics are well understood on the Great Barrier Reef, this thesis contributes with two major future goals: (1) to rank Micronesian parrotfish species according to their relative contribution to grazing impact and (2) to aid the generation of maps of grazing.

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LIST OF ABBREVIATIONS

(Part 1)

AM	Morning
ANCOVA	Analysis of covariance
ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
B	Biomass
CASI	Compact Airborne Spectrographic Imager
CMO	Consolidated <i>Montastraea</i> reefs
CRS	Completely Regularized Spline function
CRTR	Coral Reef Targeted Research & Capacity Building for Management project
CRU	Consolidated rubble
D	Density
DEMs	Digital elevation models
DMIL	Dead <i>Millepora</i>
E1	RoxAnn's acoustic roughness
E2	RoxAnn's acoustic hardness
EAARL	Experimental Advanced Airborne Research Lidar
EAM	Epilithic algal matrix
G	Gape size
GI	Grazing impact
GI _d	Total daily grazing impact
GI _h	Individual hourly grazing impact
GI _m	Monthly grazing impact
GLM	General linear model
GBR	Great Barrier Reef
GPL	Gorgonian plains
GPS	Global Positioning System
HAL	Halimeda spp.
HIG/OUT	High tide together with the first hour of outgoing tide
HSD	Honestly significant difference
IP	Initial phase

LIST OF ABBREVIATIONS

(Part 2)

ISR	<i>In situ</i> rugosity
LCO	Live coral
LRU	Loose rubble
LOW/INC	Low incoming tide
LOW/OUT	Low outgoing tide
MED/INC	Medium height incoming tide
MED/OUT	Medium height outgoing tide
MERIS	Medium Resolution Imaging Spectrometer
MID	Midday
MPA	Marine protected area (s)
NASA	National Aeronautics and Space Administration
OTH	Other substrata
PICRC	Palau International Coral Reef Center
PM	Afternoon
QTCView	Quester Tangent's acoustic seabed discrimination system
SAN	Sand patches
SH1	Sheltered barrier reef 1 (Survey site 1, Chapter 4: Ngederrak reef)
SH2	Sheltered barrier reef 2 (Survey site 2, Chapter 4: Lukes reef)
SPOT	Satellite Pour l'Observation de la Terre
TL	Fish total length
TM	Thematic Mapper
TP	Terminal phase
UMO	Unconsolidated <i>Montastraea</i> reefs
W	Width of the portion of a parrotfish jaw that is in contact with the substratum during a bite.
WBR	Exposed site in the Western barrier reef (Survey site 3, Chapter 4: New Drop-off)
z	RoxAnn's acoustic depth
ZANB	Zero Altered Negative Binomial models

DECLARATION FROM THE AUTHOR

The research questions addressed in this Doctoral dissertation were developed within the framework of objectives of the Remote Sensing Working Group of the World Bank/Global Environmental Facility. As a result, many of the scientific papers included here have been co-authored. Co-authorship was conferred to acknowledge researchers who contributed with skills that were essential to complete underwater survey procedures or that provided assistance on the use of specific computer software and the interpretation of its outputs, which were necessary to complete one or more stages of data analysis. However, under supervision the first author of the papers led and planned each of the survey and analysis procedures referred to here, and ensured they followed a logical rationale to resolve the proposed research questions.

In the following paragraphs I will describe in detail the nature of the contribution of the different authors to each of the main chapters included here.

Chapter 2 and 3:

Dr. John D. Hedley, member of the Marine Spatial Ecology Lab (Exeter) trained me in the use of the softwares ERDAS and ArcGIS to achieve the objectives of Chapter 2.

Dr. Ian Sotheran specialist of ENVISION UK (Newcastle Upon Tyne) provided the expertise in the use of RoxAnn and led the acquisition of acoustic data in April 2005. Dataset was used in Chapters 2 and 3.

Chapter 4:

Mr. Victor Ticzon, PhD student of the Remote Sensing Working Group (RSG/World Bank) at the University of the Philippines provided essential support to complete the underwater surveys making possible the collection of enough replicate observations of reef fish feeding.

CHAPTER 1: INTRODUCTION

1. INTRODUCTION

1. 1. *Coral reef ecosystems today*

Coral reefs are regarded as some of the most biologically diverse and productive ecosystems on Earth and the providers of a wealth of ecological goods and services vital for numerous human populations in tropical regions. Such goods and services include renewable food resources, protection of the physical structure of the shoreline, maintenance of habitats and biodiversity, export of organic production, recreational support, and aesthetic and cultural value among others (Richmond 1993; Moberg and Folke 1999). However, coral reefs as we know them today are changing worldwide. Local natural biological and physical disturbances such as hurricanes, typhoons, floods, earthquakes, low tides, diseases or predator outbreaks affect coral reefs recurrently (Hughes and Connell 1999; McClanahan et al. 2002). In addition, reefs are threatened worldwide by disturbances of anthropogenic origin which are increasing in diversity, frequency and scale (Salvat 1992; Hughes et al. 2003; Wilson et al. 2006), as uncontrolled human development continues altering coastal areas (Rogers 1990; Gomez et al. 1994; Munday 2004). Sedimentation, sewage-related nutrient enrichment, pollution from industrial sources (Richmond 1993) and from agriculture and land development (Salvat 1992; Hughes et al. 2003), coral and sand mining (Salvat 1992), overfishing and globalization of the reef fish markets (Jackson et al. 2001; Sadovy and Vincent 2002; Pandolfi et al. 2003) and destructive fishing practices (Edinger et al. 1998) are only some of the widely recognised anthropogenic threats to coral reefs.

Both natural or anthropogenic disturbances can be of acute or chronic duration (Connell 1997; Edinger et al. 1998). And, anthropogenic impacts can act synergistically in concert

with natural disturbances changing the conditions for reef recovery (Richmond 1993). Regardless of their origin, disturbances are generally followed by severe coral mortality and the subsequent colonization of space by algae (Done 1992). Transitions from coral dominance to macroalgal dominance are known as phase-shifts. These constitute fundamental changes in the benthic community structure of coral reefs with remarkable implications for their trophic balance (Dahl 1974) and have been widely documented (e.g. Hughes 1994; McClanahan and Muthiga 1998; McCook 1999; Gardner et al. 2003; Aronson et al. 2004). Phase-shifts have not only been associated with the deficit of reef accretion compared to the physical and biological erosion but also with a significant depletion of reef fisheries (Done 1992) and the impairment of coral settlement (Hughes 1989). As a result of phase-shifts, several reef areas around the world provide examples of once structurally complex, coral dominated systems that are no longer capable of providing the goods and services they used to when in healthier conditions (Done 1992; Goreau 1992; Moberg and Folke 1999; White et al. 2000; Rogers and Beets 2001; Gardner et al. 2003; Folke et al. 2004; Graham et al. 2006).

Region-wide catastrophic phase-shifts have been associated with sea-atmosphere processes of unusual magnitude such as the 1998 El Niño event which caused severe water-temperature anomalies in the Indian, Pacific, Caribbean and wider Atlantic oceans (Berkelmans and Oliver 1999; Stone et al. 1999; Wilkinson et al. 1999; Goreau et al. 2000). Drastic climatologic oscillations such as El Niño served as clear warnings of the imminent implications of global warming for the fate of coral reefs (Hayes and Goreau 1991; Goreau et al. 2000). Although it was earlier challenged by sceptical views, climate change is now a widely recognised reality manifest in several oceanographic changes among others (Walther et al. 2002). Among these changes, the temperature rise and ocean acidification

are critical because they compromise two essential aspects of reef-building corals: the maintenance of their symbiotic associations with zooxanthellae and their calcification (Hoegh-Guldberg et al. 2007). Pessimistic future scenarios of reef degradation have been predicted (see Hoegh-Guldberg et al. 2007) as a result of the synergies and feedbacks that climate change may produce in concert with local episodic threats to coral reefs (Newton et al. 2007).

Today, managers, conservationists, and direct users of coral reefs are witnessing these fragile systems being pushed towards their tolerance thresholds. Major ecological concerns are driving efforts to determine whether algal-dominated reefs are an alternative stable state of the ecosystem or a reversible result of a phase change (e.g. Mumby et al. 2007b). It is in this panorama of uncertainty regarding the future of reefs worldwide, where the term “resilience” has re-emerged in recently published literature. There, resilience has evolved rapidly as a concept and it is regarded today as a desirable attribute of modern coral reefs.

1.2. What is resilience and what are its sources?

A few definitions of the concept of resilience have been cited and adapted by reef ecologists as further understanding on the dynamic nature of reefs is gained (Nyström and Folke 2001; West and Salm 2003). In the broad context of ecosystems, Walker et al (2004) defined resilience as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks”. Early definitions of resilience concentrated on the stability of systems near a single equilibrium state whereas recently proposed definitions of “ecological resilience” do not assume that systems rebound to their previous state but that these can flip to a new alternate stable state (Nyström et al. 2000).

Resilience is understood today as an attribute that reefs must have in order to cope with disturbance and to avoid exceeding ecosystem thresholds to an alternate stable state; but most importantly, as an attribute that can be altered by humans (Nyström and Folke 2001). The fate of a coral reef after disturbance will depend on which sources of resilience are present for self-organization (Nyström et al. 2000).

Sources of resilience have been reviewed by Nyström and Folke (2001), McClanahan et al (2002) and West and Salm (2003) among others. Some of the most important sources are the functional diversity, diversity within functional groups, species redundancy, patterns of ocean currents and connectivity, rate of larval recruitment, the innate ability of different corals to produce competent larvae that will recruit successfully, healthy populations of grazers (Nyström and Folke 2001; McClanahan et al. 2002; West and Salm 2003; Obura 2005; Mumby et al. 2007b) and reef's connectivity to mangroves (Mumby and Hastings 2008).

1.3. Grazing as an important source of resilience

The grazing function in coral reefs relies on certain families of reef fish and sea urchins. Fish grazing plays a key role in the recovery of reefs (McClanahan et al. 2006) not only because it is one of the major forces regulating the distribution and abundance of benthic algae (Steneck 1988) but also because it is linked to the reduction of coral mortality (Hughes et al. 2007) and the increase in coral recruitment (Mumby et al. 2007a). Parrotfishes are major contributors to the grazing process because in most fish communities they comprise diverse and abundant species assemblages (Russ 1984a; Jennings et al. 1996; Jennings and Polunin 1996; Wantiez et al. 1997; Letourneur et al. 1998) that graze on the benthos continuously and actively throughout the day (Bruggemann et al. 1994a; Bellwood

1995). Parrotfishes have strong jaws and their grazing mechanisms include scraping or excavating the substrate, removing turf, endolithic algae and detritus (Bellwood and Choat 1990; Bruggemann et al. 1994b; Streebman et al. 2002). Therefore, these common herbivores are also significant contributors to reef bioerosion (Bellwood 1995) and sediment production (Bellwood 1996).

It has been widely recognized that in order to protect the resilience of reefs, herbivorous fish grazing needs to be actively managed (Nyström et al. 2000; Bellwood et al. 2004) and that this can be attained through fishing restrictions (Roberts 1995; Rakitin and Kramer 1996). However, understanding the ecological importance of the process to be managed is only the first step. Parrotfishes are heavily targeted not only in those places where fisheries have depleted the stocks of large predators (Munro 1983; Pauly et al. 2002) but also as an important part of traditional culture in several countries (Johannes 1978). Both the characterization of the socio-economic aspects of the fisheries of herbivorous fishes and a comprehensive set of information regarding the fish grazing process should be ideally available for practitioners.

1.4. Effective ecosystem management of today's coral reefs

In response to the numerous threats to coral reefs and their associated fisheries local strategies such as the implementation of marine protected areas (MPAs) and fishing regulations have emerged (Agardy 1994; Holland and Brazee 1996; Polunin and Roberts 1996; Agardy et al. 2003; Halpern 2003). Although marine reserves can be powerful management and conservation tools and have accounted for a number of local successes rewarding the efforts to mitigate certain impacts (e.g. Roberts and Polunin 1994; Chiappone et al. 2000; Graham et al. 2003; Samoilys et al. 2007), they fail to alleviate problems that

originate outside reserve boundaries, such as pollution, climate change, or overfishing (Lubchenco et al. 2003).

The severity of global-scale coral reef declines and the recognition of the complexity of factors that underlie recovery have prompted the reassessment of current management practices (Bellwood et al. 2004). Firstly, in the context of fisheries management for example, greater sustainability is likely to be achieved through incorporating multispecies interactions and influences of the physical environment on the abundance of fish resources (Botsford et al. 1997). Secondly, effective management practices must encompass multiple spatial scales and habitat types (Kuffner et al. 2007). And thirdly, because many acute disturbances cannot be mitigated directly, management must focus on the understanding and protection of key processes that underpin reef resilience rather than on measuring static attributes of reefs (Folke et al. 2004; Pressey 2004). Processes of coral recovery must be enhanced through the management of watersheds, nutrient-runoff, and grazers (Bellwood et al. 2004; Obura 2005).

1.5. The importance of scale for management

The urgency of regional-scale management has become obvious in the light of the unequivocal evidence of the importance of large-scale processes on coral reef ecosystem sustainability and function (Roberts 1997; Mumby and Steneck 2008). Several physical and biological attributes and processes of reefs often vary across large spatial scales: On the Great Barrier Reef for example, strong latitudinal cross shelf gradients of salinity, nutrient input, water clarity and exposure to prevailing wind exist (Wilkinson and Cheshire 1988). Moreover, scarid abundance and biomass vary at both the cross shelf scale (of tens of kilometres) and between sites (hundreds to thousands of metres apart) (Gust et al. 2001).

Lastly, coral recruitment and presumably the rate of post-recruitment survival also vary across geographic regions (Hughes et al. 1999). Not only attributes, but also processes vary on wide spatial scales. Several reef sites off Palau experienced differential rates of recovery after the 1998 bleaching event, and such variability was related to local circumstances of reefs including habitat type, depth, water-flow rates, seasonal irradiance and temperature extremes, adjacent refuges, and coral species composition (Golbuu et al. 2007). Furthermore, ocean currents transport pelagic eggs and larvae of coral reef organisms on the scale of tens to hundreds of kilometres, generating interconnections among fairly distant reefs (Cowen 2002). Strong connectivity may occur among distant reef areas implying that local populations in reefs may depend on processes occurring elsewhere (Roberts 1997).

Conducting surveys to capture the scales at which natural variability of attributes and processes of coral reefs occur is often impossible or prohibitively expensive. Economic constraints usually limit the scope of monitoring programs and environmental assessments by forcing a trade-off between an adequate temporal resolution and sufficient spatial coverage to adequately represent the study area.

1.6. The role of remote sensing

The use of satellite imagery for the assessment of coral reefs was first explored by Smith et al (1975) and its application to science and management has been exhaustively investigated ever since (Mumby et al. 1997). Habitat maps based on remotely sensed data have emerged as a fundamental tool for management because they summarize ecologically-meaningful information across extensive geographic scales in a cost-effective manner (Mumby and Harborne 1999). Such maps can be used to stratify reserve designation by representative habitat types (McNeill 1994; Fernandes et al. 2005), delineate reserve boundaries (Biña

1982), stratify ecological survey and monitoring, map reef communities (Dustan et al. 2001; Palandro et al. 2003), identify hotspots of habitat diversity (Harborne et al. 2006), detect coral bleaching (Andréfouët et al. 2002), and on occasion, quantify coral cover (Mumby et al. 2001).

The accuracy achieved using optical instruments to map reefs is hindered by a number of factors. Firstly, with the exception of the CASI, optical sensors with the greatest spectral resolution have insufficient spatial resolution to distinguish common reef features, whereas those with higher spatial resolution, have limited capacity to separate reef spectra (Mumby et al. 1998b; Mumby and Edwards 2002). Furthermore, spectral data do not reflect patterns of seabed reflectance directly. Variations in water depth and apparent optical properties (e.g., turbidity) strongly influence the recorded signal and confound interpretation (Maritorea et al. 1994; Mumby et al. 1997; Green et al. 2000).

The accuracy achieved in the discrimination of coral reef habitats with optical remote sensing can be improved using the depth-invariant transformation of spectral bands (Lyzena 1978), textural information derived from satellite data (Mumby and Edwards 2002), contextual editing (Mumby et al. 1998a), estimating bathymetry from multispectral images (see Lyzena et al. 2006; Lesser and Mobley 2007), or using ancillary depth data recorded by acoustic instruments to adjust the reflectance recorded in satellite spectral data to a uniform depth (Purkis and Riegl 2005; Riegl et al. 2005; Riegl and Purkis 2005). The uses of remote sensing have tended to be limited to mapping certain attributes of systems whereas less attention has been paid to the representation of spatial patterns of reef processes. Moreover, several important attributes that reflect the state of coral reefs such as coral cover, macroalgal cover, coral recruits and density and sizes of reef fish cannot be

measured routinely using remote sensing. The use of remote sensing should be directed towards obtaining predictions of the levels of key processes (e.g. grazing) across seascape scales. Maps of grazing, for example, would have obvious management applications because they would convey large scale information on the spatial patterns of reef resilience.

1.7. Synopsis of this thesis

The four chapters comprising this thesis aim to contribute to the three different management needs summarised in section 1.3 of this introduction and illustrated in Figure.

1. In the following subsections the contribution of each chapter to these management needs is described in detail:

1.7.1. Combining optical and acoustic data to enhance the accuracy of coral reef habitat maps

Geomorphological zones of coral reefs comprise a mosaic of communities denominated “habitats” in the context of habitat mapping, which can be defined as naturally-occurring assemblages of benthic macro-organisms and substrata (Mumby et al. 1997). Some of these habitats may be strikingly different in their topographic complexity whereas some others may have a similar topographic complexity but one might comprise mostly live coral and other might be dominated by algal turfs. The contrasting structural characteristics that may exist between habitats will drive important differences in the associated fish communities and possibly in the levels of fish grazing.

Although of ecological importance, the discrimination and mapping of habitats within geomorphological zones of reefs from optical satellite data has proved challenging (Mumby et al. 1997). The accuracy of such habitats maps is severely hindered by a number of factors

that affect spectral data and that will be detailed in Chapter 2. Acoustic remote sensing instruments provide data fundamentally different from spectra and are therefore unaffected by some of the limitations of optical sensors, such as variable water depth. While it seems reasonable to expect that acoustic sensors may also have an added benefit of helping to discriminate reef habitats and that the combination of good quality optical and acoustic products will work synergically to enhance accuracy, the magnitude of such enhancement has not yet been quantified. Taking optical data as a starting point, Chapter 2 explores the accuracy that can be achieved for the discrimination of coral reef habitat types by adding three new data axes: seabed roughness (E1), hardness (E2), depth (z), and the use of acoustic depth to adjust the reflectance recorded in satellite spectral data to a uniform depth. The chapter assesses the impact of combining optical and acoustic data on the accuracy with which key forereef habitats can be discriminated in a Caribbean system.

1.7.2. Predicting the structural complexity of reefs and fish abundance using RoxAnn

Reef fish communities depend fundamentally on the structural integrity of their physical environment (Sale 1991; Chabanet et al. 1997). The three-dimensional framework of reefs does not only provide transient and permanent refuges from predation to fishes of a variety of sizes and shapes (Caley and St John 1996) but also provides fishes with foraging, spawning and nesting sites (Robertson and Sheldon 1979) and can help them maintain themselves in high-flow environments (Johansen et al. 2008).

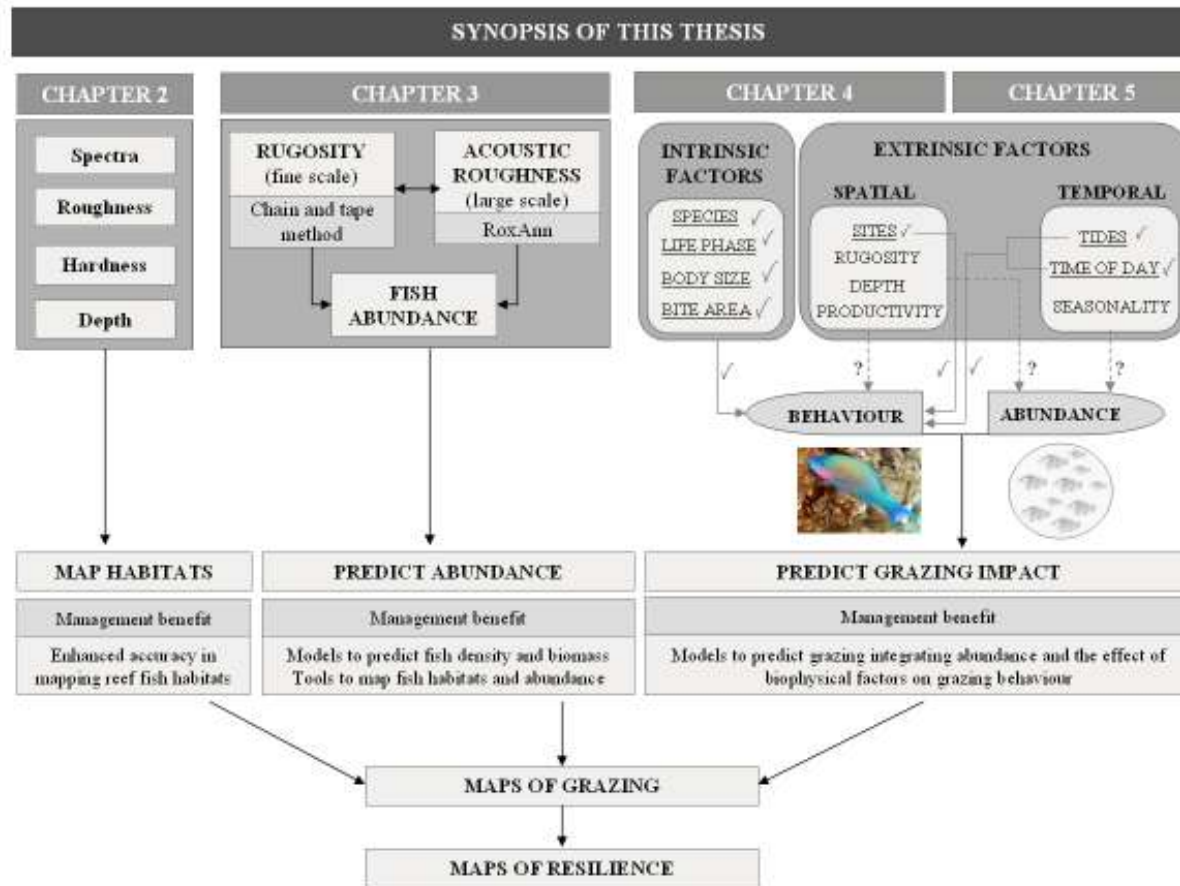


Fig. 1. Synopsis of the chapters comprising this thesis. Chapters 2 and 3 developed tools to predict habitat distribution and those spatial patterns of fish density and biomass that follow patterns of rugosity in Caribbean reefs. Chapters 4 and 5 focused on predicting the grazing impact of parrotfishes on Pacific reefs integrating the effects of several biophysical factors on feeding behaviour. Among the factors affecting the behaviour and abundance components of the grazing process only those marked and underlined were addressed in this thesis and their effect (solid arrows) was quantified. Some of the unmarked factors and their effects (dashed arrows) have been quantified in other studies and others will be the focus of my future research.

The influence of topographic complexity on a number of attributes of reef fish communities is well known (Luckhurst and Luckhurst 1978; Carpenter et al. 1981; Sale and Douglas 1984; Caley and St John 1996; Rooker et al. 1997; Friedlander and Parrish 1998a, b; Ohman and Rajasuriya 1998; Nanami and Nishihira 2002; Friedlander et al. 2003; Gratwicke and Speight 2005a, b), but information on species-specific responses to changes in topographic complexity is scarce (Lawson et al. 1999; Mumby and Wabnitz 2002; Gratwicke and Speight 2005a). Chapter 3, addresses Caribbean reef fish-habitat relationships to generate models to predict patterns of the density and biomass of 34 functionally and commercially important species as a function of spatial variation of *in situ* rugosity. Furthermore, by examining the relationship of *in situ* rugosity with a large-scale measurement of topographic complexity that can be obtained from the return signals of scientific quality echo-sounders (RoxAnn), the scope of acoustic remote sensing for mapping reef fish abundance patterns is explored.

1.7.3. *Predicting parrotfish grazing impact in Palau, Micronesia*

The grazing intensity of parrotfish communities is often assumed to be directly proportional to their biomass and therefore biomass has usually been quantified (Russ 1984a, b; Gust et al. 2001; Russ 2003; Mumby and Dytham 2006) with the implicit expectation that this can be interpreted as a direct surrogate for the grazing function. However, this approach ignores both intra and interspecific differences in grazing behaviour and the physical and biological factors that might drive such differences. More accurate estimates of the overall parrotfish grazing impact might be obtained by recognizing that fish grazing is a function of the abundance of grazers and their feeding behaviour. It is essential to understand and quantify the effect of intrinsic factors that control the grazing behaviour of a fish such as species, life phase, body size, area grazed of each bite and extrinsic factors that may cause temporal and spatial variability on both

behaviour and abundance of grazers such as seasonality, time of day, tidal regime, depth, primary production, availability of grazing substrates and substrate complexity. By focusing on the understanding of the process of grazing on Micronesian reefs from a biophysical perspective, Chapters 4 and 5 aimed to provide models to predict the grazing impact of populations of grazers from abundance data, incorporating sources of spatio-temporal variability in their grazing behaviour.

1.8. *Creating continuous maps of fish grazing: a future goal*

Chapters 1 and 2 are concerned with mapping important reef fish habitats and patterns of reef fish density and biomass across a gradient of topographic complexity. Chapters 3 and 4 are concerned with predicting the grazing of a particular fish community. Taken together these studies take important steps towards creating maps of fish grazing.

The creation of such maps is outside of the scope of this thesis because the opportunities to collect data were separated into two biogeographic regions (Belize in the Caribbean and Palau in the Pacific). The remote sensing-oriented studies described here were conducted in the Caribbean in response to the priorities of the existing funding and the wealth of remote sensing studies available for the region. Fish grazing studies were conducted on Pacific reefs because it is in this region where a larger number of species of grazers occur and quantitative aspects of their grazing behaviour were relatively poorly understood.

My future research will be directed to make the spatial predictions of the abundance of a parrotfish community and the models to predict its grazing impact available for the same geographic location.

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CHAPTER 2:
COMBINING OPTICAL AND ACOUSTIC DATA TO ENHANCE THE
ACCURACY OF CORAL REEF HABITAT MAPS

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Combining optical and acoustic data to enhance the accuracy of coral reef habitat maps

Sonia Bejarano^{1*}, Peter. J. Mumby¹, John D. Hedley¹ and Ian Sotheran²

* *Corresponding author*

¹ *Marine Spatial Ecology Lab, School of Biosciences, Hatherly Laboratories, Prince of Wales Road, University of Exeter, Exeter, Devon, EX4 4PS, United Kingdom.*

² *Envision UK. Horsley, Newcastle upon Tyne. NE15 0NY, United Kingdom.*

ABSTRACT

Maps of coral reef habitats are fundamental tools for reef management and high map accuracy is desirable to support appropriate decisions, such as the stratification of marine reserves by habitat class. While satellite sensors have been used to map different reef communities, the accuracy of these maps tends to be low (overall accuracy <50%) and optical airborne methods with high spectral resolution have, to date, been the most effective (if expensive) means of achieving higher accuracy. A potential means of compensating for the low spectral and radiometric resolution of optical satellite data, which is a major cause of its poor performance, is to combine satellite data with acoustic remote sensing. This study quantified the benefit of the combination between optical satellite data (IKONOS) and acoustic (RoxAnn) sensors. The addition of acoustic data provided 3 new data axes for discriminating habitats; seabed roughness (E1), reef depth (z), and the depth correction of satellite spectral data to uniform depth. Seabed hardness (E2) was not an informative channel in our study. The use of z to conduct the water-column correction of the optical bands to uniform depth is a potential improvement over applying the depth-invariant index approach to optical data in the absence of ancillary information on depth. Habitat maps of Glovers reef (Belize, Central America) were created using k -means unsupervised classification on nine different

treatment images constructed from various combinations of optical and acoustic data layers. The maximum benefit of data combination was achieved by depth-correcting the optical bands. The accuracy of maps based on the depth invariant optical index was not enhanced when E1, E2 or z were added as separate layers but was enhanced when these three acoustic measures were added in concert. The combination of data can improve the accuracy of habitat maps and the availability of both datasets allows practitioners to take advantage of each techniques' additional strengths such as providing synoptic continuous imagery for education and general management planning (in the case of optical imagery) and maps of reef rugosity (in the case of acoustic data).

Keywords: IKONOS, RoxAnn, acoustics, habitat mapping, accuracy, coral reefs.

1. Introduction

Coral reefs are globally important ecosystems supporting a wealth of biodiversity and providing many goods and services for human populations (Moberg and Folke 1999). However, reefs are among the most severely threatened ecosystems from both local anthropogenic disturbance and global climate change (Hoegh-Guldberg et al. 2007). The need for coral reef management is great and many conservation programmes exist, most of which utilise maps of reef habitats as a basis for decision-making (Green et al. 1996; Holden and LeDrew 1998).

Coral reef habitat maps based on remotely sensed data are a fundamental tool for management because they summarise ecologically-meaningful information across extensive geographic scales in a cost-effective manner (Mumby and Harborne 1999). Such maps can be used to stratify reserve designation by representative habitat types

(McNeill 1994; Fernandes et al. 2005), delineate reserve boundaries (Biña 1982), stratify ecological survey and monitoring, map reef communities (Dustan et al. 2001; Palandro et al. 2003), identify hotspots of habitat diversity (Harborne et al. 2006), detect coral bleaching (Andréfouët et al. 2002), and on occasion, quantify coral cover (Mumby et al. 2001). Because coral reef habitat maps, derived from remotely sensed data, play a role in decision-making, there is an imperative for these maps to be produced both as accurately and cost-effectively as possible.

Most coral reef mapping studies have used optical satellite products (26 of 32 papers reviewed, and also see Green et al. 1996). Optical products from a range of satellite sensors have successfully mapped the geomorphological zones of reefs (e.g., forereef, crest, algal rim, spur and groove) with moderate accuracy (Biña 1988; Bour 1988; Kuchler et al. 1988; Ahmad and Neil 1994). However, the discrimination of reef communities (hereafter referred to as habitats to be consistent with the term ‘habitat mapping’) within each geomorphological zone has proved challenging for optical satellite data (Mumby et al. 1997). Communities or habitat classes are defined as naturally-occurring assemblages of benthic macro-organisms and substrata (Mumby et al. 1997). Unfortunately, many reef communities have similar spectral reflectance signatures. For example, habitats dominated by brown macroalgae (e.g., *Dictyota pulchella*) can resemble habitats dominated by live coral because the dominant organisms in both habitats contain photosynthetic pigments with similar absorption spectra (Hedley and Mumby 2002). Satellite sensors available today were not designed for application to coral reef environments. Therefore, their spectral configuration (i.e. number, location and band width of spectral bands) is not optimised to discriminate coral reef habitats. Due to the spatial heterogeneity of coral reefs sensors of high spectral and spatial resolution would be ideal for habitat mapping. However, sensors

with the greatest spectral resolution (e.g., MERIS, HYPERION) have insufficient spatial resolution to distinguish common reef features, whereas those with higher spatial resolution, such as IKONOS, have limited capacity to separate reef spectra (Mumby et al. 1998b; Mumby and Edwards 2002).

The accuracy achieved using optical instruments to map reefs is also hindered by uncertainty in the interpretation of spectral data. Ideally, the spectral data would reflect patterns of seabed reflectance directly, but variations in water depth and apparent optical properties (e.g., turbidity) strongly influence the recorded signal and confound interpretation (Maritorena et al. 1994; Mumby et al. 1997; Green et al. 2000). Uncertainty in water depth can be partly mitigated by using the depth-invariant transformation of spectral bands (Lyzenga 1978), which has been found to offer some improvements in map accuracy over using untransformed bands (Mumby et al. 1998a). However, the depth-invariant method remains vulnerable to within-image changes to the diffuse attenuation coefficient of light in each spectral band, which might occur if, say, turbidity varies along the reef.

The limitations of spectral data, particularly in areas with high turbidity, has motivated a wealth of acoustic remote sensing studies, that utilize data from the return signals of scientific quality echo-sounders. Many studies of acoustic remote sensing for seabed mapping have focused on soft bottom environments. Several studies have demonstrated that simple point-based acoustic systems are able to discriminate a variety of substrate types (Pinn et al. 1998; Morrison et al. 2001; Foster-Smith and Sotheran 2003; Freitas et al. 2003a; Freitas et al. 2003b; Foster-Smith et al. 2004; Freitas et al. 2005; Freitas et al. 2008) and that resulting habitat maps can yield reasonably high accuracies (i.e. Foster-Smith and Sotheran 2003; Foster-Smith et al. 2004). Relatively few studies have

examined the acoustic discrimination of hardbottom habitats such as coral reefs, though some revealing studies do exist (i.e. White et al. 2003; Purkis and Riegl 2005; Riegl et al. 2005; Riegl and Purkis 2005). High accuracies i.e. $\tau > 60$ have been achieved for coral reef habitat maps of coarse resolution using RoxAnn data layers (White et al. 2003) but also using acoustic depth (z) to conduct the water-column correction of optical bands for actual depth (Purkis and Riegl 2005; Riegl et al. 2005; Riegl and Purkis 2005).

Fundamentally, acoustic and optical instruments provide distinct but potentially complementary data on the nature of benthic communities (Malthus and Mumby 2003; Riegl and Purkis 2005). Taking optical data as a starting point, the addition of acoustic imagery provides 3 new data axes potentially useful to discriminate hardbottom habitats; seabed roughness (E1), hardness (E2) and depth (z), and the use of such ancillary data on reef depth to adjust the reflectance recorded in satellite spectral data to a uniform depth, usually the water surface. While it seems reasonable to expect that the combination of good quality optical and acoustic products will work complementarily to enhance accuracy, the magnitude of such enhancement has not been yet been quantified. The present study compared the accuracy of mapping coral reef habitats using (a) only optical data, (b) only acoustic data and (c) combinations of acoustic and optical data. The following questions were addressed.

- 1) Benefit of optical-acoustic data combination: To what extent does the combination of optical and acoustic data enhance the accuracy of coral reef habitat maps?
- 2) Relative contribution of acoustic parameters: What is the relative contribution of E1, E2 and z to the accuracy enhancement, if any?

3) Value of water-column correction using z : To what extent is the accuracy enhanced by the depth-correction of optical bands using a layer of z ?

2. Methods

2.1. Study area

The study was conducted on the forereef of Glovers Reef Atoll (16° 44' N, 87° 50' W) in Belize, Central America. Acquisition of acoustic data, optical and ground-truth surveys took place between March and April 2005. The forereef comprises a gently sloping calcareous terrace descending from the emergent reef crest to an escarpment at a depth ranging from approximately 10 m to 20 m where *Montastraea* spp. are the major reef-building corals. Three habitats were identified at a depth of 5 m to 20 m: 1) Consolidated *Montastraea* reefs, denoted CMO, typically with a density of nearly 1 colony m⁻², 2) Unconsolidated *Montastraea* reefs, denoted UMO, typically with a colony density of approximately 0.2 per square metre), 3) communities of gorgonians established on hard bottom plains, with very few hard coral colonies, denoted GPL, and 4) sand patches, denoted SAN (Fig. 1).

2.2. Acquisition of optical data

IKONOS imagery was selected as a high spatial resolution source of optical satellite data because it is relatively good at discriminating coral reef features (Andréfouët et al. 2003). The IKONOS image used in this study encompassed the south-western region of Glovers Atoll and was acquired in March 2005 under favourable weather conditions, with calm sea surface and no cloud cover. Only the multispectral data were used in this study, comprising blue and green channels with a spatial resolution of 4 m x 4 m (Maeder et al. 2002).

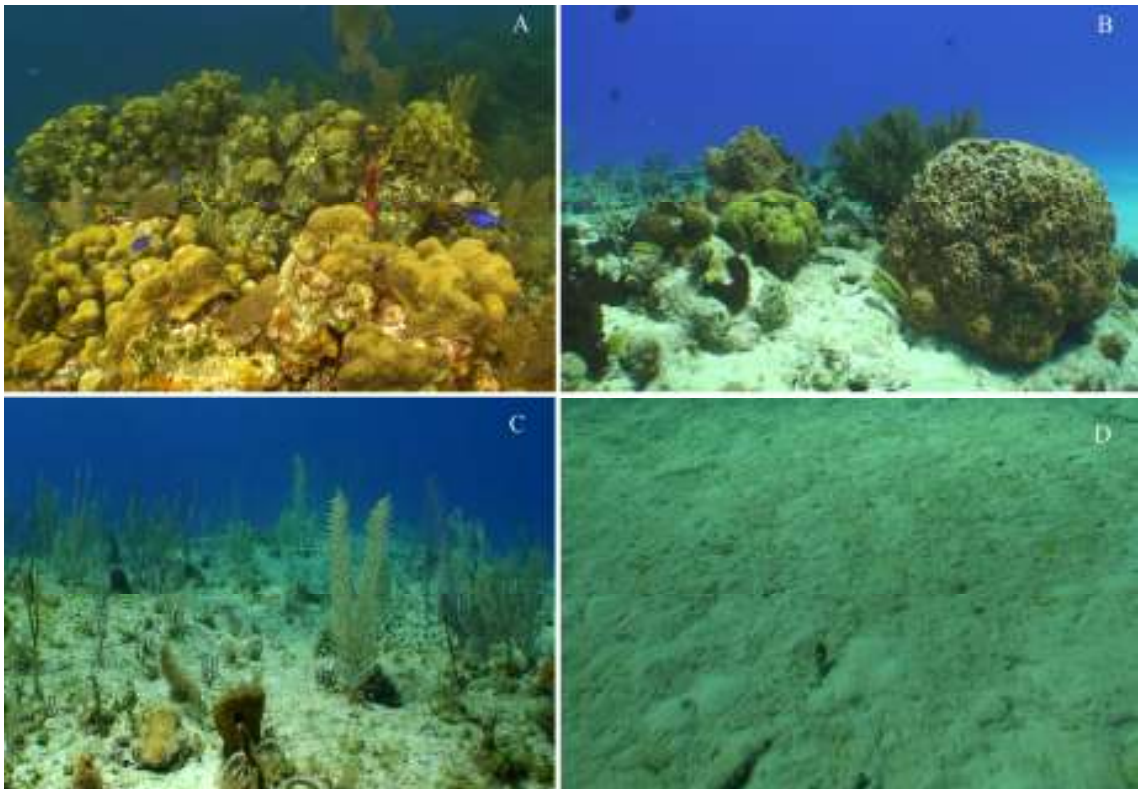


Fig. 1. Habitat classes mapped in this study: A) Consolidated *Montastraea* reefs with the highest substrate complexity comprised by densely grouped colonies of *Montastraea* spp. (Mean rugosity index: 1.9), B) Unconsolidated *Montastraea* reefs with sparse medium sized colonies of *Montastraea* spp. (Mean rugosity index: 1.3), C) Gorgonian plains: communities of gorgonians densely or sparsely distributed and mixed with macroalgae or small-sized colonies of scleractinian corals (Mean rugosity index: 1.2) and D) Sand patches.

2.3. Acquisition of acoustic data

Acoustic data were collected using the RoxAnn™ signal processor. Although RoxAnn uses a dual frequency echo sounder (Furuno FCV-600L, 50 and 200 kHz) it was operated at 200kHz during our survey. Geographical co-ordinates were provided by an integrated GPS receiver (Furuno GP-37/GP-32). Beam width at 200 kHz was set at 10° which gave a footprint of approximately 17 % of water depth. Since depth logged by RoxAnn was between 3 and 22 m, the diameter of the footprint ranged from

approximately 0.51 m in the shallowest areas to 3.74 m in the deepest areas. Vessel speed was kept constant at 8 km h⁻¹. A data point was logged every 2 to 5 m and the distance between the tracks was approximately 100 m.

2.4. Ground-truthing

The study site was chosen because of the range of reef habitats available but also because the locations of each habitat are well known from extensive field surveys. The 12 km stretch of reef considered has been subjected to more than 1000 hours of underwater field observation by one author (PJM) in which sections of reef habitat have been mapped underwater and surveyed for both benthos and fish. Additional field surveys were carried out in March 2005 to mark the boundaries of reef habitat types in which divers and snorkelers swam along 1 km transects towing a GPS. A total of 1873 ground data were extracted from the underwater maps and survey transects. Half of the points in this dataset (hereafter referred to as the "calibration data") were used to assign a habitat class to each of the initial classes resulting from the unsupervised classification. The remaining half of the dataset (hereafter referred to as the "validation data") was used to conduct the accuracy assessment of the final 4-habitat class maps. Validation data were stratified along the length of the forereef of Glovers Atoll and were located at least 200 m apart from each other. The image registration was good and the location of sand patches in the image, matched unequivocally the sand patches observed in the field.

2.5. Data processing

2.5.1 Optical data

A typical satellite sensor (such as IKONOS) can penetrate up to 8 m in the blue band, 6 m in green, and 2 m in red region (Mishra et al. 2005). Because most of the forereef habitats considered in this study were located between 6 and 12 m, only the blue (450 – 520 nm) and the green (520 – 600 nm) bands of the image were utilised during image processing. Image processing was completed using ENVI. Firstly a radiometric correction was conducted by applying a simple dark pixel subtraction (Jensen 1996). Secondly, two procedures were applied to remove the effects of water column attenuation on benthic reflectance; the first – depth-invariant index – was based only on optical data, and the second – depth correction – utilised the actual depth data from the acoustic sensor. Both procedures started by obtaining the natural logarithm of reflectance for a uniform substratum (sand) at various depths. The depth-invariant optical index (layer I, Table 1) did not require measurements of depth as only the ratio of attenuation coefficients between the blue and green spectral bands were estimated using Lyzenga's algorithm (Lyzenga 1978):

$$D_{bg} = \ln(b) - [k_g/k_b] \times \ln(g) \quad \text{Equation (1)}$$

where k_g/k_b is the ratio of attenuation coefficients between the green and blue bands.

This method resulted in a single depth-invariant index of bottom type.

The second procedure corrected the reflectance data in each spectral band to a uniform depth of the water surface (layers II and III, Table 1). Estimates of k_g and k_b were derived from the slope of the regression between the natural logarithm of reflectance for

sand and the acoustic depth (Mumby et al. 2004). The reflectance of every pixel in the image was then standardised to a depth of zero metres (R_0) by resolving:

$$R_0 = R_z / \exp(-kz) \quad \text{Equation (2)}$$

where z for every pixel was obtained from the interpolated surface of the acoustic depth (z) (see below) and k is k_g or k_b depending on the band to be corrected.

2.5.2. Acoustic data

The RoxAnnTM signal processor logs the depth (z) and derives two parameters of the substrate by integrating components from the first and second seabed echoes: E1 is an integration of the tail of the first echo and represents the roughness and E2 integrates the whole second echo and represents the hardness (Greenstreet et al. 1997). The acoustic dataset of the RoxAnn system was imported into a spreadsheet for filtering and normalisation. Records of E1 and E2 above the 95th percentile or below the 1st percentile were discarded as outliers and all remaining records were normalised by dividing them by the 95th percentile to stretch the range of values between 0 and unity (Riegl et al. 2005). Filtered and normalised data of E1, E2 and z were interpolated to create grids of equal size to the pixels of the IKONOS imagery. Grids were created by interpolating the tracks using the Completely Regularized Spline function (CRS) to produce a single value of E1, E2 and z for each satellite pixel. The CRS belongs to the Radial Basis Functions, a family of exact interpolators, and assumes that the surface should pass through or close to the data points while being as smooth as possible (Talmi and Gilat 1977).

2.6. Unsupervised classification of different treatments

In order to quantify the utility of the different optical and acoustic data layers and the benefit of combining data sources, a series of habitat maps were generated using *k*-means unsupervised classification on nine different images (hereafter referred to as treatments) constructed from various combinations of the optical and acoustic data layers (Table 1). In all cases 32 initial unsupervised classes were generated and later merged into the four habitat classes of interest (Fig. 1). For consistency among treatments, we used the same calibration data (935 field data points) and a standardised procedure to determine which of the initial classes should be merged. Firstly, we calculated the total number of calibration data points classified within each of the 32 unsupervised classes. For each of the unsupervised classes, we then calculated the percent of calibration data points belonging to each habitat class (CMO, UMO, GPL and SAN). Each unsupervised class was then assigned a habitat category based upon the modal habitat category from field calibration data. Unsupervised classes of the same overall habitat category were then merged.

2.7. Accuracy assessment

The accuracy of all habitat maps was determined using an independent validation data set (938 field data points) and represented using error matrices that quantify overall accuracy (i.e. the percentage of correctly classified reference sites), the user's accuracy per habitat class and the Tau coefficient which accounts for the agreement obtained after removal of the random agreement expected by chance (Næsset 1996). The Tau coefficients of 10 pairs of treatments were systematically compared using Z-tests (see Ma and Redmond 1995) to answer the main and secondary research questions of our study as indicated in Table 2. The difference between the coefficients of two treatments was significant at the 95 percent significance ($Z_{0.05} = 1.96$) when the Z- statistic > 1.96

and the p-value < 0.05. Supervised classification using the maximum likelihood decision rule (Mather 1987) was conducted on all the multiple layer treatments (E – K, Table 1).

Table 1. Treatments (as rows) of optical and acoustic data layers (as columns) used separately or as part of different combinations to produce habitat maps of Glovers Reef. The asterisks indicate the layers comprising each treatment.

		Layers					
		Optical data			Acoustic data		
		I	II	III	IV	V	VI
Treatment	Description	Depth invariant index	Depth-corrected blue band	Depth-corrected green band	Roughness (E1)	Hardness (E2)	Depth (z)
A	Only optical	*					
B	Only acoustic roughness				*		
C	Only acoustic hardness					*	
D	Only acoustic depth						*
E	Only acoustic (roughness, hardness and depth)				*	*	*
F	Combined optical and roughness (without depth or hardness)	*			*		
G	Combined optical and hardness (without roughness or depth)	*				*	
H	Combined optical and depth (without roughness or hardness)	*					*
I	Combined optical plus roughness, hardness and depth.	*			*	*	*
J	Depth corrected optical		*	*			
K	Combined depth corrected optical and all acoustic parameters		*	*	*	*	*

Table 2. Comparisons between treatments used to answer each of the main and secondary research questions of our study.

Research question	Comparison of treatments
1) Benefit of optical-acoustic data combination	
1.1. <i>Enhancement of optical data by acoustic data</i>	1.1.1. Does the accuracy of habitat maps (constructed only with optical data) increase significantly when optical data are combined with data layers of acoustic depth, roughness and hardness? A - I
	1.2.1. Does the accuracy of habitat maps (constructed only with data layers of acoustic roughness hardness and depth) increase significantly when all acoustic layers are combined with optical data? E - I
1.2. <i>Enhancement of acoustic data by optical data</i>	1.2.2. Does the accuracy of habitat maps (constructed only with a data layer of acoustic roughness) increase significantly when the roughness data layer is combined with optical data? B - F
	1.2.3. Does the accuracy of habitat maps (constructed only with a data layer of acoustic depth) increase significantly when the depth data layer is combined with optical data? D - H
	1.2.4. Does the accuracy of habitat maps (constructed only with a data layer of acoustic hardness) increase significantly when the hardness data layer is combined with optical data? C - G
2) Relative contribution of acoustic parameters	
2.1. <i>Enhancement of optical data by roughness data</i>	2.1.1. Does the accuracy of habitat maps (constructed only with optical data) increase significantly when optical data are combined with a data layer of acoustic roughness? A - F
2.2. <i>Enhancement of optical data by hardness data</i>	2.2.1. Does the accuracy of habitat maps (constructed only with optical data) increase significantly when optical data are combined with a data layer of acoustic hardness? A - G
2.3. <i>Enhancement of optical data by depth data</i>	2.3.1. Does the accuracy of habitat maps (constructed only with optical data) increase significantly when optical data are combined with a data layer of acoustic depth? A - H
3) Value of in-band depth correction	
	3.1.1. Does the accuracy of habitat maps (constructed only with optical data), increase significantly when optical bands are depth corrected using a data layer of acoustic depth? A - J
	3.1.2. Does the accuracy of habitat maps (constructed only with optical data), increase significantly when depth corrected optical bands are combined with roughness, hardness and depth? A - K
3.1. <i>Enhancement of optical data by depth correction</i>	3.1.3. What causes a larger accuracy enhancement in habitat maps (constructed with only optical data): the depth correction of bands using a data layer of acoustic depth, or the combination of optical data with data layers of acoustic roughness, hardness and depth? (A - J) - (A - I)
	3.1.4. How much more is the accuracy (of habitat maps constructed with only optical data) enhanced by combining depth corrected optical bands with roughness, hardness and depth layers? (A - J) - (A - K)

3. Results

The use of acoustic data layers in conjunction with high-resolution optical data was found to improve the accuracy of habitat maps over that possible using optical data alone. The highest Tau coefficient was obtained conducting unsupervised classification on depth-corrected optical layers. Equivalent treatments run with supervised classification were qualitatively similar to those obtained from unsupervised classification and therefore the results of supervised classifications are not presented here.

3.1. Benefit of optical-acoustic data combination

Habitat maps generated using only optical data, i.e., the depth-invariant index, had a moderate accuracy (0.43, Figs. 2-3, Table 3). Map accuracies from acoustic data varied widely depending on which parameter was used. Poor accuracy was achieved using only roughness (E1) (0.32) or only hardness (E2) (0.30), whereas higher accuracies were achieved using acoustic depth (z) either on its own (0.42) or in combination with E1 and E2 (0.51, Figs. 2-3, Table 3).

Sensor synergy significantly increased the accuracy of habitat maps based solely on the depth-invariant optical index when E1, E2 and z were added, constituting an increase in accuracy of Tau Coefficient of 0.05 (A vs. I, $Z = 2.31$, $p = 0.03$, Fig. 2). The main cause of this rise in accuracy was an increase in the separability of gorgonian plains (GPL) from other coral-dominated habitats (Table 3). However, adding the depth-invariant optical index to any form of acoustic data constituted either a minimal improvement over that possible with acoustic alone (for E1, B vs. F, $Z = 2.64$, $p = 0.02$) or no improvement at all (for E2, C vs. G, $Z = 1.36$, $p = 0.15$; for z , D vs. H, $Z = 0.24$, $p =$

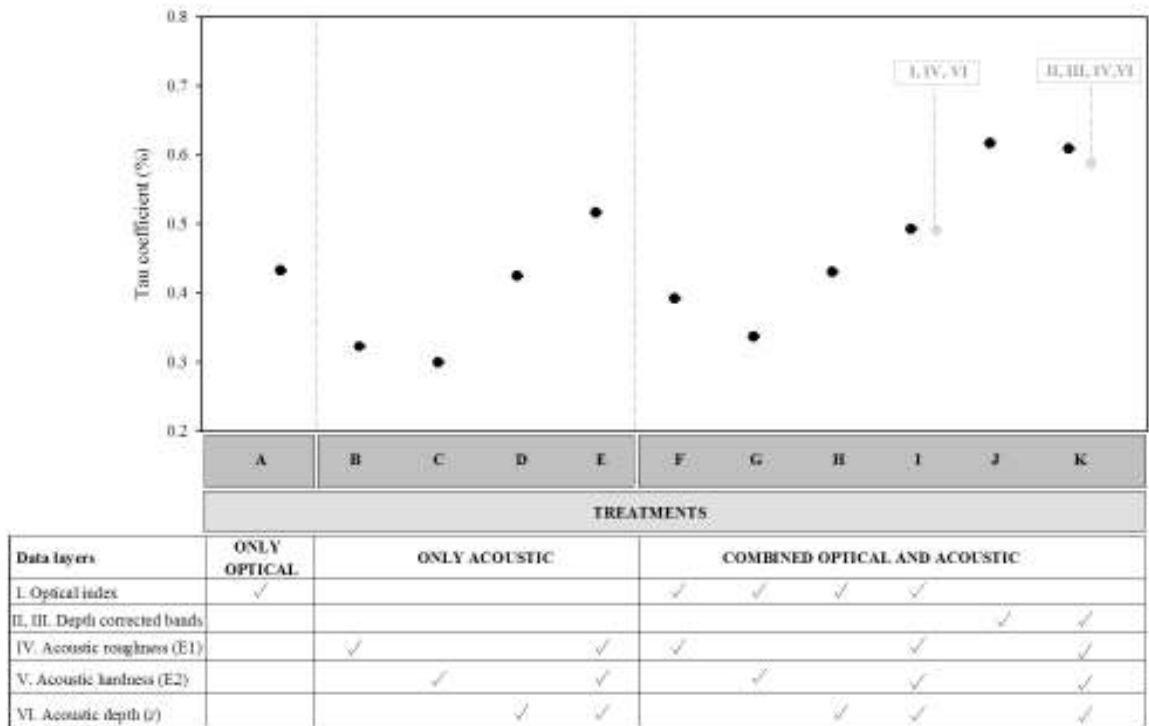


Fig. 2. Overall accuracies expressed as the Tau coefficients of habitat maps constructed using different combinations of data layers (treatments). Note that although the confidence intervals are also presented, these are very small.

0.83; for all E1, E2 and z, E vs. I, $Z = 0.94$, $p = 0.76$, Fig. 2). The highest accuracy was obtained by using acoustic depth to depth-correct the original optical bands to uniform depth (Figs. 2-4).

3.2. Relative contribution of acoustic parameters

The addition of separate layers of roughness (E1) or depth (z) provided no accuracy enhancement for maps generated using the depth-invariant optical index layer (A vs. F and A vs. H, $Z < 1.96$ and $p > 0.05$, Figs. 2-3). Interestingly, combining the depth-invariant optical index with the hardness layer (E2) caused a significant decrease in

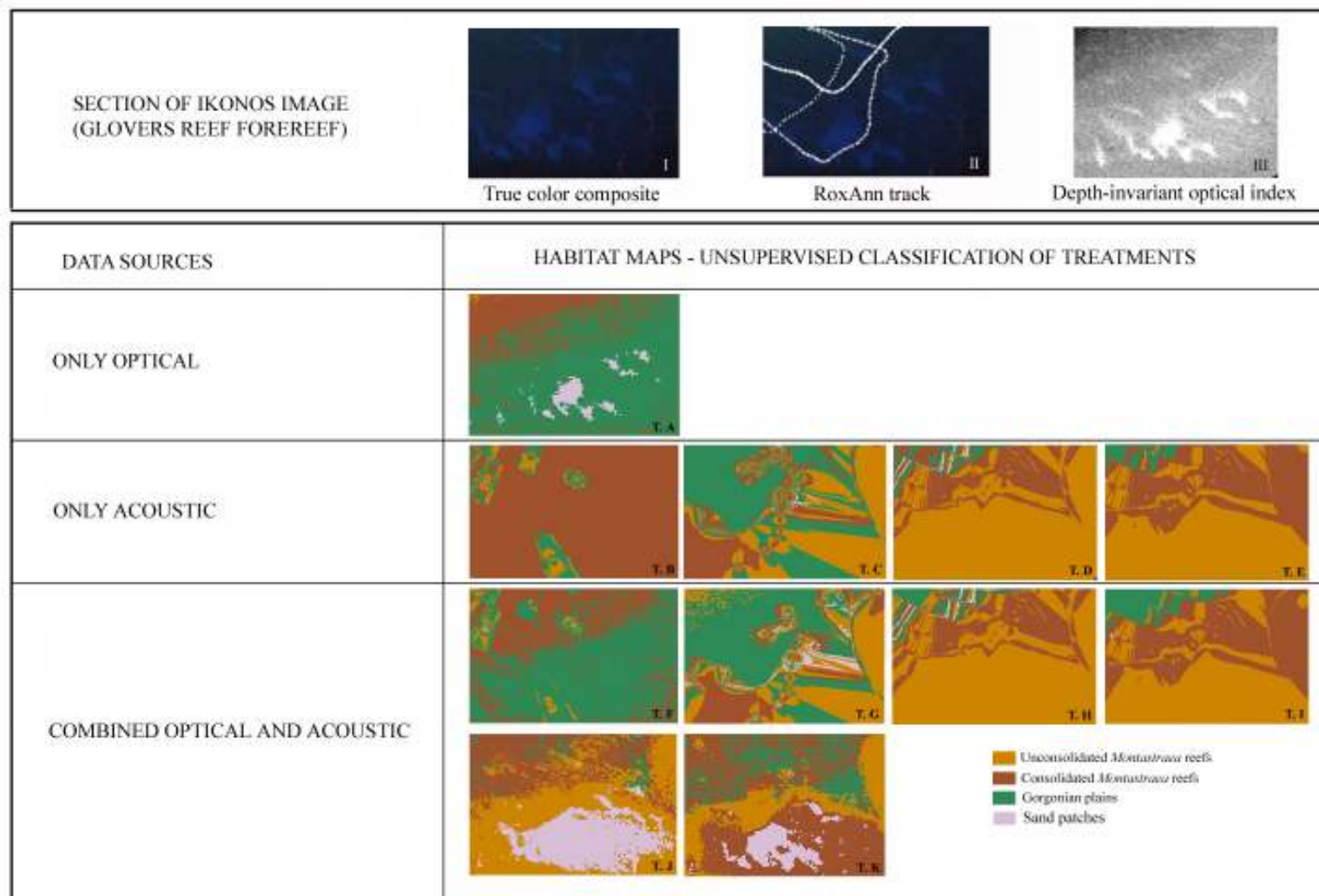


Fig. 3. A sample section of the IKONOS image of the forereef of Glovers Atoll presenting the I. true colour composite, II. Depth-invariant optical index and the habitat maps constructed using different combinations of data layers or treatments (T.A – T.K). For a detailed description of the treatments see Table 1.

Table 3. User's accuracy per habitat class, overall accuracy and Tau coefficients of habitat maps created using unsupervised classification on treatments that include optical data (A), acoustic data (B - E) or different combinations of optical and acoustic data layers (F - K).

User's accuracy per habitat class							
Treatment	Layers included	Consolidated <i>Montastraea</i> reefs (CMO)	Unconsolidated <i>Montastraea</i> reefs (UMO)	Gorgonian plains (GPL)	Sand patches (SAN)	Overall accuracy	Tau Coefficient
A	I	0.55	0.67	0.52	0.95	0.56	0.43
B	IV	0.43	0.49	0.68	0.50	0.48	0.32
C	V	0.55	0.48	0.44	0.67	0.46	0.26
D	VI	0.48	0.46	0.63	0.08	0.53	0.42
E	IV, V, VI	0.50	0.50	0.73	0.77	0.61	0.51
F	I, IV	0.50	0.43	0.61	0.47	0.52	0.39
G	I, V	0.61	0.57	0.43	0.0	0.34	0.22
H	I, VI	0.51	0.44	0.64	0.14	0.54	0.43
I	I, IV, V, VI	0.50	0.47	0.68	0.77	0.59	0.48
J	II, III	0.63	0.51	0.85	0.83	0.70	0.62
K	II, III, IV, V, VI	0.68	0.47	0.78	0.90	0.70	0.61

accuracy (A vs. G, $Z = 3.55$ and $p < 0.001$, Figs. 2-3). Combining either E1 or z with the depth-invariant optical index seemed to improve the separability of the gorgonian plains (GPL) from other coral-dominated habitats but impaired the distinction between unconsolidated and consolidated *Montastraea* reefs (UMO and CMO) and decreased the separability of sand patches (SAN) from other habitats, specially from GPL. Combining E2 with the depth-invariant optical index severely impaired the distinction between SAN and GPL (Table 3). Accuracy of maps made from the depth-invariant optical index improved when the three acoustic parameters were used in concert (Figs. 2-3). Given the poor contribution of E2, an accuracy improvement of equivalent magnitude occurred combining the depth-invariant optical index with both E1 and z (Fig. 2).

3.3. The value of in-band depth correction

Unsupervised classification using acoustic depth (z) for water-column correction of optical layers yielded the most accurate habitat map in our study (Figs. 2-4). This map was 43% more accurate than those obtained from the depth-invariant optical index layer alone (A vs. J, $Z = 7.31$, $p < 0.001$) and from the combination of the depth-invariant optical index layer with the z layer (H vs. J, $Z = 7.46$ $p < 0.001$).

Both depth-correcting optical layers (treatment J) and adding acoustic layers to the depth-invariant index (treatment I) increased the separability of gorgonian plains (GPL) from other coral-dominated habitats. However, despite this overall rise in accuracy, fusing these data sources increased the confusion between unconsolidated and consolidated *Montastraea* reefs (Table 3).

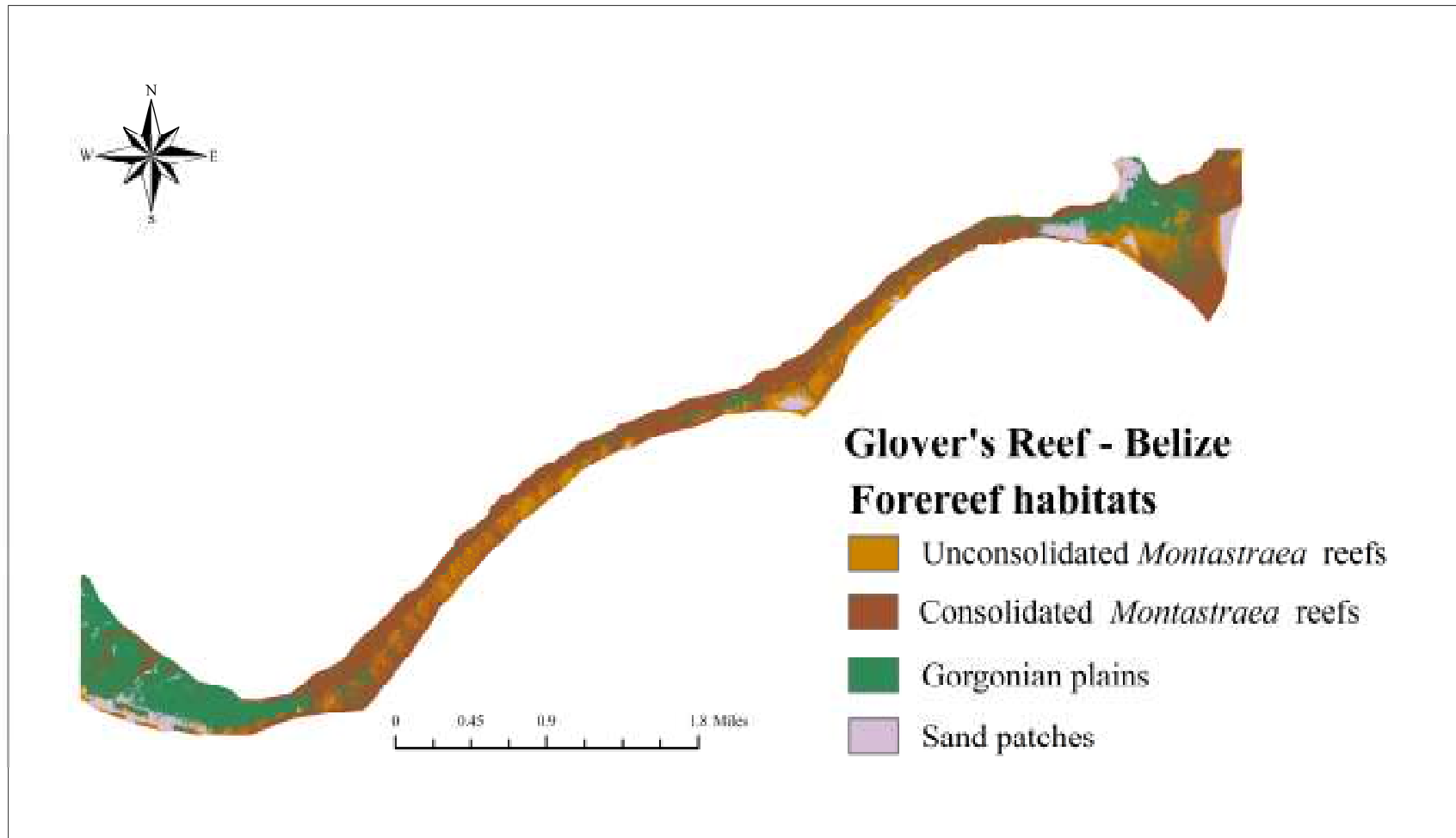


Fig. 4. Habitat map of the forereef of Glovers Atoll obtained using unsupervised classification of the optical bands (blue and green) depth-corrected using a data layer of acoustic depth.

Interestingly, the combination of depth-corrected optical layers with acoustic roughness (E1), hardness (E2) and z did not produce a map of superior accuracy compared to that obtained simply from depth-corrected optical layers alone (K vs. J, $Z = 0.34$, $p < 0.83$ Fig. 2). Indeed, combining all acoustic data with the depth-corrected optical layers caused a slight increase in the confusion between unconsolidated *Montastraea* reefs and gorgonian plains (Table 3).

4. Discussion

Results from this study indicate that moderate improvements of accuracy can be achieved for habitat maps of Caribbean reefs by combining acoustic data derived from single-beam acoustic systems (e.g. RoxAnn) with high-resolution optical data (IKONOS). Larger accuracy improvements can be obtained by using acoustic depth data to correct for depth variations in the spectral bands. Using acoustic depth for depth-correction seemed to have eliminated the confounding influence of variable depth on those habitats with a low albedo such as *Montastraea* reefs. Our conclusions apply to a fairly ambitious discrimination of forereef habitats, that include three forereef communities: unconsolidated *Montastraea* reef, consolidated *Montastraea* reef, and gorgonian plains. It should be borne in mind that many lower-resolution reef mapping programmes would not discriminate these classes and would tend combine all three under a forereef slope category.

Four major results can be highlighted from the present study: 1) the combination of RoxAnn and IKONOS data improved significantly the accuracy of habitat maps created from the optical depth-invariant index, 2) when combined separately with the depth-invariant optical index acoustic roughness (E1) and z had no effect on the accuracy of

habitat maps whereas acoustic hardness (E2) had a significant detrimental effect, with Tau declining from 0.56 to 0.24 (Table 3). The simultaneous addition of the three parameters was required to achieve an accuracy enhancement, 3) the maximum accuracy enhancement was achieved by applying unsupervised classification to depth-corrected optical layers, and 4) the addition of E1, E2 and z to depth-corrected optical layers caused no further accuracy enhancement.

The poor contribution of E2 to accuracy results easy to understand considering that underlying substrate of most coral dominated habitats is a carbonate matrix of a fairly homogeneous hardness. The relative contribution of E1 and z in determining accuracy was not clear because, contrary to our expectations, no accuracy improvement occurred when E1 and z were combined separately with the depth-invariant optical index (accuracy only improved when both measures were used in concert). It is difficult to provide a full explanation of these results at this stage but some insight can be sought. When only optical information was used, spectrally contrasting habitats such as sand patches were easily distinguished from the coral-dominated habitats but the three coral habitats were difficult to separate because of similar spectral characteristics (see Hedley and Mumby 2002). When either E1, or z were added, gorgonian plains were easily distinguished from coral-dominated habitats but were acoustically-confused with sand patches, resulting in low map accuracies for sand. Adding E2 on its own provided no useful information to separate GPL from other coral dominated habitats or from sand patches. It is likely feasible that the limited vertical structure of the sand and gorgonian habitats renders them acoustically similar in terms of roughness, whereas the difference in albedo (sand being greater) allows these habitats to be discriminated on a spectral basis. Contrary to expectation E2 did not facilitate the separation of sand patches from

presumably harder habitats, causing these to be severely misclassified as gorgonian plains.

Also surprisingly, the depth-invariant index failed to correct the misclassification of sand when used with either of E1, E2 and z but succeeded when the three acoustic channels, or only the two most informative ones (E1 and z) were added. One possible explanation is that the sites used for mapping can be partitioned differently when axes of E1 or z are involved, either in isolation or with a depth-invariant band. In other words, rather than being partitioned by our definition of habitat, the sites will primarily be partitioned on the basis of their depths when z is used, and their structural complexity when E1 is used. Only when z and E1 are used together does the partitioning by habitat category occur in the multivariate space used for the discriminant analysis. Such results may reflect the partly arbitrary nature of habitat classification in which a series of habitat categories are chosen from say a biological perspective, but alternative means of categorising reefs also exist (e.g., based on their physical structure) which may be more consistent with remotely-sensed data.

The accuracy of habitat maps created from the depth-invariant optical index improved modestly, by a rise in the Tau coefficient of 0.06 when combined with the three acoustic parameters (a rise of 14%). However, the improved accuracies were still low (<50%). Only when the original spectral bands were depth-corrected using acoustically-derived depth did the accuracy improve dramatically, from a Tau coefficient of 0.43 to 0.62 (a rise of 43%), or from an overall accuracy of 56% to 70% (a rise of 25%). Combining optical data with all acoustic parameters caused a more moderate accuracy enhancement than the one achieved using acoustically-derived depth for depth-correction or applying some other processing steps to optical data. For example, the use of textural information

derived from IKONOS data improved the overall accuracy for a map of fine level of discrimination (13 habitats) of Turks and Caicos by 20% (see Mumby and Edwards 2002). Moreover, using contextual editing and the depth invariant-optical indices derived from the satellite SPOT multispectral, the accuracy was significantly improved by 27% for maps of coarse discrimination (4 habitats) and was almost doubled for maps of finer discrimination (8 and 13 habitats) (see Mumby et al. 1998a).

The clear accuracy improvement achieved by depth-correcting the spectral bands with acoustic depth may lead the reader to ask whether simply determining bathymetry directly from the imagery (see Lyzenga et al. 2006; Lesser and Mobley 2007) would be feasible. However, the value of combining acoustic and optical data lies in the generation of three independent axes with which to discriminate marine habitats: depth-corrected reflectance, depth, and roughness of the seabed and their integration improves accuracy over basic spectral classification. It is also worth bearing in mind that while estimates of bathymetry from optical data can be quite accurate (Stumpf and Holderied 2003), the methods are still susceptible to the confounding influence of variable inherent optical properties and therefore acoustic data are a superior means of determining bathymetry.

Practitioners considering the benefits of coupling acoustic and optical remote sensing should be aware of the inherent limitations of both approaches in order to determine whether to use their products separately or in concert. Unlike optical data that can be interpreted through reference to spectral libraries, data obtained by RoxAnn need to be calibrated on an image by image basis, which likely necessitates more field survey than is necessary for optical data. Acoustic data also require interpolation in order to create continuous maps and this inevitably introduces errors, particularly in areas with high

levels of habitat patchiness such as lagoons with small patch reefs (bommies). Optical imagery may have the desirable attributes of being relatively easy to interpret and providing a continuous, synoptic data source, but its use is severely limited by light attenuation and spectral confusion. Previous studies have shown that optical imagery can be used to map reefs to a maximum depth of approximately 20 m when the water clarity is high (Case 1) but this depth penetration declines rapidly with rising attenuation (Green et al. 2000). Moreover, high spectral and spatial resolution is needed to discriminate relatively subtle spectral differences between reef communities in the same geomorphological zone (Mumby et al. 1998b). Neither of these spectral problems besets acoustic data and indeed, acoustic methods are the only feasible solution for mapping deep reefs or areas with high turbidity (Riegl and Purkis 2005). In summary, fusion of optical and acoustic methods is likely to be appropriate when light penetration to the reef is significantly impaired (i.e., if depth exceeds 0.5 m) but still measurable (i.e., not exceeding a depth of 20 m). Further, the combination of optical and acoustic data is likely to be particularly useful where terrestrial runoff causes local changes in water inherent optical properties that confound the interpretation of optical data or where reef habitats vary in their topographic complexity such that acoustic roughness provides useful discrimination (e.g. identifying patches of reef that have been flattened by hurricanes or where bioerosion has severely degraded the reef structure).

4.1. Comparison with other studies

Habitat maps resulting from the unsupervised classification of the depth-invariant optical index had relatively low values of Tau coefficient (< 0.45) compared to maps with a similar level of habitat discrimination derived from IKONOS data for other areas (Table 4). This is likely to reflect the difficulty of separating our 3 coral-dominated habitat types based on their spectral characteristics. Higher accuracies achieved

particularly in other studies using IKONOS, may have resulted from choosing broader classes with all coral-dominated habitats grouped within the same class (e.g. forereef, brown algae, seagrass/Lobophora and seagrass in Andréfouët, 2003; coral, macroalgae, seagrass and sand in Mumby and Edwards, 2002; rubble, sand, algae and coral in Capolsini et al. 2003)

Although examples of coral reef habitat maps based only on acoustic information are less common in the literature, some examples are available for comparison (Table 4). The map of the forereef of Glovers Atoll resulting from combined acoustic data (E1, E2 and z) was less accurate than maps of similar descriptive resolution of Negros Occidental (Philippines) using RoxAnn (White et al. 2003) (if Tau coefficients of supervised classification are compared). Only the maps resulting from unsupervised classification (but not those resulting from supervised classification) of combined acoustic data (E1, E2 and z) were more accurate than those of a reef area on the south-eastern Arabian Gulf using QTCView (Riegl and Purkis 2005).

Table 4. Overall accuracies and Tau coefficients (as percentages) obtained in this study compared with values observed in other coral reef studies.

Sensor (number of habitats)	Ecosystems (Location)	Classification technique (additional data or processing steps)	Overall accuracy	Tau coefficient	Reference
<i>Using optical sensors</i>					
Aerial photography (4, 6, 9) Landsat TM (4)	Mangrove, seagrass and fringing reefs. (Anguilla)	Drawing-digitization- Cluster Analysis (Colour, texture and grain)	68, 62, 57%	55, 52, 48%	Sheppard et al. (1995)
Spot XS (4) Landsat MSS (4)	Seagrass and fringing reefs (Turks and Caicos)	SIMPER Analysis- Supervised (Lyzenga's depth compensation)	67%	50%	Mumby et al. (1997)
Casi (4, 9)	Seagrass and fringing reefs (Turks and Caicos)	Supervised (Lyzenga's depth compensation) (Contextual editing)	89, 81%	84, 79%	Mumby et al. (1998b)
Ikonos (4, 9)	Seagrass and fringing reefs (Turks and Caicos)	Supervised (Lyzenga's depth compensation) (Addition of textural layers)	83, 65%	74, 56%	Mumby and Edwards (2002)
Ikonos (5,11) Landsat TM (6)	Seagrass, forereef and reef lagoon (Glovers Atoll, Belize) Patch reefs and gorgonian plains (Lee Stocking Island, Bahamas)	Unsupervised (Lyzenga's depth compensation) (Contextual editing)	77, 50%	Not available	Andréfouët et al. (2003)
Ikonos (4, 9) Multi-Spectral Camera System (6)	Shallow barrier reef (Taapuna Reef, Tahiti) Sand channel and coral-algal communities on spur and grove (Kailua bay, Hawaii)	Supervised (No depth compensation, depths < 2m)	75, 72%	67, 69%	Capolsini et al. (2003)
Landsat ETM + (5) Quickbird (5)	Fringing reefs, non-framebuilding corals on bedrock, and sandy and muddy bottoms. (Las Perlas, Panama) As above	Supervised (SU) Object-oriented classification (OOC) (Lyzenga's depth compensation) As above	SU: 57% OOC: 81%	Not available	Benfield et al. (2007)
Ikonos (6) CASI (10)	Seagrass and fringing reefs (Bunaken Island, Indonesia) Forereef (Pulau Nukaha, Indonesia)	Supervised (images obtained in 2001 and 2004) Semi-unsupervised-hierarchical clustering (Depth compensation using bathymetry generated from radiative transfer models)	2001: 78% 2004: 81%	Not available	Newman et al. (2007)
Ikonos (4) Treatment A	Forereef (Glovers Atoll, Belize)	Unsupervised (Lyzenga's depth compensation)	63%	61%	Bertels et al. (2008)
			56%	43%	This study

Table 4. (Continuation) Overall accuracies and Tau coefficients obtained in this study presented along with values observed in other coral reef studies.

Sensor (number of habitats)	Ecosystems (Location)	Classification technique (additional data or processing steps)	Overall accuracy	Tau coefficient	Reference
<i>Using optical sensors and bathymetry measured in-situ</i>					
Landsat TM 5 (7)	Fringing reefs. (Marsa Shagra, Egypt)	Supervised (Water column correction using bathymetric data collected in the field and the Bierwirth model)	76%	71%	Purkis and Pasterkamp (2004)
<i>Using acoustic sensors</i>					
RoxAnn (E1, E2, z) (3, 4, 5, 10)	Fringing reefs (Negros occidental, Philippines)	Supervised	86, 60, 54, 28%	63, 46, 43, 26%	White et al. (2003)
QTCView (4)	Seagrass, sand, macroalgal plains, and corals on a subtidal ramp (Abu-Dhabi).	Cluster analysis-Bayesian approach using QTC specific software.	56%	46%	Riegl and Purkis (2005)
QTCView (3)	Seagrass and macroalgal plains (Indian River Lagoon, Florida)	Cluster analysis-Bayesian approach using QTC specific software.	50 KHz: 61%, 200 KHz: 60%	50 KHz: 47% 200 KHz: 45%	Riegl et al. (2005)
RoxAnn (4) Treatment B		Unsupervised	48%	32%	
RoxAnn (4) Treatment C	Forereef	Unsupervised	46%	26%	This study
RoxAnn (4) Treatment D	(Glovers Atoll, Belize)	Unsupervised	53%	42%	
RoxAnn (4) Treatment E		Unsupervised / Supervised	61% / 57%	51% / 45%	
<i>Using a combination of optical and acoustic sensors</i>					
Ikonos-QTCView (8)	Seagrass, sand, macroalgal plains, and corals on a subtidal ramp (Jebel Ali, Abu-Dhabi).	Multi-variate-normal probability density function (Depth-correction of optical layers using acoustic z)	69%	65%	Purkis and Riegl (2005)
Ikonos-Fugro SeaSTAR GPS (7)	As above	As above	70%	64%	Purkis (2005)
Ikonos (4) Treatment I		Unsupervised / Supervised	59% / 68%	48% / 57%	
Ikonos (4) Treatment J	Forereef	Unsupervised / Supervised	70% / 60%	62% / 50%	This study
Ikonos (4) Treatment K	(Glovers Atoll, Belize)	Unsupervised / Supervised	70% / 71%	61% / 61%	

The maximum benefit of the combination of acoustic and optical remote sensing instruments was achieved using the z layer within the algorithm for water-column correction of the optical bands (treatment H). The accuracy resulting from such approach (Tau = 62 %, 4 classes) was comparable to the accuracy obtained by Riegl and Purkis (2005) (Tau = 65 %, 8 classes) using acoustic depth (z) derived from QTCView to depth-correct an IKONOS image of a reef area in Dubai (Table 4). In short, while direct comparisons between different types of reef architecture are difficult to make, the range of accuracies reported here are consistent with those elsewhere, even from different sensors.

5. Conclusions

Alternative means of acquiring depth data to supplement optical imagery exist such as the NASA experimental Advanced Airborne Research LIDAR (EAARL) (Brock et al. 2004). However, the costs are likely to be impractical for most practitioners. This study evaluated the benefits of combining optical and acoustic data at Glovers Reef in Belize. The results should be widely applicable in the Caribbean because the reef habitats studied are found throughout the region (Geister 1977). It is not unreasonable to expect that the combination of optical and acoustic data could also facilitate habitat discrimination on Indo-Pacific coral reefs. First, the inherent optical properties of many Indo-Pacific reefs are similar to those at Glovers Reef (Mumby and Hedley, unpublished data) and the limitations of optical data appear to be comparable between regions (Andréfouët et al. 2002). Second, the morphological diversity of corals is much greater in the Indo-Pacific (Veron 2000) which is likely to favour the discrimination of coral communities by acoustic sensors (White et al. 2003; Riegl and Purkis 2005). Whether 14% represents a sufficiently-great increase in accuracy to warrant data fusion instead of using either optical or acoustic sensors alone, remains a

decision for practitioners and will likely depend on the objectives involved. It should be borne in mind, however, that in addition to creating habitat maps, both sensors have additional mutual benefits that were not quantified here. For example, optical data provide useful media for education and outreach whereas acoustic data can also be used to quantify reef structural complexity and possibly be related to reef fish species richness (Pittman et al. 2007).

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CHAPTER 3:
PREDICTING STRUCTURAL COMPLEXITY OF REEFS AND FISH
ABUNDANCE USING ROXANN

This chapter comprises of a paper that has been submitted to Marine Biology

Predicting structural complexity of reefs and fish abundance using RoxAnn

Sonia Bejarano^{1*}, Peter. J. Mumby¹ and Ian Sotheran²

* *Corresponding author*

¹ *Marine Spatial Ecology Lab, School of Biosciences, Hatherly Laboratories, Prince of Wales Road, University of Exeter, Exeter, Devon, EX4 4PS, United Kingdom.*

² *Envision UK, Horsley, Newcastle upon Tyne. NE15 0NY, United Kingdom.*

ABSTRACT

The relationship between the topographic complexity of coral reefs and their fish fauna has been widely documented. In this study we aimed to determine whether the acoustic roughness (E1) of Caribbean reef habitats can be used as an accurate proxy for their topographic complexity and as a significant predictor of the fish abundance they support. Abundance of 46 reef fish species was measured in April 2005 at 25 sites along the forereef of an atoll in Belize using underwater census techniques. *In situ* rugosity (ISR) was estimated at each site using the “chain and tape” method and acoustic data were acquired using RoxAnn at the same time as the field surveys. The relationship between the acoustic roughness (E1) and ISR was tested using linear models. The relationship of both E1 and ISR with the density and biomass of each of the *common* species were tested using linear models whereas the effect of ISR and E1 on the presence and the abundance (if present) of *uncommon* species was tested using hurdle models. Model interpretation demonstrated that E1 is a significant and reasonably strong predictor of the topographic complexity of reefs ($R^2 = 0.66$). Fourteen fish species were unaffected by ISR or E1 and the remaining species (and life phases) varied in their nature and degree of association with the ISR. Chaetodontids and pomacanthids seemed unaffected by topographic complexity whereas all species of scarids, pomacentrids, haemulids, most species of acanthurids and lutjanids, and

some species of serranids and labrids were correlated with ISR or E1. Not all species increased in number linearly in response to high topographic complexity. E1 was a reasonable predictor of the presence or abundance patterns of 21% of the species recorded. Small changes in E1 (i.e. 0.05 - 0.07) translated into subtle but significant differences in the abundance of a parrotfish species strongly influenced by topographic complexity (~1 individual 200 m⁻² and 116 g 200 m⁻²). In order to detect a change of 0.05 in E1 between two sites on a typical forereef habitat, a minimum of 70 RoxAnn echoes per site need to be recorded.

Keywords: RoxAnn, rugosity, roughness, Caribbean, Belize, reef fish, density, biomass.

1. Introduction

Caribbean coral reefs have degraded rapidly over the past few decades (Aronson and Precht 2001; Gardner et al. 2005) and today continue to be threatened by several natural and anthropogenic disturbances. A number of these disturbances including thermally induced bleaching events, hurricanes, sedimentation and uncontrolled coastal development can cause coral mortality over large reef areas (Rogers 1990; Gardner et al. 2005; Donner et al. 2007). Coral mortality caused either by natural or anthropogenic impacts often results in the collapse of the reef framework (e.g. Woodley et al. 1981; Kaufman 1983; Shepherd et al. 1992; Bellwood et al. 2004; Graham et al. 2006; Alvarez-Filip et al. 2009) on which reef fish communities depend fundamentally (Sale 1991; Chabanet et al. 1997). The three-dimensional framework of reefs does not only provide transient and permanent refuges from predation to fishes of a variety of sizes and shapes (Caley and St John 1996) but also provides fishes with foraging, spawning and nesting sites (Robertson and Sheldon 1979) and can help them maintain themselves in high-flow environments (Johansen et al. 2008).

The topographic complexity of reefs varies across a range of spatial scales as a result of natural structural differences among habitats or their differential susceptibility to disturbances. Due to the strong relationship that fishes hold with the structure of reefs, patterns of topographic complexity are reflected in the associated fish communities. The positive relationship between topographic complexity and species richness, diversity, total biomass and abundance is well known (Luckhurst and Luckhurst 1978a; Carpenter et al. 1981; Sale and Douglas 1984; Caley and St John 1996; Rooker et al. 1997; Friedlander and Parrish 1998a, b; Ohman and Rajasuriya 1998; Nanami and Nishihira 2002; Friedlander et al. 2003; Gratwicke and Speight 2005a, b). However, the nature of the relationship between topographic complexity and the density or biomass of individual species has rarely been described (but see Ebersole 1985; Mumby and Wabnitz 2002) and needs further investigation. Different degrees of association with habitat complexity may exist depending on fish size (Choat and Bellwood 1991) mobility, home range and feeding habits (Chabanet et al. 1997) and territoriality (Mumby and Wabnitz 2002). Small fishes may have a stronger need of shelter because of their increased vulnerability to predators (Mumby and Wabnitz 2002) and strongly site-attached fish, or fishes with obligate associations, tend to have higher correlations with the substratum than more widely ranging species or life stages (McCormick 1994). Species with small home ranges may yield strong relationships with habitat variables, as a result of the scale at which these variables are measured (Jennings et al. 1996). Understanding the relationship between topographic complexity and fish abundance at a species level would allow more detailed and useful predictions of spatial and temporal patterns of fish abundance. If such predictions were both readily available for species with critical functional roles or commercial importance and applicable at large spatial scales, these would provide ecologically meaningful information to support stock assessments and the design of management strategies.

Topographic complexity has traditionally been measured as the ratio of the actual contour of the reef relative to linear distance (Luckhurst and Luckhurst 1978a) using what is known as the “chain and tape” method. Although a fine-scale proxy of the vertical relief is obtained using this method, it involves considerable underwater effort and therefore is generally unsuitable for use across wide spatial scales. The need for alternative large scale and continuous measurements of topographic complexity that allow a) predictive models and b) the possibility to map topographic complexity continuously at large scales has been recognized and recently addressed using remote sensing techniques (Kuffner et al. 2007; Pittman et al. 2007; Purkis et al. 2008). The study of the correlation between remotely sensed rugosity and in-situ rugosity is in its infancy and would benefit if the spectrum of viable instruments is broadened.

The acoustic ground discrimination system RoxAnn provides a cost-effective approach to measure the acoustic roughness (E1) of the sea bottom and discriminate benthic coral reef habitats with different topographic complexity with relative detail (Hamilton et al. 1999; White et al. 2003). However, the beam-width of RoxAnn causes each measurement of E1 to be recorded from a 2-dimensional patch of reef surface (beam footprint) which differs from the 1-dimensional nature of the “chain and tape” method. Thus, each method measures a different aspect of reef complexity but a comparison between them is warranted because of the widespread use of the “chain and tape” approach. There is no *a priori* reason why one metric of complexity will be superior to the other and the relationship between each metric and the fish abundance parameters might differ and vary further according to species or body size.

The capacity of satellite remote sensing to predict habitat complexity at a scale relevant to fish has been recently demonstrated (Purkis et al. 2008). Fish community parameters such as species richness (Kuffner et al. 2007; Pittman et al. 2007), diversity (Purkis et al. 2008) as well as the abundance of fish at a family level (Kuffner et al. 2007) within size, trophic and mobility guilds (Purkis et al. 2008) can be predicted over large spatial scales. The present study aimed to take these predictions forward to a species and life-phase level (in the case of parrotfishes). Within families, species may display differences in behaviour, degrees of territoriality and food requirements which may affect their use of refugia and their degree of association with the topographic complexity of reefs. Furthermore, although certain trophic guilds (e.g. parrotfishes) play a crucial ecological role in the reduction of macroalgal biomass (Mumby et al. 2006), the reduction of coral mortality (Hughes et al. 2007) and the increase in coral recruitment (Mumby et al. 2007a), species or life phases within the guild may contribute differently to these functions (Bruggemann et al. 1994). In addition some of these species (or life phases) may be preferentially targeted by fishers and therefore more susceptible to overfishing than others. In such cases, prioritization of management strategies may be required. Mapping fish diversity and richness at large scales provides managers with novel tools to improve ecosystem-based management (Pittman et al. 2007) and identify potential sites for marine protected areas (Purkis et al. 2008). By extending spatial predictions to a further level of detail we aim to support targeted management measures oriented to the protection of key species and their habitats. Abundance predictions for certain grazers which play a crucial ecological role could be used to orient conservation efforts to the enhancement of resilience of reefs. Biomass predictions of commercially important species (e.g. groupers and snappers) could be used to direct conservation efforts to maintain desirable levels of fish stocks.

In summary, the present study aimed to determine whether the RoxAnn's acoustic roughness (E1) is as a reasonable predictor of the topographic complexity of Caribbean reef habitats and therefore the abundance of reef fishes they support. Relationships are analysed at the level of species and life phase, and also quantify the capacity of acoustic remote sensing to predict patterns of spatial variability in the abundance of key fish species. The following hypotheses were tested:

- 1) Despite the differences in scale between the E1 and the *in situ* rugosity (ISR), E1 is a good predictor of the topographic complexity of a reef.
- 2) The abundance (density/biomass) of most reef fish species is positively correlated with ISR and E1.
- 3) When the abundance and/or biomass of a species are significantly related with the ISR, it will have the same type of relationship with E1.
- 4) Juveniles and small-bodied species have the strongest relationship with the topographic complexity.
- 5) Species that according to the literature are strongly territorial or have small home ranges will be strongly related to the small scale measure of topographic complexity (ISR), whereas species with larger home ranges will be strongly related with the large-scale measure of topographic complexity (E1).

2. Methods

2.1. Study area

The study was carried out on the forereef of Glovers Atoll (16° 44' N, 87° 50' W) in Belize (Fig. 1). This forereef comprises a gently sloping calcareous terrace descending from the emergent reef crest to an escarpment at a depth ranging from approximately 10 m to 20 m where *Montastraea* spp. are the major reef-building corals. Surveys were conducted at 25

sites within the same forereef zone and at comparable depths (~10 m) including a range of typical forereef habitats such as consolidated *Montastraea* reefs, unconsolidated *Montastraea* reefs, dense and sparse gorgonian communities established on hard bottom plains with very few hard coral colonies, and spurs and grooves with predominance of hard bottom with small hard coral colonies and a medium relief.

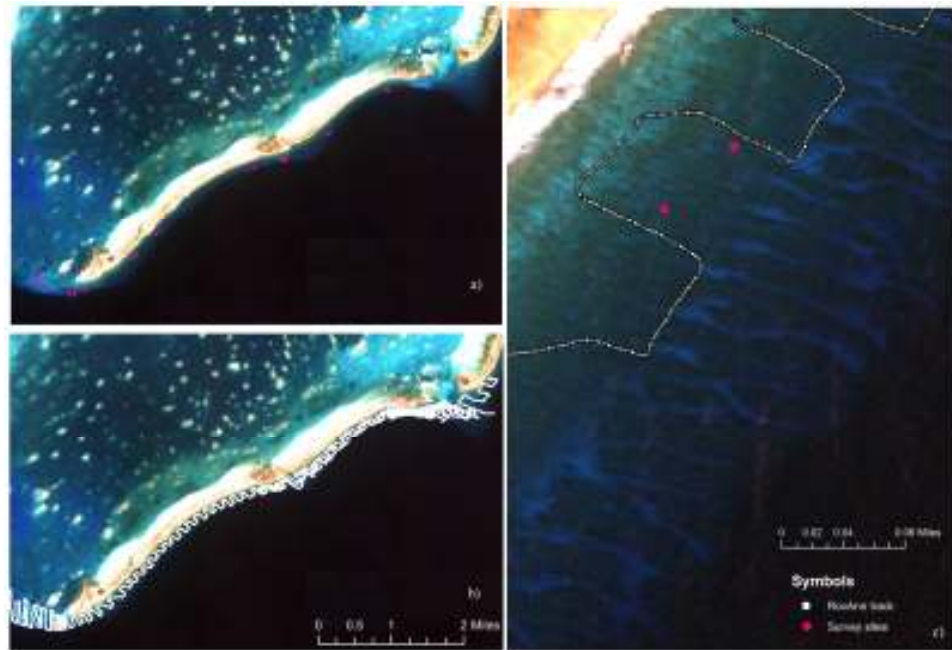


Fig. 1. Sections of an IKONOS image of Glovers Atoll indicating a) the location of the survey sites and b) the RoxAnn track. Image c shows a detailed view of two of our survey sites.

2. 2. Field surveys

2.2.1. Fish census and topographic complexity

The number of individuals of 39 species of reef fish including the families Scaridae, Acanthuridae, Haemulidae, Chaetodontidae, Serranidae, Lutjanidae, Carangidae, Kyphosidae, Sphyraenidae, Sparidae, Labridae, Balistidae and Pomacanthidae (Table 1) were quantified by a surveyor within 30 x 4 m belt transects (10 per site). Life phase (for every parrotfish) and total length (TL) were recorded for every fish encountered in the

transects. The choice of species aimed to include the most common, the important functional groups, and commercially important species.

Seven additional species including the smaller, more abundant and site attached damselfishes and the commonest squirrelfish were surveyed in transects of a narrower area (30 x 2 m belt transects) to ensure accurate estimates of their abundance. Two of these transects were surveyed per site counting and recording the TL of the every individual of following species: *Stegastes planifrons*, *S. partitus*, *S. leucostictus*, *S. diencaeus*, *S. adustus*, *Microspathodon chrysurus* and *Holocentrus rufus*.

The topographic complexity at each site was measured using a modification of the “chain and tape” method (Risk 1972). A chain of 4 meters long with spherical links of 2mm of diameter was moulded to the contour of the substratum at randomly selected starting positions (n = 10 – 14 per site). *In situ* rugosity (ISR) was calculated as the ratio of the length of the chain to the linear distance between its start and end point (McCormick 1994).

2.2.2. Acquisition of acoustic data

Acoustic data were collected along a track encompassing the forereef of Glovers Atoll using the RoxAnn signal processor (Fig. 1b). Although RoxAnn uses a dual frequency echo sounder (Furuno FCV-600L, 50 and 200 kHz) it was operated at 200kHz during our survey. Geographical co-ordinates were provided by an integrated GPS receiver (Furuno GP-37/GP-32). Beam width at 200 kHz was set at 10° which gave a footprint of approximately 17% of water depth. Since depth logged by RoxAnn was between 3 and 22 m, the diameter of the footprint ranged from approximately 0.51 m in the shallowest areas to 3.74 m in the

Table 1. Species of reef fish counted within 30 x 4 m band transects (10 per site) in Glovers Atoll, Belize (Central America).

Family	Species
Scaridae	<i>Sparisoma aurofrenatum</i> (Red band parrotfish)
	<i>Sparisoma viride</i> (Stoplight parrotfish)
	<i>Sparisoma rubripinne</i> (Yellowtail parrotfish)
	<i>Sparisoma atomarium</i> (Green blotch parrotfish)
	<i>Sparisoma chrysopterum</i> (Red tailed parrotfish)
	<i>Scarus taeniopterus</i> (Princess parrotfish)
	<i>Scarus iserti</i> (Striped parrotfish)
	<i>Scarus coelestinus</i> (Midnight parrotfish)
Acanthuridae	<i>Acanthurus coeruleus</i> (Blue tang)
	<i>Acanthurus bahianus</i> (Ocean surgeonfish)
	<i>Acanthurus chirurgus</i> (Doctorfish)
Haemulidae	<i>Haemulon flavolineatum</i> (French grunt)
	<i>Haemulon sciurus</i> (Bluestriped grunt)
	<i>Haemulon plumieri</i> (White grunt)
Chaetodontidae	<i>Chaetodon striatus</i> (Banded butterflyfish)
	<i>Chaetodon capistratus</i> (Foureye butterflyfish)
	<i>Chaetodon ocellatus</i> (Spotfin butterflyfish)
Serranidae	<i>Cephalopholis fulva</i> (Coney)
	<i>Cephalopholis cruentata</i> (Graysby)
	<i>Epinephelus striatus</i> (Nassau grouper)
	<i>Epinephelus guttatus</i> (Red hind)
	<i>Epinephelus adscensionis</i> (Rock hind)
	<i>Mycteroperca venenosa</i> (Yellowfin grouper)
	<i>Mycteroperca tigris</i> (Tiger grouper)
	<i>Mycteroperca bonaci</i> (Black grouper)
Lutjanidae	<i>Lutjanus apodus</i> (Schoolmaster)
	<i>Lutjanus mahogoni</i> (Mahogany snapper)
	<i>Ocyurus chrysurus</i> (Yellowtail snapper)
Carangidae	<i>Caranx ruber</i> (Bar jack)
Kyphosidae	<i>Kyphosus sectator</i> (Bermuda sea chub)
Sphyraenidae	<i>Sphyraena barracuda</i> (Great barracuda)
Sparidae	<i>Calamus calamus</i> (Saucereye porgy)
Labridae	<i>Lachnolaimus maximus</i> (Hogfish)
	<i>Bodianus rufus</i> (Spanish hogfish)
Balistidae	<i>Balistes vetula</i> (Queen triggerfish)
Pomacanthidae	<i>Pomacanthus arcuatus</i> (Gray angelfish)
	<i>Holacanthus ciliaris</i> (Queen angelfish)
	<i>Holacanthus tricolor</i> (Rock beauty)

deepest areas. Vessel speed was kept constant at 8 km h⁻¹. A data point was logged every 2 to 5 m and the distance between the tracks was approximately 100 m (Fig. 1b-c).

2.3 Data analysis

2.3.1. Fish abundance and biomass

Biomass for each species was estimated using TL of individual fish and the published allometric scaling relationships between length and weight (Bohnsack and Harper 1998). Mean density (individuals 200 m⁻²) and biomass (g 200 m⁻²) was calculated separately for each species, and within each species separately for each life phase (in the case of parrotfishes) and for juvenile damselfishes (which were very abundant).

2.3.2. Acoustic roughness (E1)

To extract the mean acoustic roughness for each of our survey sites we overlaid the geo-referenced acoustic track on an IKONOS image of our study area (acquired in March 2005) (Fig. 1a-c). Between 2 and 5 echo returns containing E1 data were available on the exact location of our survey sites. To obtain a more representative number of E1 measurements per site we conducted an unsupervised classification of the IKONOS image generating 15 spectral classes (Mumby and Edwards 2002; Andréfouët et al. 2003). The maximum possible number of RoxAnn echoes acquired from the immediate vicinity of each site and from areas of the same spectral class were selected (Fig. 1b). All echoes with E1 data above the 95th and below the 1st percentile were discarded as outliers possibly originated by problematic echo acquisition (primarily resulting of the pitch and roll of the boat) and a mean E1 was calculated per site.

2.3.3. Scope of RoxAnn's E1 to predict topographic complexity

To determine whether the acoustic roughness (E1) of Caribbean reef habitats can be used as a proxy for their topographic complexity, a linear model was fitted to our benthic data. The

model tested whether there was a significant relationship between the ISR and E1. Model adequacy was evaluated by examining (a) the plot of residuals vs. fitted values to look for heteroscedasticity and (b) the normality Q-Q plot to test for the normality of errors (Crawley 2002).

2.3.4. Species relationships with topographic complexity and E1

Fish species were classified in three groups: 1) including *common* species and/or life phases that were observed in > 16 sites (17 species), 2) including *uncommon* species and/or life phases that were observed in \leq 16 sites and therefore contained a substantial proportion of zeros in their data sets (19 species) and 3) including *extremely rare* species (i.e. 1 individual observed at no more than 4 sites and, therefore, their relationship with ISR and E1 could not be tested).

2.3.4.1. Common species

For each of the *common* species simple linear regression models were fitted to test for the relationships between 1) density and ISR, 2) density and E1, 3) biomass and ISR and 4) biomass and E1. The adequacy of the models was evaluated by examining (a) the plot of residuals vs. fitted values to look for heteroscedasticity and (b) the normality Q-Q plot and the Shapiro test to assess the normality of errors (Faraway 2005). In cases of non-constant variance, non-normality of errors or evidence of non linearity, the response variable was transformed using either \sqrt{y} , $\log(y)$ or $\log(y + 1)$ as appropriate. In cases where the relationship between variables could not be adequately represented by a straight line, one or more polynomial terms were added to the linear model and retained in it subject to their significance and the adequacy of the model's diagnostics (Faraway 2005). In the case of

parrotfishes, adequate models were fitted separately for juveniles, initial phase (IP's) and terminal phase (TP's) individuals.

2.3.4.2. *Uncommon species*

Uncommon species were treated as having skewed and zero-inflated datasets with an excess of true zeros (Martin et al. 2005). The relationships of each of these species with our two measurements of topographic complexity were evaluated using ZANB or hurdle models which involved two steps (see Zuur et al. 2009 for details). First the presence-absence of each species was modelled separately as a function of ISR and E1 using logistic regression. Second, the abundance if present (total number of individuals of each species per site) was modelled separately as a function of ISR and E1 using negative binomial general linear models (GLMs) with zero-truncated Poisson distributions (Fletcher and Faddy 2007; Zuur et al. 2009).

A total of 108 parametric tests were conducted to assess the relationships between pairs of variables for *common* species. Usually the significance of such a high number of multiple tests should be tested using Bonferroni adjusted alpha values (α) of 0.0004 and 0.001 (for our common and uncommon species respectively) (Sidak 1968; Simes 1986). However, the interpretation of the significance of tests using strictly adjusted α values has been strongly contested as these reduce the probability of Type I error only at the cost of inflating the probability of the equally deleterious Type II error (see Perneger 1998). Therefore, significance of the relationships examined here was tested using an alpha of 0.05.

2.3.5. *Scope of RoxAnn's E1 to predict patterns of fish abundance*

The minimum difference in fish abundance (density and biomass) that has to exist between two sites for it to be detected using RoxAnn's E1 data was determined in 3 steps using the

fitted values of the model and its confidence intervals for an example species (i.e. TP *Sparisoma aurofrenatum*) (Fig. 2). In step 1, a point “P1” along the regression line representing the relationship between E1 (x axis) and density (or biomass) of TP *Sp. aurofrenatum* (y axis) was randomly selected. In step 2 the location of a second point “P2” just outside the upper limit established by the 95% confidence intervals of the regression line was then determined. In step 3 the difference between the values corresponding to P1 and P2 on the y axis (density or biomass) was calculated and comprised the minimum difference in fish density or biomass (ΔD or ΔB) that can be detected between two sites of different E1 ($\Delta E1$).

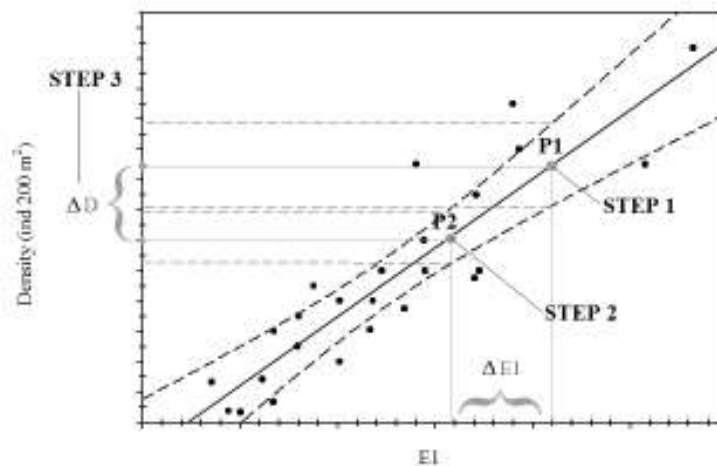


Fig. 2. Example plot of a linear regression curve between the acoustic roughness (E1) in the x axis and the fish density in the y axis. Steps 1 to 3 illustrate the procedure to determine the minimum difference that has to exist between two sites in fish abundance for it to be detected using RoxAnn’s E1 (ΔD). See methods for details.

The number of acoustic echoes (n) required to detect a significant difference in E1 of size $\Delta E1$ between two sites which would result in differences in the density and biomass of *Sp. aurofrenatum* of sizes ΔD and ΔB respectively, was calculated using sample size power

calculations (Faul et al. 2007). To find the sample size n , the significance level was set to 0.05, the power at 0.80 and the effect size (d) was determined by:

$$d = (\mu_1 - \mu_2) / \sigma$$

where $(\mu_1 - \mu_2)$ equalled the difference we want to detect ($\Delta E1$) and σ is the population standard deviation, in this case taken as the standard deviation of the RoxAnn's E1 across Glover's forereef.

3. Results

3.1. Scope of E1 to predict topographic complexity

The ISR of our study sites was a relatively good predictor of their E1 (Fig. 3). The high fit of the linear model including polynomial terms ($R^2 = 0.66$) indicates that E1 could be used as a comparable proxy for the topographic complexity of Caribbean reefs to that obtained with widely-used *in situ* methods.

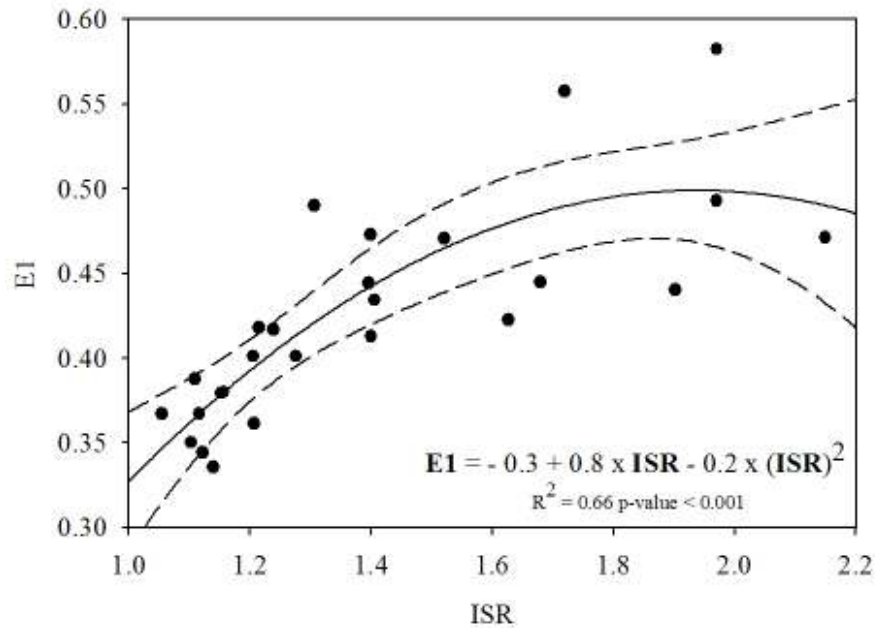


Fig. 3. Relationship between *in situ* rugosity (ISR) measured with the “chain and tape” method and the acoustic roughness (E1) measured with RoxAnn. Points represent the 25 sites surveyed on the forereef of Glovers Atoll. Dashed lines indicate the 95% confidence intervals.

3.2. Species relationships with topographic complexity and E1

Some of the species targeted within our censuses were very rarely observed (i.e. 1 individual at no more than 4 sites and, therefore, their relationship with ISR and E1 could not be tested. These species were the large groupers: *Epinephelus striatus*, *E. adscensionis*, *Mycteroperca venenosa*, *M. tigris*, *M. bonaci*, the parrotfishes *Scarus coelestinus*, *Sc. vetula*, *Sc. taeniopterus*, the Bermuda sea chub (*Kyphosus sectator*) and the Great barracuda (*Sphyraena barracuda*).

3.2.1. Predicting the abundance of common species

The abundance of *Chaetodon striatus*, *C. capistratus*, *E. guttatus*, *Sp. chrysopterus*, *Cephalopholis fulva*, *Ocyurus chrysurus* and *Holocentrus rufus* was not significantly

correlated with ISR or E1. However, the density and biomass of the remaining 10 *common* species found in our study were significantly related to the ISR (Figs. 4-6, Table 2). Significant relationships occurred between E1 and both abundance parameters of most of these species, but not between E1 and the biomass of *Acanthurus coeruleus*, *Stegastes partitus* and juveniles of *Sp. aurofrenatum* or between E1 and the density of *Haemulon plumierii* and juveniles of *Sp. aurofrenatum*. The strongest relationships between fish abundance and the ISR ($R^2 > 0.60$) occurred in strongly territorial species (i.e. *Sc. iserti*, *S. planifrons*, *Sp. aurofrenatum* and *Sp. viride*). The R^2 values indicated that the relationship between the abundance of a species and the ISR was generally stronger than its relationship with E1. Usually both measures of topographic complexity had a relatively stronger effect (higher R^2) on the density than on biomass of the species observed.

The density and biomass of 5 species, namely *A. coeruleus*, *S. planifrons*, *Sp. viride*, *Sc. iserti* and *C. cruentata* increased linearly as ISR increased (Figs 4a,g, 5c,e and 6e). Except for the biomass of *A. coeruleus*, both abundance parameters of all these species also increased linearly with E1 (Fig. 4b,h, 5d,f and 6f).

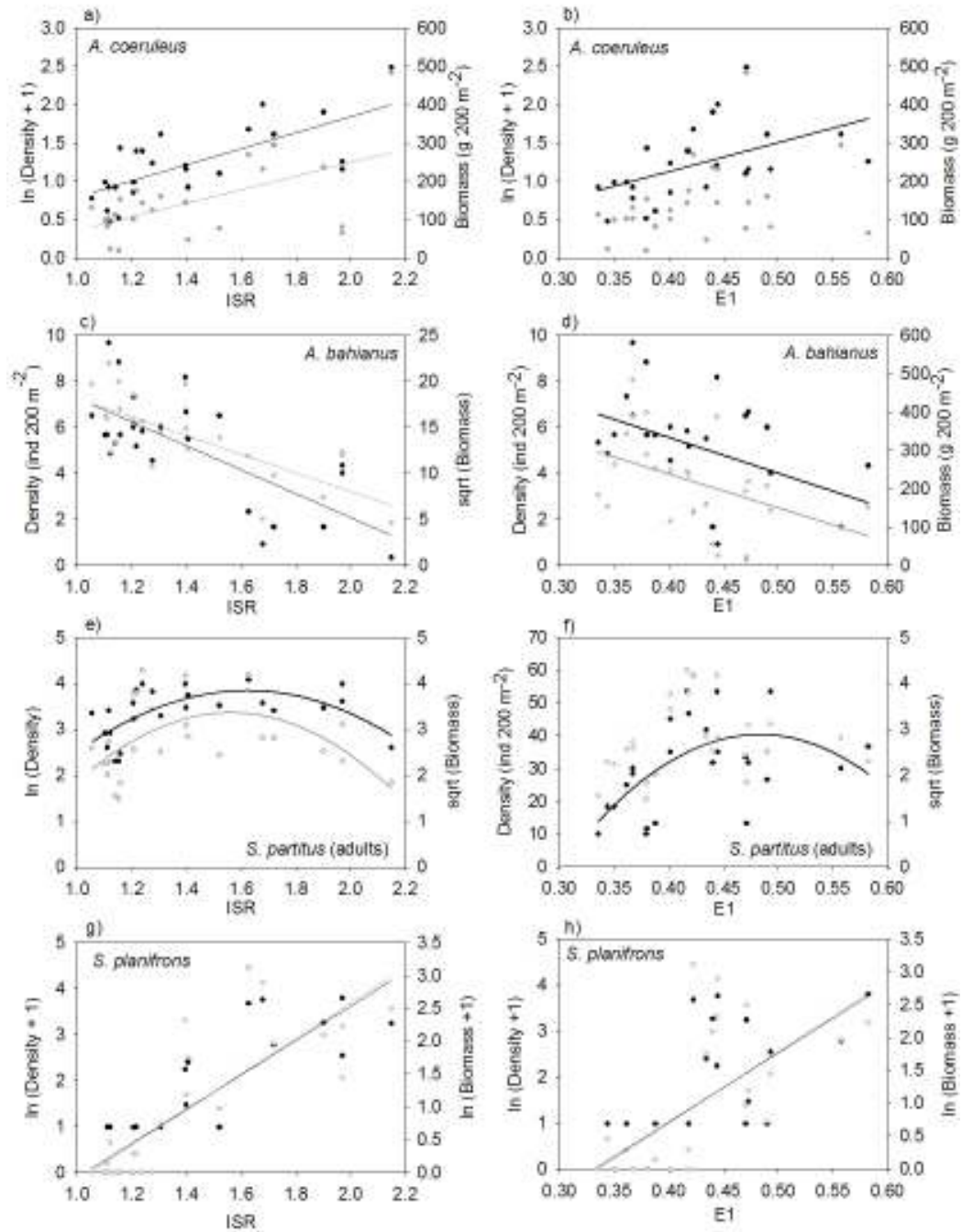


Fig. 4. Paired scatter-plots for a-b) *A. coeruleus*, c-d) *A. bahianus*, e-f) *S. partitus* and g-h) *S. planifrons*. Predictors on the x axis are: topographic complexity – ISR (left) and acoustic roughness – E1 (right). Response variables are density (individuals 200 m^{-2}) represented by solid dots (on the left y axis) and biomass (grams 200 m^{-2}) represented by light gray dots (on the right y axis) on each plot. Variables were transformed when necessary for models to meet the normality assumptions, but curves were only fitted when relationships between variables were statistically significant (for equations and significance see Table 2).

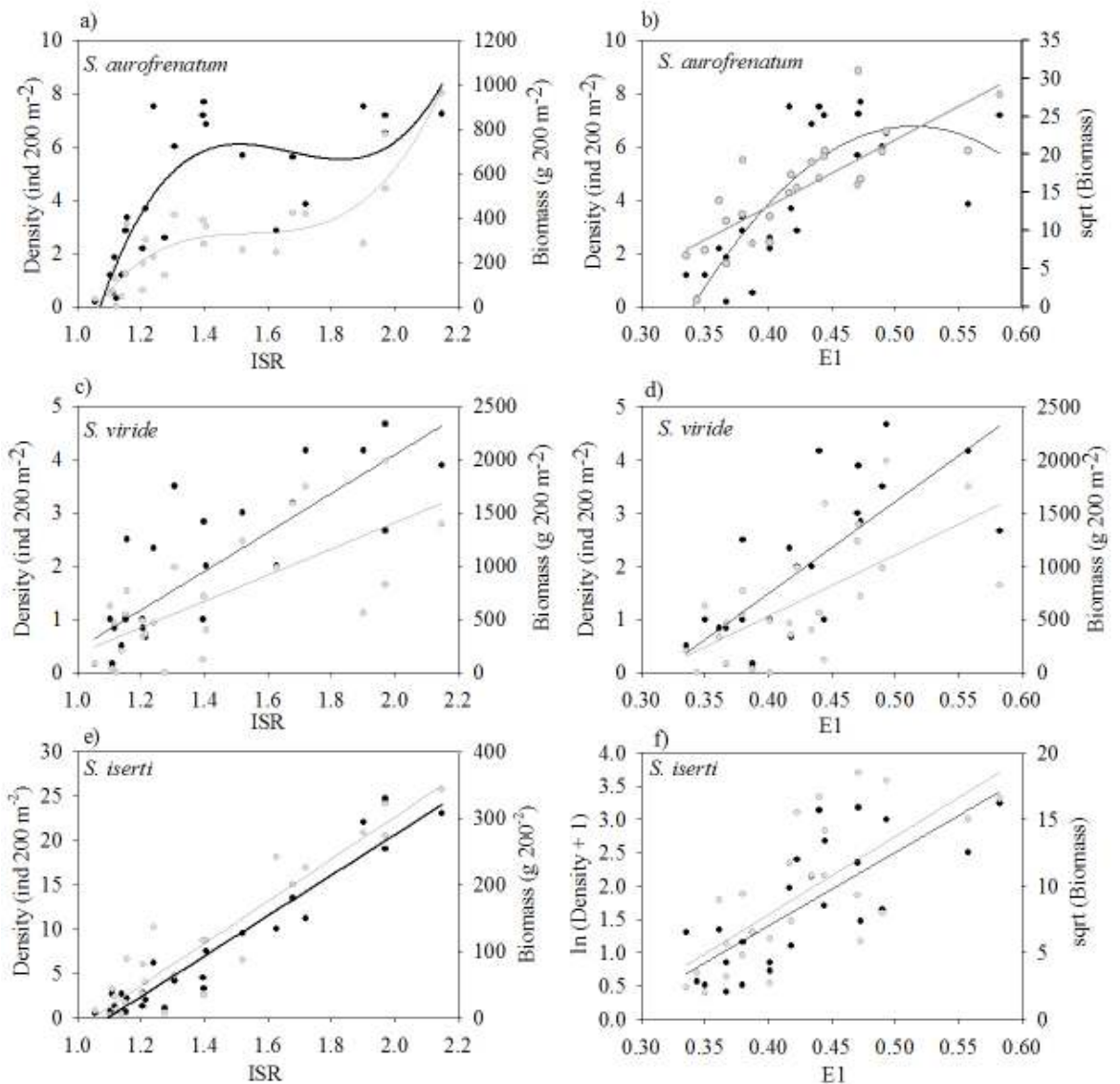


Fig. 5. Paired scatter-plots for a-b) *Sp. aurofrenatum*, c-d) *Sp. viride* and d-e) *Sc. iserti*. Predictors on the x axis are: topographic complexity – ISR (left) and acoustic roughness-E1 (right). Response variables are density (individuals 200 m^{-2}) represented by solid dots (on the left y axis) and biomass (grams 200 m^{-2}) represented by light gray dots (on the right y axis) on each plot. Variables were transformed when necessary for models to meet the normality assumptions, but curves were only fitted when relationships between variables were statistically significant (for equations and significance see Table 2).

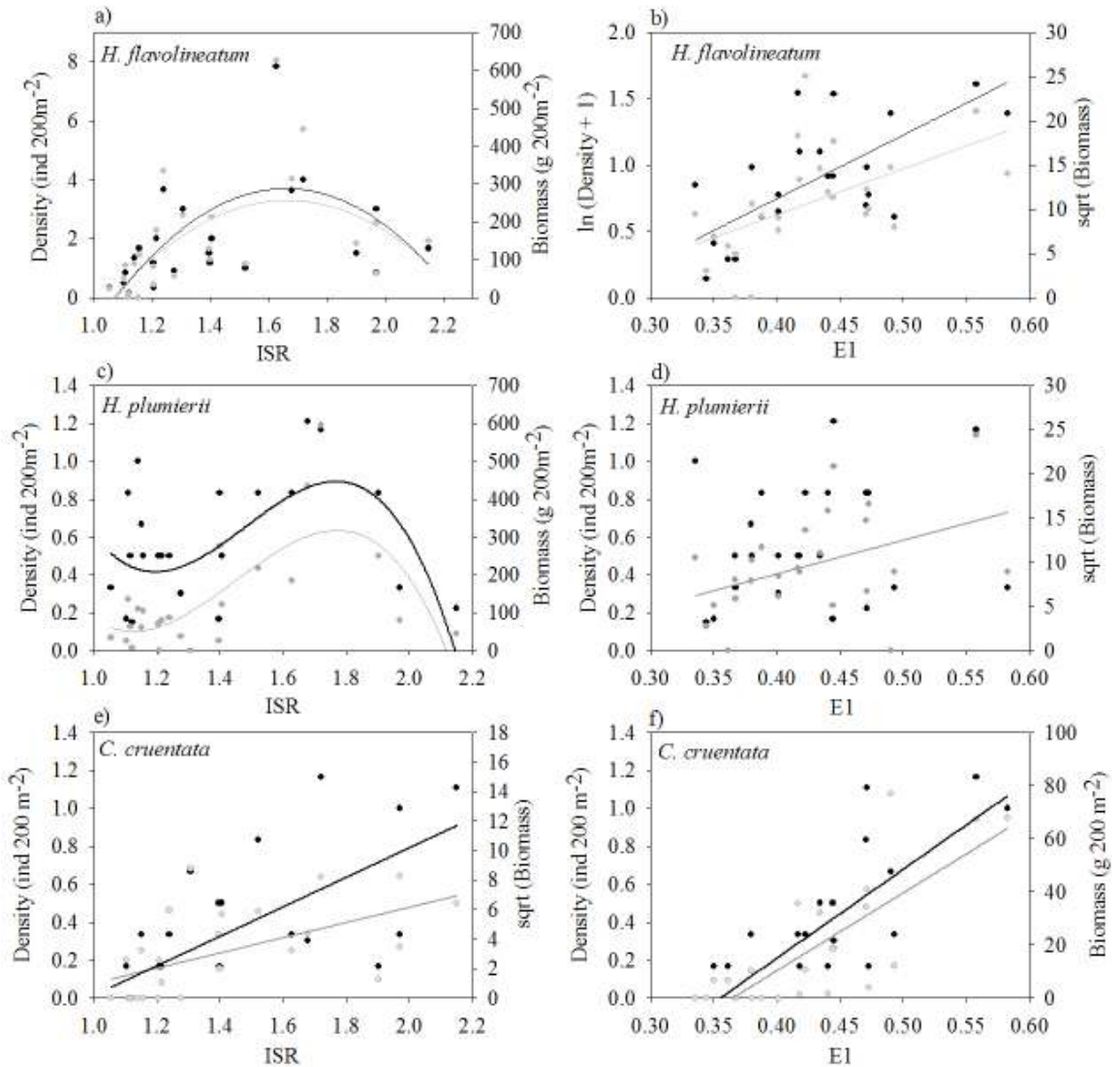


Fig. 6. Paired scatter-plots for a-b) *H. flavolineatum*, c-d) *H. plumierii* and e-f) *C. cruentata*. Predictors on the x axis are: topographic complexity – ISR (left) and acoustic roughness-E1 (right). Response variables are density (individuals 200 m⁻²) represented by solid dots (on the left y axis) and biomass (grams 200 m⁻²) represented by light gray dots (on the right y axis) on each plot. Variables were transformed when necessary for models to meet the normality assumptions, but curves were only fitted when relationships between variables were statistically significant (for equations and significance see Table 2).

Table 2. (Part 1.) Models to predict density (**D**, ind 200 m⁻²) and biomass (**B**, g 200 m⁻²) of 10 fish species as a function of the *in situ* rugosity (**ISR**) and the acoustic roughness (**E1**). An * indicates significant relationships at the 95% confidence intervals ($\alpha = 0.05$).

Common species			
Species	Function	R ²	P
<i>Surgeonfishes</i>			
<i>A. coeruleus</i>	$\ln(\mathbf{D}+1) = -0.25 + 1.05 \times \mathbf{ISR}$	0.48	7.4 E-5 *
	$\ln(\mathbf{D}+1) = -0.39 + 3.78 \times \mathbf{E1}$	0.22	0.010 *
	$\mathbf{B} = -104.8 + 176.61 \times \mathbf{ISR}$	0.29	0.003 *
	Not significant relationship between B and E1	-	-
<i>A. bahianus</i>	$\mathbf{D} = 12.47 - 5.20 \times \mathbf{ISR}$	0.49	6.0 E-5 *
	$\mathbf{D} = 11.80 - 15.60 \times \mathbf{E1}$	0.14	0.036 *
	$\sqrt{\mathbf{B}} = 28.23 - 10.10 \times \mathbf{ISR}$	0.53	2.4 E-5 *
	$\mathbf{B} = 592.2 - 885.2 \times \mathbf{E1}$	0.19	0.017 *
<i>Damselfishes</i>			
<i>Stegastes partitus</i>			
Adults	$\ln(\mathbf{D}) = -4.85 + 10.74 \times \mathbf{ISR} - 3.32 \times (\mathbf{ISR})^2$	0.34	0.004 *
	$\mathbf{D} = -242.6 + 1171.4 \times \mathbf{E1} - 1212.4 \times (\mathbf{E1})^2$	0.24	0.020 *
	$\sqrt{\mathbf{B}} = -8.28 + 14.91 \times \mathbf{ISR} - 4.78 \times (\mathbf{ISR})^2$	0.21	0.029 *
	$\sqrt{\mathbf{B}} = -12.73 + 68.68 \times \mathbf{E1} - 74.24 \times (\mathbf{E1})^2$	0.17	0.053
Juveniles	No significant relationship observed	-	-
<i>S. planifrons</i>			
All stages	$\ln(\mathbf{D} + 1) = -3.84 + 3.73 \times \mathbf{ISR}$	0.73	3.0 E-8 *
	$\ln(\mathbf{D} + 1) = -4.99 + 15.02 \times \mathbf{E1}$	0.44	0.001 *
	$\ln(\mathbf{B} + 1) = -2.83 + 2.71 \times \mathbf{ISR}$	0.65	6.3 E-7 *
	$\ln(\mathbf{B} + 1) = -3.63 + 10.82 \times \mathbf{E1}$	0.39	0.001 *
Adult and juvenile	See table 3 (uncommon species and stages)		
<i>Parrotfishes</i>			
<i>Sp. aurofrenatum</i>			
All phases	$\mathbf{D} = -150.98 + 287.08 \times \mathbf{ISR} - 173.57 \times (\mathbf{ISR})^2 + 34.66 \times (\mathbf{ISR})^3$	0.65	1.4 E-5 *
	$\mathbf{D} = -52.58 + 230.84 \times \mathbf{E1} - 224 \times (\mathbf{E1})^2$	0.66	3.0 E-6 *
	$\mathbf{B} = -9868.7 + 19755.5 \times \mathbf{ISR} - 12789.7 \times (\mathbf{ISR})^2 + 2767 \times (\mathbf{ISR})^3$	0.78	1.0 E-7 *
	$\sqrt{\mathbf{B}} = -21.97 + 87.80 \times \mathbf{E1}$	0.62	2.1 E-6 *
Terminal phase	$\ln(\mathbf{D} + 1) = -0.90 + 1.05 \times \mathbf{ISR}$	0.62	1.9 E-6 *
	$\ln(\mathbf{D} + 1) = -1.82 + 5.65 \times \mathbf{E1}$	0.69	1.6 E-7 *
	$\sqrt{\mathbf{B}} = -11.91 + 16.65 \times \mathbf{ISR}$	0.62	1.6 E-6 *
	$\sqrt{\mathbf{B}} = -26.06 + 88.29 \times \mathbf{E1}$	0.68	1.6 E-7 *

Table 2. (Part 2). Models to predict density (**D**, ind 200 m⁻²) and biomass (**B**, g 200 m⁻²) of 10 fish species as a function of the *in situ* rugosity (**ISR**) and the acoustic roughness (**E1**). An * indicates significant relationships at the 95% confidence intervals ($\alpha = 0.05$).

Common species			
Species	Function	R ²	P
<i>Parrotfishes</i>			
<i>Sp. aurofrenatum</i>			
Initial phase	D = -58.97 + 111.01 × ISR – 66.14 × (ISR) ² + 13.1 × (ISR) ³	0.59	7.2 E-5 *
	D = -30.51 + 136.63 × E1 -138.24 × (E1) ²	0.58	3.0 E-5 *
	B = -5287.4 + 10702.8× ISR – 6969.2×(ISR) ² +1492×(ISR) ³	0.48	0.001 *
	B = -1379.2 + 62.99.8 × E1 – 6.462.8 × (E1) ²	0.23	0.021 *
Juveniles	D = -13.02 + 18.89 × ISR – 6.0 × (ISR) ²	0.19	0.039 *
	√ D = -0.36 + 3.03 × E1	0.10	0.066
	B = -29.17 + 40.76 × ISR - 12.76 × (ISR) ²	0.29	0.010 *
	No significant relationship between B and E1	-	-
<i>Sp. viride</i>			
All phases	D = -3.21 + 3.65 × ISR	0.63	1.2 E-6 *
	D = -5.44 + 17.31 × E1	0.54	1.7 E-5 *
	B = -1053.8 + 1230.7 × ISR	0.49	5.7 E-5 *
	B = -1780.7 + 5775.9 × E1	0.41	0.004 *
Terminal phase	ln(D + 1) = -0.92 + 0.95 × ISR	0.60	3.5 E-6 *
	ln(D + 1) = -1.50 + 4.52 × E1	0.51	3.6 E-5 *
	√ B = -24.06 + 28.21 × ISR	0.56	9.3 E-6 *
	√ B = -43.78 + 139.56 × E1	0.53	2.3 E-5 *
Initial phase	ln(D + 1) = - 0.37 + 0.67 × ISR	0.35	0.001 *
	ln(D + 1) = -0.83 + 3.31× E1	0.32	0.002 *
	No relationship between B and ISR	-	-
	No relationship between B and E1	-	-
Juveniles	See table 3 (uncommon species and life phases)	-	-
<i>Scarus iserti</i>			
All phases	D = -24.96 + 22.80 × ISR	0.93	4.9E-14*
	ln(D + 1) = -3.03 + 11.06 × E1	0.56	1.0 E-5 *
	B = -332.10 + 316.86 × ISR	0.89	1.4E-12 *
	√ B = -15.63 + 58.66 × E1	0.48	6.9 E-5 *
Terminal phase	D = -5.49 + 5.01 × ISR	0.86	1.8E-11 *
	ln(D + 1) = -2.09 + 6.69 × E1	0.48	7.9 E-5 *
	B = -194.62 + 183.77 × ISR	0.82	3.3E-10 *
	√ B = -13.47 + 47.44 × E1	0.44	0.001 *

Table 2. (Part 3). Models to predict density (**D**, ind 200 m⁻²) and biomass (**B**, g 200 m⁻²) of 10 fish species as a function of the *in situ* rugosity (**ISR**) and the acoustic roughness (**E1**). An * indicates significant relationships at the 95% confidence intervals ($\alpha = 0.05$).

Common species				
Species	Function	R ²	P	
<i>Parrotfishes</i>				
<i>Scarus iserti</i>				
Initial phase	$\sqrt{\mathbf{D}} = -1.96 + 2.45 \times \mathbf{ISR}$	0.79	1.7 E-9 *	
	$\sqrt{\mathbf{D}} = -2.70 + 9.85 \times \mathbf{E1}$	0.48	8.3 E-5 *	
	$\sqrt{\mathbf{B}} = -5.73 + 7.99 \times \mathbf{ISR}$	0.66	5.9 E-7 *	
	$\sqrt{\mathbf{B}} = -8.51 + 32.96 \times \mathbf{E1}$	0.41	0.001 *	
	Juveniles	$\mathbf{D} = -9.69 + 8.72 \times \mathbf{ISR}$	0.89	1.2E-12 *
		$\ln(\mathbf{D} + 1) = -2.83 + 8.94 \times \mathbf{E1}$	0.52	2.6 E-5 *
		$\mathbf{B} = -34.14 + 31.18 \times \mathbf{ISR}$	0.86	1.2E-11 *
		$\sqrt{\mathbf{B}} = -5.38 + 18.72 \times \mathbf{E1}$	0.43	0.001 *
<i>Grunts</i>				
<i>H. flavolineatum</i>	$\mathbf{D} = -22.13 + 30.56 \times \mathbf{ISR} - 9.180 \times (\mathbf{ISR})^2$	0.32	0.006 *	
	$\ln(\mathbf{D}+1) = -1.17 + 4.80 \times \mathbf{E1}$	0.29	0.003 *	
	$\mathbf{B} = -2027.5 + 2789.5 \times \mathbf{ISR} - 840.2 \times (\mathbf{ISR})^2$	0.35	0.003 *	
	$\sqrt{\mathbf{B}} = -11.34 + 51.85 \times \mathbf{E1}$	0.27	0.004 *	
<i>H. plumierii</i>	$\mathbf{D} = 15.29 - 32.16 \times \mathbf{ISR} + 22.57 \times (\mathbf{ISR})^2 - 5.08 \times (\mathbf{ISR})^3$	0.22	0.040 *	
	No relationship between D and E1	-	-	
	$\mathbf{B} = 5320.8 - 11884 \times \mathbf{ISR} + 8637.3 \times (\mathbf{ISR})^2 - 1988.8 \times (\mathbf{ISR})^3$	0.45	0.001 *	
	$\sqrt{\mathbf{B}} = -6.53 + 38 \times \mathbf{E1}$	0.14	0.037 *	
<i>Serranids</i>				
<i>C. cruentata</i>	$\mathbf{D} = -0.77 + 0.78 \times \mathbf{ISR}$	0.46	0.001 *	
	$\mathbf{D} = -1.67 + 4.69 \times \mathbf{E1}$	0.65	6.7 E-7 *	
	$\sqrt{\mathbf{B}} = -4.20 + 5.16 \times \mathbf{ISR}$	0.29	0.003 *	
	$\mathbf{B} = -107.02 + 293.44 \times \mathbf{E1}$	0.60	3.3 E-6 *	

A humpshaped curve was found to be the model that better explained the relationship of the density and biomass of *H. flavolineatum*, *H. plumierii* and adult *S. partitus* with ISR. However, the same type of relationship occurred only between the density of *S. partitus* responded and E1 (Fig. 4f). Interestingly, both the density and biomass of *H. flavolineatum* and only biomass of *H. plumierii* increased linearly with the E1 rather than with the

quadratic (humpshaped) relationship found for ISR. Further, E1 was not a significant predictor of the density of *H. plumierii* (Figs. 6b,d).

The response of the abundance of the Redband parrotfish *Sp. aurofrenatum* to changes in ISR was best explained by a polynomial model including a cubic term (Fig. 5a). The response of *Sp. aurofrenatum* abundance to changes in E1 was slightly different. Biomass of *Sp. aurofrenatum* increased linearly with E1 whereas increases in its density described a polynomial shaped curve (Fig. 5b).

An unusual response to the increase of ISR and E1 was the consistent linear decrease of *A. bahianus* in density and biomass. Unlike most reef fish species, large numbers of individuals, and consequently a higher biomass of *A. bahianus*, were recorded in less structurally complex reefs (Fig. 4c,d).

In the case of parrotfishes, the nature and strength of the relationships between abundance and reef complexity differed among life phases. The abundance of juveniles of *Sc. iserti* was strongly related with both ISR and E1 ($R^2 = 0.43-0.89$, Table 2) whereas juveniles of *Sp. aurofrenatum* were not as strongly affected by reef complexity ($R^2 = 0.10-0.29$, Table 2). Both density and biomass of terminal phase individuals (TP's) of these 3 species of parrotfishes increased linearly with ISR and E1 and these relationships were strong ($R^2 = 0.44-0.86$, Table 2). R^2 values indicated that the relationships between the initial phase individuals (IP's) and both measurements of topographic complexity were generally weaker than those of TP's (Table 2).

Both the abundance and biomass of the *Sc. iserti* IP's increased linearly with ISR and E1, whereas only the density, but not the biomass of *Sp. viride* IP's increased linearly with ISR and E1 (Table 2). Specific trends of the abundance of *Sp. aurofrenatum* IP's were virtually identical to those described for the overall abundance of this species. Both density and biomass increased in a steep curve from flat reefs towards reefs with low ISR (~1.4), the density was relatively stable throughout reefs of intermediate ISR (1.4 - 1.9) and then increased again in reefs with the highest ISR. Only the density of *Sp. aurofrenatum* IP's was also related to E1 (by a polynomial shaped curve, Table 2).

3.2.2. Predicting the abundance of uncommon species

19 species of the families Acanthuridae, Pomacentridae, Scaridae, Haemulidae, Pomacanthidae, Lutjanidae, Chaetodontidae, Carangidae, Labridae, Balistidae and Sparidae were classified and analysed as being uncommon in our study (Table 3). Additionally, some life phases and stages of common species were uncommon when counted separately. Such was the case of adult and juvenile *S. planifrons* and juvenile *Sp. viride*.

The occurrence of *A. chirurgus*, *Holacanthus ciliaris*, *H. tricolor*, *Pomacanthus arcuatus*, *C. ocellatus*, *Caranx ruber*, *Balistes vetula*, *Calamus calamus* and *Lachnolaimus maximus* and the abundance of these species (when present) were unaffected by either measure of topographic complexity. Both the occurrence and abundance (if present) of *S. diencaeus*, *S. leucostictus*, adult *S. planifrons* and *Lutjanus apodus* were significantly and positively affected by ISR (Table 3). E1 was a significant predictor for the occurrence of all these species but was not significantly related to the abundance (when present) of any of them.

Table 3. P-values indicating the significance of the relationships between two measurements of topographic complexity (ISR, E1) and the presence of a species and its abundance given presence (Hurdle models). Asterisks (*) indicate significant relationships at the 95% confidence intervals ($\alpha = 0.05$).

Species	Effect of ISR		Effect of E1	
	On Presence	On abundance given presence	On Presence	On abundance given presence
	Pr ($> z $) Logistic	Pr ($> z $) Neg. binomial	Pr ($> z $) Logistic	Pr ($> z $) Neg. binomial
<i>Acanthurus chirurgus</i>	0.566	0.547	0.361	0.718
<i>Stegastes diencaeus</i>	0.021*	< 0.001*	0.015*	0.313
<i>Stegastes leucostictus</i>	0.028*	0.029*	0.040*	0.447
<i>Stegastes planifrons</i> (adults)	0.026*	0.028*	0.010*	0.495
<i>Stegastes planifrons</i> (juveniles)	0.024*	0.054	0.07	0.161
<i>Stegastes adustus</i>	0.076	< 0.001*	0.242	0.336
<i>Microspathodon chrysurus</i>	0.010*	0.177	0.019*	0.674
<i>Sparisoma rubripinne</i>	0.045	0.004*	0.045	0.372
<i>Sparisoma atomarium</i>	0.020*	0.444	0.091	0.593
<i>Sparisoma viride</i> (juveniles)	0.017*	0.854	0.133	0.285
<i>Haemulon sciurus</i>	0.030*	0.267	0.072	0.278
<i>Holacanthus ciliaris</i>	0.875	0.102	0.533	0.496
<i>Holacanthus tricolor</i>	0.118	0.392	0.287	0.828
<i>Pomacanthus arcuatus</i>	0.097	0.443	0.716	0.216
<i>Lutjanus apodus</i>	0.019*	0.004*	0.018*	0.878
<i>Lutjanus mahogoni</i>	0.017*	0.952	0.028*	0.055
<i>Chaetodon ocellatus</i>	0.337	0.163	0.624	0.098
<i>Caranx ruber</i>	0.113	0.681	0.048	0.306
<i>Bodianus rufus</i>	0.038*	0.757	0.040*	0.620
<i>Balistes vetula</i>	0.801	0.479	0.128	0.449
<i>Calamus calamus</i>	0.416	0.969	0.339	0.392

The occurrence but not the abundance of *Microspathodon chrysurus*, *H. sciurus*, *L. mahogoni*, *Bodianus rufus*, *S. atomarium*, juvenile *S. viride* and juvenile *S. planifrons* was also significantly and positively related to ISR. However, only the occurrence of the first 4 was also related with E1 (Table 3). Conversely, the abundance but not the occurrence of *S.*

adustus and *S. rubripinne* was significantly and positively related to ISR, but unaffected by E1.

3.3. Scope of E1 to predict patterns of fish abundance

Terminal phase red band parrotfish *Sp. aurofrenatum* held the strongest relationships with E1 and provided a good example of the application of the models generated in this study (Fig. 7). Using the RoxAnn's E1 a minimum difference of 0.9 ind 200 m⁻² and 116 g 200 m⁻² can be predicted for *Sp. aurofrenatum* (Fig. 7) between two sites.

Two sites are likely to support significantly different densities of TP *Sp. aurofrenatum* if their differ at least 0.07 units in E1 and will support significantly different biomass of the same species if they differ at least 0.05 units in E1.

The standard deviation of E1 across the forereef of Glovers Atoll was 0.09. Therefore to detect differences in E1 that would reflect in significant differences in the density of the red band parrotfish ($\Delta E = 0.07$) a minimum of 37 RoxAnn's echoes per site need to be acquired. If the aim was to detect significant differences in E1 that would reflect in different biomass of the red band parrotfish ($\Delta E = 0.05$), a minimum of 70 RoxAnn's echoes per site need to be acquired.

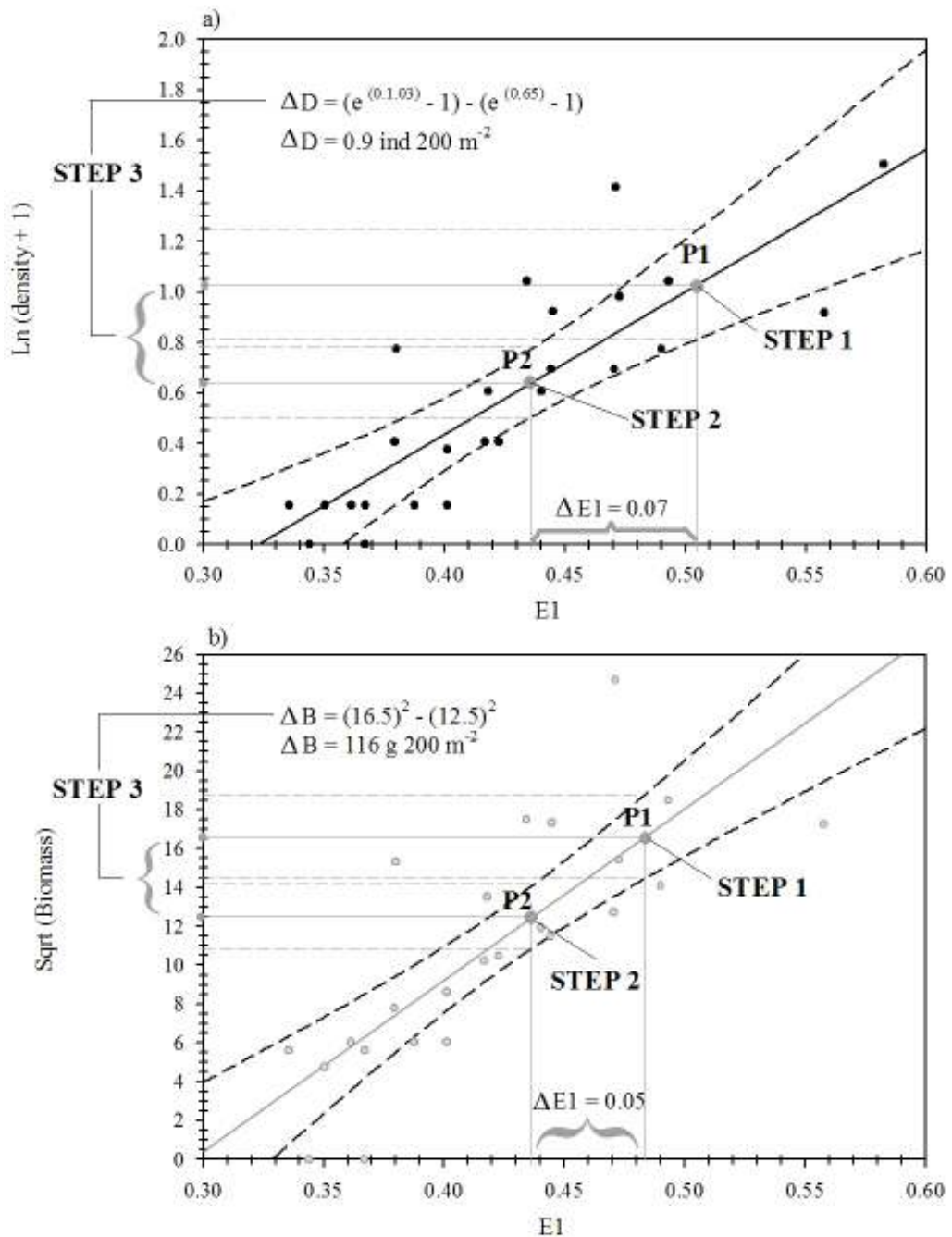


Fig. 7. a) Linear regression between x: E1 vs. y: transformed density of *Sp. aurofrenatum* (Ln (density + 1)) and b) x: E1 and y: square root of biomass of *Sp. aurofrenatum*. Regression line fitted in plot a) is used to illustrate that the smallest difference in density of *Sp. aurofrenatum* that can be predicted with E1 is 0.9 ind 200 m⁻² and would occur in sites that are 0.07 units of E1 different from each other. Plot b) illustrates that the smallest difference in biomass of *Sp. aurofrenatum* that can be predicted with E1 is 116 g 200 m⁻² and would occur in sites that are 0.05 units of E1 different from each other.

4. Discussion

This study demonstrates that despite the differences in scale between the *in situ* measurement of ISR and RoxAnn's E1, the latter can be used as a reasonably good proxy for the topographic complexity of Caribbean reefs. The curvilinear shape of the relationship between ISR and E1 indicates that E1 could sense differences among reefs with lower to intermediate topographic complexity and between reefs with very low and very high topographic complexity relatively easily. However, E1's capacity to reflect the differences among reefs with medium to high complexity is rather limited. Such limitation may arise from the large foot print over which E1 is measured on the bottom (typically at least 30 cm in diameter). Highly complex reefs may differ subtly in their availability of small refuges or other fine-scale attributes that fail to be detected by the sonar.

Fish species included in our surveys hold close relationships with the substratum for a number of reasons. Nocturnal foragers such as grunts, squirrelfish and snappers use physical refuges during the day (Ehrlich 1975; Burke 1995; Ménard et al. 2008) whereas those species that are active during the day such as butterflyfishes, parrotfishes, surgeonfish and damselfish seek refuges during the night (Robertson and Sheldon 1979). Some are prominent stationary predators that spend a large amount of time hiding in refuges such as groupers and hinds (Shpigel and Fishelson 1991). And among these, herbivores and grazers also hold permanent territories and/or feed on the bottom continuously and intensively (Robertson et al. 1976; Thresher 1976; Mumby and Wabnitz 2002). Sites with higher topographic complexity have higher surface area and a greater diversity and availability of shelter and/or foraging sites would be available (Luckhurst and Luckhurst 1978a; Bell and Galzin 1984). Therefore it seemed reasonable to expect that the abundance of most if not all our species would be affected by topographic complexity. Furthermore, given that it has

been suggested that the strongest relationships between fish and topographic complexity may occur in those species that have smaller home ranges or territories and/or are more vulnerable to predation due to their small body size (Roberts and Ormond 1987; Choat and Bellwood 1991; Mumby and Wabnitz 2002) we expected this to be the case in our study. Given the significant relationship observed between ISR and E1, we expected that those species that were significantly correlated with ISR would be also significantly affected by E1.

50% of our species (10 *common* and 13 *uncommon*) had significant relationships with ISR in forereef habitats of Glovers Atoll. These included all the surveyed species of parrotfishes damselfishes and grunts, 67% of the species of surgeonfish and snappers, one species of wrasse and the graysby. The significant relationship of a species with ISR did not always imply a significant relationship with E1. E1 was a significant predictor of the abundance patterns for all the common species but only for 53% of the uncommon species that were significantly affected by ISR. The fact that *Sc. iserti* and *S. planifrons* held the strongest relationships with ISR ($R^2 = 0.93$ and $R^2 = 0.73$) is consistent with our expectations. Both these grazing species are small bodied. *Sc. iserti* has the smallest territory size among species of parrotfish (i.e. 41 – 120 m²) (Mumby and Wabnitz 2002) and territories of *S. planifrons* are only about a meter in diameter (Hixon 1996) or 0.25 m³ (Luckhurst and Luckhurst 1978b). Moreover, the relationships of other small territorial species with ISR were significant despite them being relatively uncommon (i.e. *Sp. atomarium*, *S. diencaeus* and *M. chrysurus*).

Because individual fish are likely to utilize the habitat characteristics on a scale proportional to their home range or foraging area (Roberts and Ormond 1987), it seemed

reasonable to expect that the larger scale measure of topographic complexity E1 would be a stronger predictor of the abundance of species with larger home ranges, whereas ISR will be a stronger predictor for site attached species or species with smaller home ranges or territories, However, ISR was always a stronger predictor for all species (except for TP *Sp. aurofrenatum*, *C. cruentata* and *Caranx ruber*) compared to E1. *Sp. aurofrenatum* did not have particularly large home ranges or territory sizes compared to other parrotfish species in Glovers Atoll or in other Caribbean areas (Munoz and Motta 2000; Mumby and Wabnitz 2002); whereas the mean home range of *C. cruentata* was 2120 m² in St. Lucia (Pople and Hunte 2005) and *C. ruber* had one of the largest movement ranges in Barbados (Chapman and Kramer 2000). The fact that *Sp. aurofrenatum*, *C. cruentata* and *C. ruber* held the strongest relationships with the large scale E1 suggest that these species may be affected by the presence of attributes of the topographic complexity such as mounds or gullies which are not captured with a 4 m chain but may be captured within the footprint of a RoxAnn echo.

A number of small bodied species, some of which are known to be highly site attached such as *Holocentrus rufus* and *Holacanthus tricolor* (Luckhurst and Luckhurst 1978b; Chapman and Kramer 2000) or with at least some individuals holding territories such as *C. capistratus*, *C. ocellatus* and *C. striatus* (Gore 1983; Bonaldo et al. 2005) were unaffected by ISR. The lack of a relationship between abundance and ISR also occurred with the juveniles of the highly site attached *S. partitus*. Two possible reasons may account for the lack of relationship between the abundance of these small site-attached species and ISR. In some cases abundance may be determined by aspects of the topographic complexity that are inadequately reflected by the ISR. Despite it being a commonly used method, the “chain and tape” method provides a measure of the vertical relief but fails to define important

characteristics of the available refuges such as distribution of holes and crevices. The number and diversity of shapes and sizes of holes plays an important role in determining the species richness and abundance of some families of fish (respectively) (Roberts and Ormond 1987). Similarly, the availability of holes matching the size of individual fish are key determinants of a species' choice for refuges (Robertson and Sheldon 1979; Hixon and Beets 1993). A larger number of refuges matching the shape and size of some of the small species or juveniles may not necessarily occur in the most topographically complex reefs. Lack of relationships between abundance and ISR may also have occurred because of an overriding influence of other demographic processes such larval supply, predator abundance, food availability and interspecific competition. For example, the distribution and abundance of chaetodontids for example may be more strongly affected by the abundance of their preferred food resources (i.e. the octocorals *Gorgonia ventalina* and *G. flabellum*, and *Zoanthus*) (Gore 1983; Bonaldo et al. 2005) than the availability of refuge holes. Moreover, the need for physical refuges may not only be a consequence of restricted home ranges or site-attachment but of the species' behaviour in response to predator attacks. When threatened, Caribbean chaetodontids have been observed to undertake a flight response, swimming long distances rather than seeking shelter (Clarke 1977), which may explain why shelter does not seem to be of prime importance to certain species (Gore 1983).

Only 5 of the 10 common species that were significantly affected by topographic complexity increased linearly in abundance as a result of the increases of ISR. Surprisingly the density and biomass of the ocean surgeonfish *A. bahianus* decreased linearly with increasing ISR and E1. Our results contrast with findings of Gratwicke and Speight (2005a) which indicate that *A. bahianus* was characteristic of highly rugose sites in Tortola. Ocean

surgeonfishes differ from other species of surgeonfish in that they consume large amounts of inorganic sediment along with algal material (Randall 1967), though their distribution has been reported to follow the availability of algae (Longley and Hildebrand 1941). It is possible that the daily abundance of *A. bahianus* at the forereef of Glovers Atoll was determined by the presence of inorganic sediment on algal turfs which tends to occur on or in the proximity of less rugose reefs (obs. pers.). In fact, high levels of wave-induced resuspension of sediments are likely to contribute to the low structural complexity at some sites on the forereef of Glovers Atoll, because the presence of sediments can inhibit coral settlement (Birrell et al. 2005). Furthermore, by schooling, *A. bahianus* gains the necessary protection from predators that allows it to utilise such low complexity habitats (Wolf 1987). Finding appropriate refuges for the night might be possible for *A. bahianus* because it has a documented ability to travel long distances (Chapman and Kramer 2000).

Three species, namely the French grunt *H. flavolineatum*, the white grunt *H. plumierii* and the adults of the bicolor damsel fish *S. partitus* reached a maximum density and or biomass in reefs of intermediate ISR. For the grunts this observation is consistent with findings of Gratwicke and Speight (2005b) who found these species to be characteristic species of moderately complex reefs. Interestingly, among the observed parrotfish species only *Sparisoma aurofrenatum* exhibited a curvilinear relationship with ISR, starting with a rapid increase in density and biomass from low to medium complexity (~1.4). This relationship was driven by the IP individuals because TP's increased linearly in density with ISR. Why females exhibit this pattern and not TP (males) remains unclear, as is the reason why it occurs only in this species of parrotfish, because all parrotfish species exhibit territoriality at Glovers Atoll (Mumby and Wabnitz 2002).

4.1. The scope of RoxAnn's E1 to predict patterns of fish abundance

Relatively few studies have studied the relationship between attributes of fish communities and measures of topographic complexity derived from remote sensing tools (see Mellin et al. 2009 for a review). Kuffner et al (2007) for example found a weak relationship between species richness and the rugosity measured from digital elevation models (DEMs) generated from the Experimental Advanced Airborne Research Lidar (EAARL) data in the Biscayne National Park, Pittman et al (2007) predicted sites of high fish species richness using GIS and a spatial layer representing differences in fine-scale topographic complexity among habitat types in the US Virgin Islands, and Purkis et al (2008) found that not only fish species richness but total abundance could be predicted by the rugosity determined with DEMs derived from an IKONOS image of the Diego Garcia Atoll (Chagos Archipelago). Our study evaluated the relationship between the RoxAnn's E1 and the occurrence, density and/or biomass of fish at the species/life phase level finding that this acoustic measurement was a significant predictor of the spatial patterns observed for 21 species of reef fish in Glovers Atoll. Moreover, small differences of E1 between sites (i.e. 0.07) resulted in subtle but significant differences in the abundance (i.e. of minimum 1 individual 200 m^{-2} or $116 \text{ g } 200 \text{ m}^{-2}$) of a species strongly affected by E1 (*Sp. aurofrenatum*).

Interestingly, only one of the studies reviewed by Mellin et al (2009) examined the relationship between the remotely sensed rugosity and the *in situ* rugosity determined with manual methods (i.e. Kuffner et al. 2007). The relatively strong fit we obtained when modelling the relationship between ISR and E1 ($R^2 = 0.66$) contrasts with the poor fit found by Kuffner et al. (2007) between ISR and Lidar rugosity (i.e. $R^2 = 0.15$). Findings of Kuffner et al (2007) indicate that the utility of EAARL rugosity to predict patterns of reef

complexity can be hindered by the choice of study environment. In patch reef areas EAARL rugosity was strongly correlated with distance from the edge of the patch reef rather than with topographic complexity. Moreover, inter-patch reef variability in the Biscayne Natural Park was responsible for most of the variability of species richness and diversity rather than the manually or acoustically determined rugosity. Although this remains untested, we can anticipate that the utility of RoxAnn to predict patterns of ISR could also decline considerably if in hindsight the variability among survey sites is likely to be a strong determinant of the patterns of habitat structure and fish community.

It is necessary to acquire a minimum of 70 RoxAnn echoes per site to detect significant differences in the biomass of species that are highly sensitive to topographic complexity, whereas a minimum of 37 echoes are enough to detect significant differences in density. Detecting subtle differences for species that do not hold a strong relationship with E1 may prove more challenging if possible. Given that the quality of the RoxAnn's signal is affected by the movements of the boat during data acquisition and several echoes need to be eliminated during the filtration of data, a larger number of echoes (100 per site) should be collected.

5. Conclusions

The results of our study highlight the utility of a relatively cost-effective acoustic instrument (see White et al. 2003) to predict variations of topographic complexity and fish abundance within a typical Caribbean coral reef. Models predicting species-specific spatial patterns of density and biomass facilitate mapping functional attributes of fish populations rather than aggregate attributes of fish communities. Accurate predictions of species richness and diversity (Kuffner et al. 2007; Pittman et al. 2007) have provided tools to aid

the design of marine protected areas sensible to fish richness and diversity. We show that the density of some functionally and commercially important species (e.g., large-bodied parrotfishes and small groupers respectively) can also be mapped using acoustic remote sensing. We anticipate that such maps will contribute towards the generation of GIS datasets representing the potential resilience of reefs (Mumby et al. 2007b) and their commercial value to fisheries or tourism. Such maps may then be integrated with other relevant physical, biological, social and economic datasets to help identify appropriate zoning for multiple uses and conservation of the coastal zone.

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CHAPTER 4:
PREDICTING PARROTFISH GRAZING IMPACT IN PALAU, MICRONESIA

This chapter comprises of a paper to be submitted to Biological Conservation

Predicting parrotfish grazing impact in Palau, Micronesia

Sonia BEJARANO CHAVARRO^a

Peter J. MUMBY^a

^a Marine Spatial Ecology Laboratory. Hatherly Laboratories, Prince of Wales Road,
University of Exeter. Exeter, Devon. EX4 4PS, United Kingdom.
(P.J.Mumby@exeter.ac.uk).

Corresponding author: S. Bejarano (sb277@exeter.ac.uk)

Phone: +44 1392 263761

Fax: +44 1392 263700

Predicting parrotfish grazing impact in Palau, Micronesia

ABSTRACT

The grazing process exerts a considerable influence on the health of coral reefs and, appealingly, is subject to management intervention through fishing restrictions. Parrotfishes are among the major grazers of Pacific reefs and their total biomass is often used as a surrogate for their grazing impact (GI). This approach assumes that GI is directly proportional to total biomass and ignores spatio-temporal variability and both intra and interspecific differences in grazing behaviour. Here, we explore an alternative approach that models grazing behaviour explicitly considering the effect of biophysical factors that generate spatial and temporal variation. Grazing was modelled in two steps using empirical studies at three sites in Palau, Micronesia; grazing rate and bite size (area grazed per bite). Bite rate was unaffected by site, but significantly affected by life phase, species and time of day. Bite area increased linearly with total fish body length (TL). The relative grazing impact (% $\text{m}^2 \text{month}^{-1}$) of intermediate phase (IP) and terminal phase (TP) *Chlorurus sordidus*, IP *Scarus psittacus*, TP *Chl. microrhinos* and TP *Cetoscarus bicolor* were calculated by combining their mean abundance with modelled values of bite rate and bite area. Relative biomass was a good proxy for the relative grazing impact in some cases but not others. At the most exposed site the relative biomass of TP *Chl. microrhinos*, TP *Chl. sordidus* and TP *Cet. bicolor* were proportional to their grazing impact, whereas at the sheltered sites the biomass of IP and TP *Chl. sordidus* and that of IP *Sc. psittacus* and IP *Chl. sordidus* did not reflect the relative grazing impact of these populations. This study extends the existing information on grazing impact of Pacific parrotfishes to two more species (i.e. *Sc. psittacus* and *Cet. bicolor*) and provides useful data on the function of two of the main targets of Palau spear-fishermen (i.e. *Chl. microrhinos* and *Cet. bicolor*). Our grazing impact estimates are a first step towards assessing the relative contribution of

different species to the process of grazing and the maintenance of resilience of Micronesian reefs.

Keywords: Parrotfish, Bite rate, Bite area, Palau, Grazing impact

1. Introduction

Although coral reefs are highly dynamic systems capable of recovering from disturbances (Done 1999; Bythell et al. 2000), the frequency and scale of human impacts may in places, exceed the recovery capacity of the ecosystem (Aronson and Precht 2006). Severe disturbances in coral reefs are often followed by extensive coral mortality (Berkelmans and Oliver 1999; Kayanne et al. 1999; Spencer et al. 2000; Loya et al. 2001) and the establishment of algal communities (Diaz -Pulido and McCook 2001) which can successfully pre-empt space and inhibit coral recruitment (McCook et al. 2001). Management strategies must seek to protect those processes and functions that comprise key sources of reef resilience.

The process of grazing, generally defined as the type of animal feeding that involves plant ingestion, plays a key role in the recovery of reefs (McClanahan et al. 2006), because it is one of the major forces regulating the distribution and abundance of benthic algae (Steneck 1988). Intensive grazing can shift the algal community dominance from macroalgae to turfs and ultimately to encrusting corallines (Steneck 1988; Steneck and Dethier 1994). Most (though not all) encrusting corallines provide suitable substrata for the settlement of coral larvae (Birkeland 1977; Harrington et al. 2004) and provide chemical cues that facilitate coral metamorphosis (Heyward and Negri 1999).

Among ecological processes on coral reefs, fish grazing is relatively easy to manage through fishing restrictions (Roberts 1995; Rakitin and Kramer 1996). Parrotfishes (Scaridae) are the dominant grazers of Caribbean reefs (Carpenter 1986; Bruggemann et al. 1996) and one of the main groups on Pacific reefs along with surgeonfish and rabbitfishes (Hiatt and Strasburg 1960; Kiene 1985, 1988; Bellwood 1995b). Within most fish communities, parrotfishes comprise diverse and abundant species assemblages (Russ 1984b; Jennings et al. 1996; Jennings and Polunin 1996; Wantiez et al. 1997; Letourneur et al. 1998) that feed on the benthos continuously and actively throughout the day (Bruggemann et al. 1994b; Bellwood 1995b). Parrotfishes have strong jaws and their grazing mechanisms include scraping or excavating the substrate removing turf, endolithic algae and detritus (Bellwood and Choat 1990; Bruggemann et al. 1994c; Streebman et al. 2002) and, in some species, biting live corals (Bellwood et al. 2003; Reyes-Nivia et al. 2004; Rotjan and Lewis 2005). Therefore, these common herbivores are also significant contributors to reef bioerosion (Bellwood 1995b, a) and sediment production (Bellwood 1996). Parrotfish grazing has not only been associated with the reduction of macroalgal biomass (Williams and Polunin 2001; Mumby et al. 2006) but has also been linked to the reduction of coral mortality (Hughes et al. 2007) and increase in coral recruitment (Mumby et al. 2007). Therefore, the overexploitation of this group can impair the resilience of corals and reduce the scope of recovery after disturbances (Hoegh-Guldberg et al. 2007; Mumby and Steneck 2008). Marine reserves have emerged as potential tools to enhance reef recovery (Hoegh-Guldberg 2006) and have been found to increase parrotfish density (Rakitin and Kramer 1996; Hawkins and Roberts 2004; Mumby et al. 2006)

Parrotfish grazing intensity is often assumed to be directly proportional to their biomass and therefore parrotfish community biomass has usually been quantified (Russ 1984a, b;

Gust et al. 2001; Russ 2003; Mumby and Dytham 2006) with the implicit expectation that this can be interpreted as a direct surrogate for their grazing function. However, this approach ignores both intra and interspecific differences in grazing behaviour and the well known diurnal periodicity of the activity of herbivorous fish. More accurate estimates of the overall parrotfish grazing impact can be obtained by recognizing that the grazing impact of an individual is a function of its bite rate and the area grazed per bite and incorporating the biophysical factors affecting these variables.

Bite rate of certain Caribbean and Pacific species is strongly influenced by the total fish length (TL) (Bruggemann et al. 1994b; Fox and Bellwood 2007), life phase and the foraging depth (Bruggemann et al. 1994b). Also, as observed in other families of tropical herbivorous fish (Polunin and Klumpp 1989; Polunin et al. 1995; Ferreira et al. 1998), grazing rates of various parrotfish species are low in the morning and high in the afternoon (Choat and Clements 1993; Bruggemann et al. 1994c; Bellwood 1995b; Polunin et al. 1995). Parrotfish bite area is positively related to fish size (Bruggemann et al. 1994b; Fox and Bellwood 2007), differs among species and life phases and it is affected by the density of the grazed substrate (Bruggemann et al. 1994a).

Only a few studies on the Great Barrier Reef (GBR) have used visually recorded abundance of parrotfish to quantify the grazing impact indirectly (Fox and Bellwood 2007; Bonaldo and Bellwood 2008; Fox and Bellwood 2008; Hoey and Bellwood 2008) applying a simple algorithm initially developed for Caribbean species (Bruggemann et al. 1996; Mumby et al. 2006). These GBR studies provided grazing impact estimates for 3 parrotfish species (i.e. *Scarus rivulatus*, *Chlorurus microrhinos* and *Bolbometopon muricatum*) on natural reef environments, across different spatial scales and including certain sources of variability of

parrotfish feeding behaviour (Fox and Bellwood 2007; Hoey and Bellwood 2008) and determined the macroalgal selectivity of three parrotfish species (i.e. *Chl. microrhinos*, *Sc. rivulatus*, and *Hipposcarus longiceps*) under experimental conditions (Mantyka and Bellwood 2007). Studies to measure the grazing impact of parrotfishes in natural reef habitats need to be extended to further parrotfish species and to areas where these are heavily targeted within the coral reef fisheries (e.g. Micronesia).

Despite their ecological importance, parrotfishes and other herbivores are heavily fished in Pacific reefs (Dalzell et al. 1996; Dulvy and Polunin 2004) sometimes to the point of threatening certain species with extinction (Donaldson and Dulvy 2004; Dulvy and Polunin 2004). In Palau (Micronesia), parrotfishes have been traditionally important for subsistence fishing and Palauan customs (Johannes 1992). Today several species continue to be extracted intensively for both subsistence and commercial purposes. Unfortunately, the management of most parrotfish communities is rudimentary and largely confined to implicit conservation within no-take marine reserves. In Palau only one species of parrotfish is specifically protected in fished areas (*B. muricatum*). Criteria to identify those species and size classes that require strict management regulations in Micronesia based on their function and contribution to the grazing process are lacking. Our study quantifies parrotfish grazing and some of the key biophysical factors affecting it. Ultimately our aim is to provide policy guidance to help prioritise the conservation of key herbivore species and identify physical conditions that favour high rates of grazing. We worked in Palau (Micronesia) which has extensive and relatively healthy coral reef systems.

The specific objectives of the present study were to (a) model the effects of key biophysical factors on parrotfish bite rate, (b) model the relationship between bite area and fish total

length (TL), and (c) estimate the local grazing impact (total and per substratum type in terms of % m² of reef grazed per month) of the commonest parrotfish species, combining abundance data from visual census and modelled values of bite rates and bite areas. This study extends the grazing impact calculations to 3 more species (i.e. *Chl. sordidus*, *Cetoscarus bicolor* and *Sc. psittacus*) and tests the generality of the results found on the GBR in some Micronesian reefs which seem to hold a higher parrotfish species diversity.

The following hypothesis were tested:

- (1) bite rate differs among reef sites
- (2) bite rate is affected by life phase, body size, and species as observed in other areas (Bruggemann et al. 1994c; Bellwood 1995b; Fox and Bellwood 2007),
- (3) grazing rates are greater in the afternoon as described for several herbivores in the Pacific (Polunin and Klumpp 1989; Choat and Clements 1993; Bruggemann et al. 1994b; Bruggemann et al. 1994c; Bellwood 1995b; Zemke-White et al. 2002),
- (4) parrotfishes graze selectively on one or more substratum types, and
- (5) bite area is positively related to the square of TL as it is in some Caribbean and Pacific species (Bruggemann et al. 1994b; Fox and Bellwood 2007).

2. Methods

2.1. Study area

The Palau Archipelago (Republic of Belau, Micronesia) is located in the western Pacific Ocean between 131°-135° E and 2° to 8° N (Kitalong and Dalzell 1994), 740 km east of the Philippines and 1300 km southeast of Guam (PICRC 2003) (Fig. 1). The archipelago comprises a relatively intact assemblage of tropical marine ecosystems including seagrass beds, mangroves, marine lakes and 500 km² of coral reefs ranging from sheltered fringing reefs to oceanic atolls (PICRC 2003). Palauan reefs harbour one of the most diverse fish

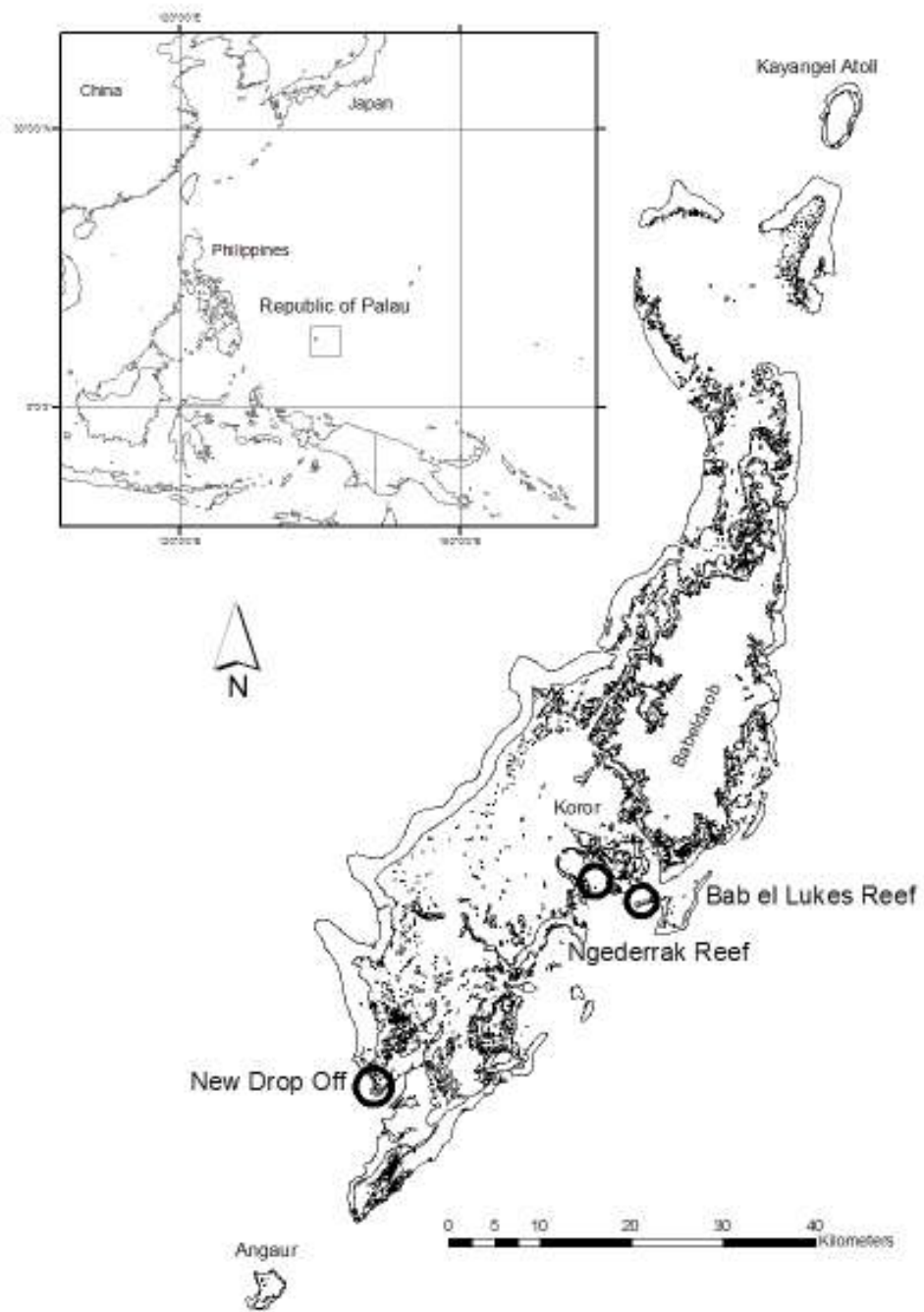


Fig. 1 - Map of the study area indicating the location of the survey sites.

fauna in all of Micronesia probably due to the geographic proximity to the “Indo-Malayan centre of Diversity” (Donaldson 2002).

Surveys were carried out from April 1 to June 5 2006 at three contrasting rock island reef sites (Fig. 1):

Ngederrak is located on the gently sloping forereef terrace of a sheltered barrier reef at ~4.8 km south from Koror. This forereef has a highly complex topographic relief resulting from a mixture of large colonies of branching corals, low coral boulders (< 1 m height), high mounds (1-3 m) and piles of consolidated rubble colonized by a variety of life forms (1-3 m height). This site is an enforced marine reserve.

Lukes reef is located on a sheltered barrier reef bordered by a gently sloping forereef terrace. The site is not fully exposed to wave action coming from the east but is less sheltered than Ngederrak. The topographically complex substratum of Lukes reef comprised a mixture of hard bottom and loose rubble (covered by encrusting and turf algae) with abundant live and dead tabulate and coarse branching corals (primarily *Acropora* spp).

New Drop-off is located on the western barrier reef in the Ngemelis area and was the southernmost of the surveyed reefs. Surveys took place within the flat portion of the reef above 12 m depth where the substrate dropped into a vertical wall. Strong currents and high levels of wave exposure typify this site, particularly during monsoonal winds in the summer months. This site had low topographic complexity and the benthos comprised hardbottom with encrusting coralline red algae and small colonies of encrusting and coarsely branched corals (primarily *Pocillopora* spp.). Like at Ngederrak, fishing is prohibited at this site.

In the following sections of this manuscript we will refer to Ngederrak and Lukes reefs as sheltered barrier reef sites 1 and 2 respectively (SH1 and SH2) and to New drop-off as the exposed site on the western barrier reef (WBR).

2.2. *Data collection*

2.2.1. *Parrotfish biomass*

Underwater visual censuses were conducted at each site to assess the abundance and biomass of each parrotfish species. All surveys were performed in the morning when tidal height was ~1.5 m. At each site, the same surveyor recorded the species, life phase and estimated TL (cm) of every individual parrotfish within 8 randomly-placed belt transects of 30 × 4 m. Parrotfish biomass was calculated from estimates of TL using existing length-weight relationships (Smith and Dalzell 1993; Gust et al. 2001). Where the length-weight relationship was unknown (7 species) the species of most similar body shape was used

2.2.2. *Parrotfish bite rate and grazing selectivity*

Feeding observations were conducted by two surveyors between 9:15 and 16:45 targeting randomly selected individuals from some of the commonest species at each site. To test the effect of the time of day, surveys that took place between 9:15 and 11:30 were grouped as morning (AM) observations, those between 11:30 and 13:30 as midday (MID) observations and those between 13:30 and 16:45 as afternoon (PM) observations. Each surveyor aimed to follow one individual at a time for 7 minutes keeping at least a 2 m distance from it and making careful movements to avoid interfering with its normal behaviour. Life phase (IP: initial phase and TP: terminal phase), total length (TL) and number of bites per substratum type were recorded during each observation.

Parrotfish community composition varied among sites and the testing of hypotheses varied accordingly. To test whether parrotfish bite rate varied among sites, the afternoon bite rate of TP *Chl. sordidus* was quantified at all sites (minimum n = 11). At SH1, where IP and TP *Chl. sordidus* was the commonest species, a total of 60 individuals were surveyed to test whether body size, life phase and time of day had a significant effect on bite rate (minimum n = 10). At SH2, where IP *Chl. sordidus* and IP *Sc. psittacus* were some of the most abundant species, a total of 22 individuals were surveyed to test whether bite rate was significantly affected by species and time of day (minimum n = 5). At WBR, where TP *Cet. bicolor*, TP *Chl. sordidus* and TP *Chl. microrhinos* were the commonest species, the afternoon bite rates were quantified to test if there were significant differences among species (minimum n = 6).

Bite counts were aggregated to obtain mean total bite rate and mean bite rate per substratum type for each species (bites min⁻¹). The availability of substratum types was quantified by surveying 12 randomly-placed point-intercept transects of 20 m length at each site. Substratum types were recorded at each 1 m interval.

2.2.3 Parrotfish bite areas and volumes

Bellwood (1995b) determined the bite area and volume of the excavator *Chl. microrhinos* by measuring visible scars directly on the substrate. However, this method proved impossible in our study because bite marks from scrapers or small parrotfishes, or bites on certain substrates (e.g. fine branching corals) were not discernible directly in the field. Instead, parrotfish bite area was estimated directly from the oral dimensions of harvested parrotfishes, caught by spear-fishermen and landed at the local fish market.

Several individuals of *Chl. microrhinos* and *Cet. bicolor* were found regularly in the fish market of Palau whereas *Chl. sordidus* and *Sc. psittacus* were never observed in the catch of Palauan fishermen. Bite areas for *Chl. sordidus* and *Sc. psittacus* were obtained from individuals landed during later surveys at the fish markets in Guam and Pohnpei. A minimum of 8 individuals of different sizes were examined for each species. Total length and gape size (G) were measured directly on the fish using a flexible measuring tape or metallic callipers. A similar amount of pressure was applied when opening the jaws of all individuals to avoid introducing handling variation when measuring G. The contours of upper and lower jaws were printed on thin layers of coloured moulding clay held inside clear plastic bags. Imprinted moulding clay layers were photographed next to a size reference and bite area was estimated for each species and life phase using G and the width of the portion of the jaw that is in contact with the substratum during a bite (W). W was estimated from the photographs of the jaw prints using the software *Image J 1.32j*. W will likely depend on the feeding strategy (excavating or scraping) of the species under consideration, how forcefully the fish bites into the substrate, and the slope, curvature, and density of the substrate. Nevertheless, for the purpose of this study, W was measured at a fixed distance of 0.01 cm from the distal end of the jaw for small-bodied species (*Chl. sordidus* and *Sc. psittacus*) and of 0.15 cm for large-bodied species (*Chl. microrhinos*, *Cet. bicolor*). These distances were equivalent to the bite depth estimated on the GBR for IP *Chl. sordidus* (15 - 20 cm SL) and the bite depth calculated from data on bite area (169.99 mm²) and volume (256.04 mm³) of *Chl. microrhinos* (35 – 44 cm SL) (Bellwood 1995b).

We assumed that parrotfish bites produced rectangular scars and calculated its total by adding the areas of substrate scraped by each jaw

$$A_{\text{Upper Jaw}} = (G/2) \times W_{\text{Upper Jaw}},$$

$$A_{\text{Lower Jaw}} = (G/2) \times W_{\text{Lower Jaw}},$$

The accuracy of these bite area estimates will be lower than had they been directly measured from scars. However, oral dimensions were measured in a standardised way such that variations observed in the potential bite area of an individual will depend mainly on the shape of its jaws.

Bite volumes (cm^3) for the excavating species (i.e. *Chl. sordidus*, *Chl. microrhinos* and *Cet. bicolor*) were determined by multiplying the estimated area by the abovementioned bite depths reported in the literature (Bellwood 1995b).

2.3. Data analysis

2.3.1. Effect of biophysical variables on parrotfish bite rate

Separate linear regression models were fitted to address the different questions of this study: (a) a one-way ANOVA to test whether the afternoon bite rate of TP *Chl. sordidus* differed among sites, (b) a two-way ANOVA to test whether life phase, body size and time of day had any effect on the bite rate of *Chl. sordidus* at SH1, (c) a two way ANOVA to test whether bite rate differed between IP *Chl. sordidus* and IP *Sc. psittacus* and between times of day at SH2 and (d) a one-way ANOVA to test whether the afternoon bite rate differed among TP *Chl. sordidus*, TP *Chl. microrhinos* and TP *Cet. bicolor* at WBR. To meet the assumptions of normality, the response variable (bite rate) was square-root transformed in the WBR dataset. The overall model adequacy was evaluated by examining

(a) the plot of residuals vs. fitted values to look for heteroscedasticity and (b) the normality Q-Q plot to test for the normality of errors (Crawley 2002).

2.3.2. Grazing selectivity

Individuals' selectivity for each of the grazed substratum types was calculated using the Vanderploeg and Scavia's E^* index (Lechowicz 1982):

$$E^* = [W_a - (1/n)] / [W_a + (1/n)]$$

where n is the total number of substratum types available within a reef site and W is a selectivity coefficient for substratum type "a" determined by:

$$W_a = [r_a/p_a] / \sum (r_a/p_a), (r_b/p_b) \dots (r_z/p_z)$$

where r is the relative number of bites of the individual on substratum types a to z and p is the mean relative cover of substratum types a to z within a reef site.

Mean E^* per species-life phases for all substratum types at each site were determined from individual's E^* . A substrate was selected at random during feeding when mean $E^* = 0$, preferred when mean $E^* > 0$ and avoided when mean $E^* < 0$.

2.3.3. Parrotfish bite area

Linear regressions were conducted to model the relationship between TL and bite area for *Cet. bicolor*, *Chl. sordidus*, *Chl. microrhinos*, and *Sc. psittacus*. Models yielded negative intercepts in most cases, therefore the adequacy of forcing the regression lines to pass

through the origin was tested. Because in most cases this step caused the regression line to be rotated away its maximum likelihood position, it was unjustified (Crawley 2002). Therefore, bite area was square-root transformed to avoid negative predicted values. The adequacy of the models was evaluated by plotting residuals against fitted values to test for heteroscedasticity and against standard normal deviates to test for normality among errors (Crawley 2002).

2.3.4. Grazing impact of four parrotfish species

Models generated here allowed us to predict the monthly grazing impact (% m² grazed month⁻¹) of the populations of IP and TP *Chl. sordidus* at SH1, IP *Chl. sordidus* and IP *Sc. psittacus* at SH2 and the hourly grazing impact in the afternoon (% m² grazed hour⁻¹) of TP *Cet. bicolor*, TP *Chl. microrhinos* and TP *Chl. sordidus* at WBR using bite areas, bite rates, and fish census data, because these were the dominant parrotfishes by species (and phase) at each site during feeding observations.

Predicted bite rate (B_r , bites min⁻¹) and area (B_a , cm²) were obtained from the models above. Individual hourly grazing impact (GI_h , m² hour⁻¹) was calculated as the product of its predicted bite rate and area:

$$GI_h = ((B_r \times B_a)/10000) \times 60$$

and the result was rescaled to the percentage of 2-dimensional reef area grazed per hour (% GI_h , % m² hour⁻¹) using the equation:

$$\% GI_h = GI_h / A_{Tr} \times 100$$

where A_{Tr} is the transect area which in this case was 120 m².

Individuals' hourly grazing impact was extrapolated to daily and monthly estimates accounting for the effect of time of day at SH1 and SH2. At these sites individuals' morning and afternoon B_r were calculated separately and multiplied by B_a to obtain morning and afternoon hourly impacts (% GI_{h-am} and % GI_{h-pm}). % GI_{h-am} and % GI_{h-pm} were then multiplied by the number of morning and afternoon active feeding hours (4.5 and 7 respectively) which were taken from the length of a feeding day observed by Bellwood (1995b) on the GBR (i.e. from 7:00 until 18:30). Finally, total daily grazing impact (% GI_d) was obtained by adding % GI_{h-am} and % GI_{h-pm} and monthly grazing impact (% GI_m) was calculated by multiplying % GI_d by 30. Because the bite rate model at WBR was constructed using afternoon observations (when bite rate of herbivorous fish tends to be higher) the effect of the time of day could not be considered at this site. Estimates of the daily grazing impacts of TP *Chl. sordidus*, TP *Chl. microrhinos* and TP *Cet. bicolor* at WBR were obtained by multiplying the afternoon hourly impact by the total number of active feeding hours in a day. As a result daily and monthly grazing impact of these species at WBR may have been slightly overestimated. However, such overestimation did not affect our main conclusions since our interpretations were drawn only from comparing the grazing impact of a species to that of the species studied within the same site.

Mean hourly, daily and monthly grazing impact for each species-life phase per site were obtained averaging corresponding transect values. Mean monthly impact per substratum

type was calculated as the product of the mean % GI_h and the proportion of bites on each substratum type.

For the excavators TP *Cet. bicolor*, TP *Chl. bicolor* and IP and TP *Chl. sordidus* the monthly grazing impact on live coral (cm³ month⁻¹) was estimated as the product of bite rate, bite volume and the proportion of bites taken from live corals at each site.

3. Results

3.1. Parrotfish biomass

A total of 18 species of parrotfish (in 4 genera) were observed in our morning visual censuses. Mean abundance (individuals 120 m⁻²) at SH1 (13±1.7) and SH2 (14.1±1.9) was significantly higher than at WBR (5.1±0.8) whereas mean biomass (g 120 m⁻²) was significantly lower at SH1 compared with SH2 and WBR (ANOVA, p-value < 0.001, Fig. 2).

An ANOSIM among sites confirmed that the structure of the parrotfish community at WBR differed significantly and strongly from that at SH1 and SH2 (R statistic > 0.60, Significance level < 0.1) whereas differences between SH1 and SH2 were limited. A SIMPER analysis indicated that the predominance of the large bodied excavator *Chl. microrhinos* and the rarity of the small scraper *Sc. psittacus* at WBR were the main two contributors to the differences between this area and SH2 (Clarke and Warwick 2001).

Biomass was dominated by the small-bodied excavator *Chl. sordidus* (60%) at SH1 by twelve scraper species (70%) at SH2 and by the large-bodied excavators *Cet. bicolor* and *Chl. microrhinos* (55.7%) at WBR (Fig. 2).

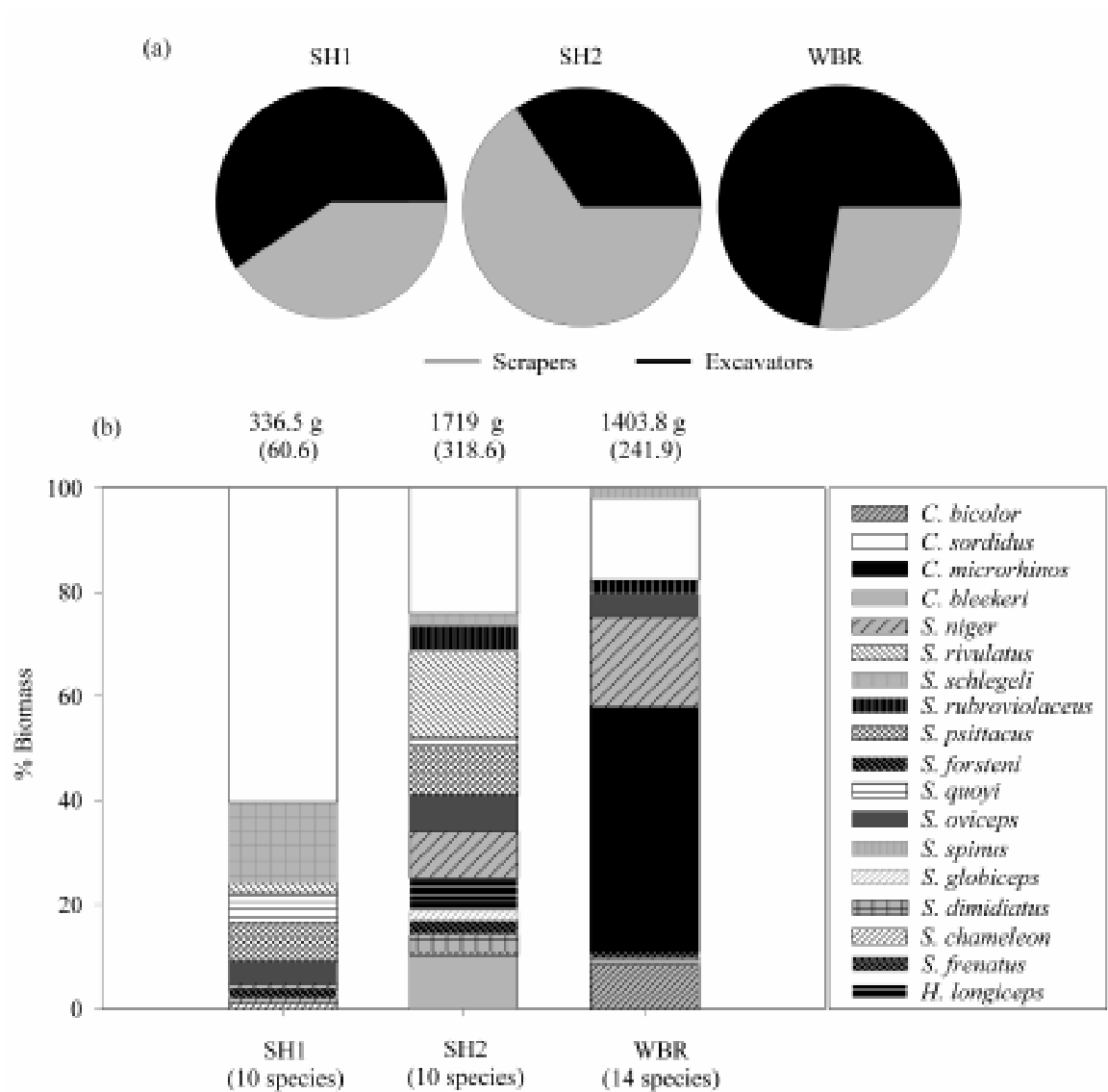


Fig. 2 - Percent biomass (g) of parrotfish (a) functional groups and (b) species at three survey reef sites of Palau (left bars). Right bars correspond to the percent density (individuals 120 m⁻²) of each species. Numbers on top of the bars indicate the mean scarid biomass and density and standard errors at each site.

3.2. Effect of biophysical variables on parrotfish bite rate

3.2.1. *Chlorurus sordidus*: effect of site, life phase, body size, and time of day

The bite rate of TP *Chl. sordidus* was not significantly different among our three study sites (Table 1). At SH1 the bite rate of *Chl. sordidus* was unaffected by body size but significantly affected by their life phase, and by the time of day. Bite rate was always higher in IP individuals than in TP individuals, and was significantly lower in the morning than at midday or afternoon. *Chl. sordidus* bite rates at midday were not significantly different from those in the afternoon (Table 1).

Table 1. Linear regression coefficients for models testing the effect of a) site on the bite rate of TP *Chl. sordidus*, b) total length, life phase and time of day on the bite rate of *Chl. sordidus* at SH1 and the differences c) between bite rates of a scraper and an excavator and d) among 3 excavators

a) <i>Chlorurus sordidus</i> effect of site				
Initial model: rate ~ site				
Final model: (No significant effect of site) (R ² = 0.03)				
	Estimate	Error	t. val.	Pr(> t)
Intercept (SH1)	15.7	1.4	11.1	< 0.001
WBR	-1.2	2.2	-0.5	0.604
SH2	0.7	1.9	0.4	0.713
b) <i>Chl. sordidus</i> at SH1: effect of total length, life phase and time of day				
Initial model: rate ~ total length + life phase + time of day				
Final model: (No significant effect of total length) (R ² = 0.34)				
Intercept (IP, Midday)	22.3	1.4	15.5	< 0.001 *
Terminal phase	-6.3	1.4	-4.4	< 0.001 *
AM	-5.2	1.8	-2.9	0.005 *
PM	0.9	1.8	0.5	0.601
c) SH2: differences between a scraper and an excavator				
Initial model: rate ~ species + time of day (R ² = 0.45)				
Intercept (AM, IP <i>C. sordidus</i>)	10.4	5.6	1.9	0.079
IP <i>Scarus psittacus</i>	27.0	6.6	4.1	0.001 *
PM	13.0	6.6	2.0	0.062 *
d) WBR: differences among excavators				
Initial Model: rate ~ species (R ² = 0.41)				
Intercept (PM, TP <i>Cetoscarus bicolor</i>)	6.71	1.1	6.3	< 0.001 *
PM, TP <i>Chlorurus microrhinos</i>	-0.4	2.2	-0.2	0.857
PM, TP <i>Chlorurus sordidus</i>	7.8	1.7	4.6	< 0.001 *

3.2.2. Lukes reef: differences between a common scraper and excavator of similar size

Bite rate was significantly higher in the scraper IP *Sc. psittacus* than in the excavator IP *Chl. sordidus*. The effect of time of day on the bite rate of the IP individuals of these species at SH2 was marginally significant ($p = 0.06$). Bite rate in the afternoon was higher than that in the morning (Table 1).

3.2.3. New-drop off: differences among excavators

The afternoon bite rate of the smallest excavator TP *Chl. sordidus*, was significantly higher than those of the larger TP *Cet. bicolor* and TP *Chl. microrhinos*. Bite rates of these large excavators were not significantly different from each other.

3.3. Grazing selectivity

The epilithic algal matrix (EAM sensu Wilson et al. 2003) established on solid hard bottom comprised the main grazing substratum for all species surveyed at all sites and was actively selected for ($E^* > 1$) (Table 2). In contrast, all fishes seemed to avoid other substratum types including live corals at all sites and the macroalgae *Halimeda* spp. ($E^* < 0$) where present. At SH1, IP and TP *Chl. sordidus* and also fed selectively on the EAM established over consolidated rubble (CRU) ($E^* > 1$) and at SH2 IP *Sc. psittacus* fed selectively on the EAM established on loose rubble (LRU) ($E^* > 1$) (Table 2).

3.4. Parrotfish bite area and volume

Mean estimated area grazed per bite (cm^2) was largest in *Cet. bicolor* (1.4 ± 0.1) and *Chl. microrhinos* (1.2 ± 0.2) and smallest in *Chl. sordidus* (0.24 ± 0.03) and *Sc. psittacus* (0.18 ± 0.02). Linear relationships between total length and square-root transformed bite area were

positive and relatively strong ($R^2 > 0.50$). *Cet. bicolor* and *Chl. microrhinos* were capable of removing an estimated mean volume of 0.2 cm³ per bite, whereas the smallest excavating species *Chl. sordidus* removed a volume of 0.002 cm³ per bite (Fig. 3).

Table 2. Mean monthly grazing impact (% of a m² grazed month⁻¹) (total and per substratum type) of the population of four parrotfish species-life phases at 3 sites in Palau. Substratum types are: CRU: Consolidated rubble, DMIL: Dead *Millepora* spp., HAL: *Halimeda* spp., EAM: Epilithic algal community, LCO: live coral, LRU: Loose rubble, SAN: Sand, OTH: Others. Note that not all substratum types were present at all sites. Underlined values indicate selectively grazed substrata ($E^* > 0$), all remaining substrata were avoided ($E^* < 0$).

Site / Species / Life phase	Monthly grazing impact (% m ² month ⁻¹)							Total
	Substratum types							
SH1	CRU	DMIL	HAL	EAM	LCO	LRU	OTH	
<i>Chlorurus sordidus</i>								
IP	<u>0.46</u>	0.15	0.03	<u>0.31</u>	0.01	0.14	0.03	1.13
TP	<u>0.63</u>	0.13	0.0	<u>0.66</u>	0.00	0.62	0.01	2.06
SH2	CRU	-	HAL	EAM	LCO	LRU	SAN	
IP <i>Chlorurus sordidus</i>	0.86	-	0.04	<u>3.10</u>	0.03	<u>0.88</u>	0.0	4.9
IP <i>Scarus psittacus</i>	0.12	-	0.03	<u>4.44</u>	0.0	1.06	0.13	5.8
WBR	-	-	-	EAM	LCO	-	-	
TP <i>Cetoscarus bicolor</i>	-	-	-	<u>4.9</u>	0.06	-	-	5.0
TP <i>Chlorurus microrhinos</i>	-	-	-	<u>9.2</u>	0.42	-	-	9.7
TP <i>Chlorurus sordidus</i>	-	-	-	<u>6.4</u>	0.02	-	-	6.4

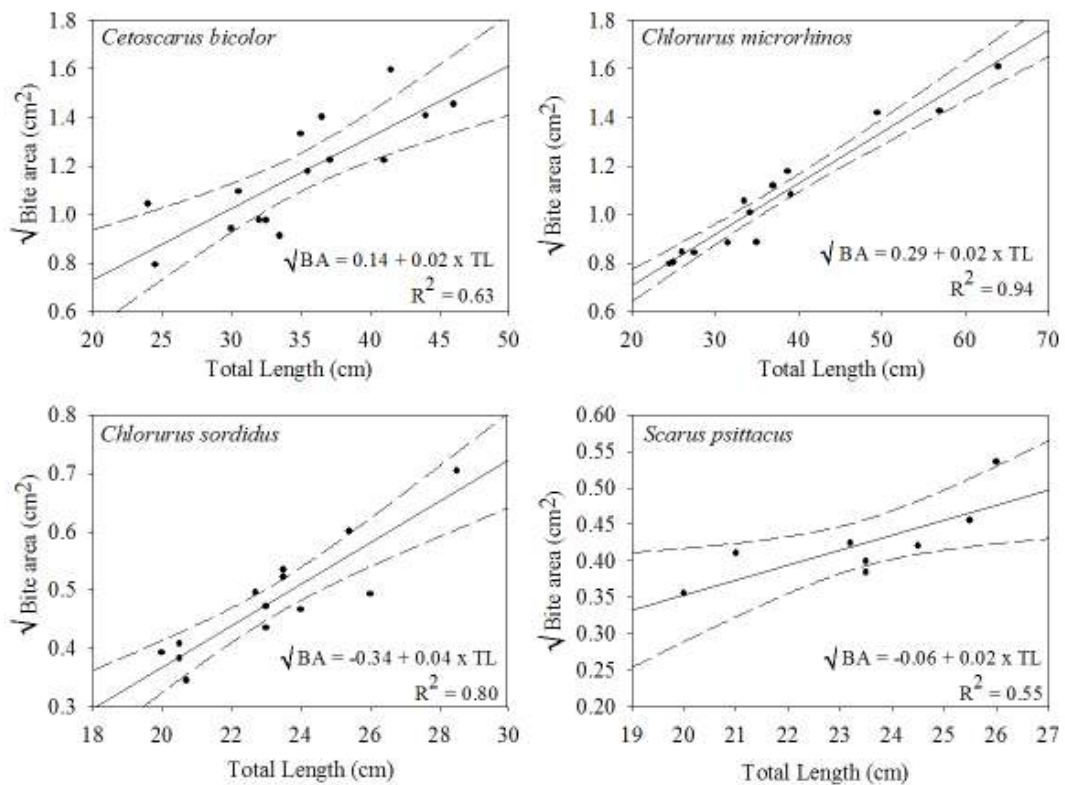


Fig. 3 - Relationship between parrotfish TL and bite area in *Cet. bicolor*, *Chl. microrhinos*, *Chl. sordidus* and *Sc. psittacus*. Regression equations and models fit (R^2) are indicated. Note that scales of both y and x axis differ among plots.

3.5. Grazing impact

The populations of large excavating species at WBR had the greatest grazing impact (Table 2). TP *Chl. microrhinos* at WBR was able to graze almost 10 % of every square metre of reef every month. While TP *Cet. bicolor* was capable of comparable grazing rates and bite sizes to *Chl. microrhinos*, its abundance was lower and overall it grazed ~5 % of every square metre per month. Populations of *Chl. sordidus* (IP and TP) grazed 3.2 % of every m^2 month⁻¹ at SH1, most of which was attributable to TP individuals (Table 2). Although comprised of small-bodied individuals with minimal areas per bite, population densities of IP *Chl. sordidus* and IP *Sc. psittacus* at SH2 were large and collectively grazed 11 % of every m^2 month⁻¹. Of all the grazed substratum types the EAM usually experienced the

greatest grazing impact while mounds of consolidated rubble (CRU) and the loose rubble also experienced considerable grazing when present. In WBR the population of TP *Chl. microrhinos* was responsible for the heaviest predation on live corals (798 cm³ month⁻¹ with a mean of 710 cm³ month⁻¹ ind⁻¹) followed by *Cet. bicolor* (82.1 cm³ month⁻¹ with a mean of 219 cm³ month⁻¹ ind⁻¹). Coral bioerosion was much weaker in *Chl. sordidus*. Despite it being the most abundant in SH1, the population of *Chl. sordidus* removed only 2 cm³ month⁻¹ (with a mean of 0.21 cm³ month⁻¹ ind⁻¹). Similarly, the TP *Chl. sordidus* population in WBR grazed 1.5 cm³ month⁻¹ (with a mean of 0.81 cm³ month⁻¹ ind⁻¹).

3.6. Is relative biomass a good proxy for relative grazing impact?

Relative biomass was a good proxy for the relative grazing impact of some species but not for others. At WBR for example, the total biomass of the population of excavating parrotfishes comprised 59% of TP *Chl. microrhinos*, 23% of TP *Chl. sordidus* and 18% of TP *Cet. bicolor*. The relative contribution of each of these species to grazing at this site reflected rather accurately their relative biomass (Fig. 4). At SH1, the biomass of *Chl. sordidus* was evenly distributed between TP (47 %) and IP (53 %) individuals yet TP's contributed more than half of the species grazing impact (65 %) whereas IP individuals were responsible for the 36 %. At SH2, although the relative biomass of IP *Chl. sordidus* (76 %) was greater than that of IP *Sc. psittacus* (25 %), IP *Sc. psittacus* was responsible for the 54 % of the total grazing impact attributable to these two species (Fig. 4).

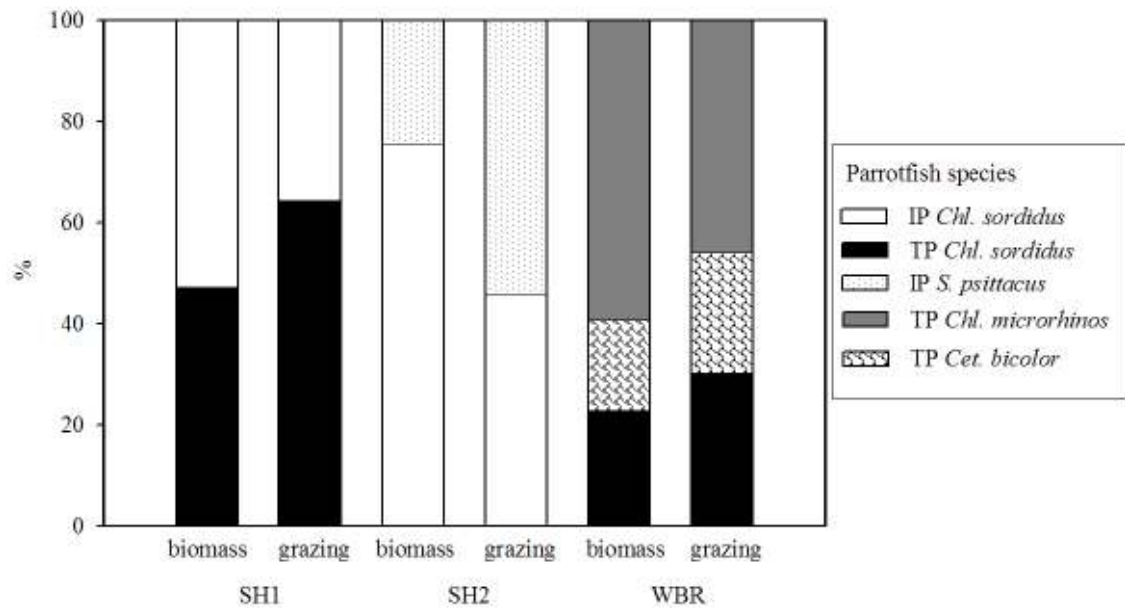


Fig. 4 - Relative biomass (% kg 200 m⁻²) indicated in the bars on the left and relative grazing impact (% m² grazed month⁻¹) in the bars on the right of IP and TP *Chl. sordidus* at SH1, of IP *Sc. psittacus* and IP *Chl. sordidus* in SH2 and of TP *Chl. microrhinos*, TP *Cet. bicolor*, and TP *Chl. sordidus* at WBR.

4. Discussion

This study quantifies the effects of several important biophysical factors on parrotfish bite rate and allows fish body size to be converted into a direct metric of grazing. Models can be used to predict the relative grazing impact of some of the most important targets of spear-fishing activities in Palau and other Micronesian countries (*Chl. microrhinos* and *Cet. bicolor*), and for some of the commonest grazers of Palauan reefs (*Chl. sordidus* and *Sc. psittacus*).

4.1. Parrotfish biomass

Our study took place at three sites with markedly contrasting conditions of wave exposure, substrate complexity, and coral cover. Varying levels of exposure to wave energy explained

the spatial variability of scarid communities on the GBR (Gust et al. 2001; Gust 2002), and are likely to explain some of the differences observed here. High flow of water at exposed sites enhances the supply and uptake of nutrients for algae causing high growth rates and high rates of primary production (Leigh et al. 1987; Carpenter et al. 1991). This mechanism might explain why at WBR, a site affected by heavy surf during monsoonal winds in the summer months, numerous large grazers (i.e. *Chl. microrhinos*, *Cet. bicolor*, *Sc. rubroviolaceus*) could be sustained, whereas these were virtually absent elsewhere. Although the rate of primary productivity was not measured at our study sites, our observations at WBR seem to be supported by findings of Russ (2003) working on the GBR who found that large grazers seemed to aggregate in zones of the highest algal turf production. At present, the importance of food quality relative to other factors such as predation rate and refuge availability in determining spatial differences in parrotfish communities remains to be determined (Fox and Bellwood 2007). Our study indicates that the scarcity of refuges at WBR did not limit the presence of large herbivores. Rather the assumed high rate of primary production at WBR seemed to support the congregation of them, despite the large numbers of parrotfish predators observed at the site. Levels of herbivores could, however, be either a cause or consequence of the patterns of algal productivity over the reef (Russ 2003). A parrotfish community dominated by large excavating species, may also be shaping the characteristics of the substratum landscape at WBR. Eroding species feed predominantly on convex surfaces (Bellwood and Choat 1990) and this may contribute to some extent to the low topographic complexity observed in this heavily grazed environment (Miller 1982).

4.2. *Effect of biophysical variables on parrotfish bite rate*

Differences among our study sites in terms of wave exposure, topographic complexity and benthic cover may be reflected in differences in the rate at which turfs are renewed and in the area effectively available for grazing. Exposed and highly productive sites will generate an increased availability of food over time compared to more sheltered sites, and structurally complex reefs could provide a larger area effectively available for grazing compared to flatter reefs (Mumby and Wabnitz 2002). Here we hypothesized that physical differences among sites would be reflected in inter-site variability of the grazing rate of parrotfishes. Higher grazing rates were expected at highly productive sites or at sites with greater availability of turfs. However, *Chl. sordidus* grazed with a similar intensity at the three studied sites. Two possible reasons can explain this observation. Physical differences among sites may elicit community-level responses, such as increases in abundance or biomass of certain species, rather than an a decrease of individual feeding rates. Alternatively, physical differences among sites may affect other unmeasured aspects of the feeding behaviour of individuals such as the size of the territories or home ranges or the display of territorial behaviour.

In recent literature, differences in the estimated parrotfish grazing impact among sites have emerged as a result of the species or size class composition of their associated scarid community or the dominance of certain species or functional groups (Fox and Bellwood 2007; Hoey and Bellwood 2008). However, accounts of inter-site variability of the grazing rate of individual parrotfishes are rare and inconsistent. Our results contrast with findings of Bellwood (1995b) who found significant differences in the bite rate of *Chl. sordidus* between two sites on a fringing reef at Lizard Island, but are consistent with findings of Bonaldo and Bellwood (2008) who found no differences in the bite rate of *S. rivulatus*

between two sites located on the leeward side of Orpheus Island. When inter-site differences have been observed they have received little explanation. Spatial variability of grazing rates needs to be addressed at wider spatial scales with a more comprehensive approach. Inter-site differences in the primary productivity need to be established empirically and several behavioural aspects of grazing (e.g. territory size, frequency of intra and inter-specific interactions) need to be assessed.

Bite rates measured by direct observation of individual parrotfishes in natural conditions have also been affected by diel periodicity (Choat and Clements 1993; Bruggemann et al. 1994b; Bellwood 1995b; Bonaldo and Bellwood 2008; Alwany et al. 2009), species or functional group (Bellwood and Choat 1990; Bonaldo et al. 2006; Fox and Bellwood 2007; Alwany et al. 2009; Cardoso et al. 2009), life phase (Bonaldo et al. 2006; Lokrantz et al. 2008) and body size (Lokrantz et al. 2008; Cardoso et al. 2009). Moreover, grazing impact of certain species calculated as the product of the bite rate and the area or volume grazed per bite holds a non-linear relationship with the body size for two Caribbean parrotfishes (Bruggemann et al. 1996) and three species from East African reefs (Lokrantz et al. 2008).

In Palau, grazing rates of *Chl. sordidus* displayed a diurnal periodicity in accordance with the patterns previously recognized for several parrotfishes across a wide geographic range (Bruggemann et al. 1994b; Bellwood 1995b; Bonaldo and Bellwood 2008; Alwany et al. 2009) but also for other herbivorous fish (Polunin and Klumpp 1989). Grazing rates of *Chl. sordidus* in Ngederrak reef were unaffected by the individual's body size but were strongly influenced by their life phase. IP individuals attained higher bite rates than TP individuals and at least to some extent this can be explained because TP individuals were involved in significantly more territorial interactions, whereas IP individuals spend more time focused

on foraging. Interestingly *Chl. sordidus* grazing rates were negatively correlated with body size and unaffected by life phase in Zanzibar (Lokrantz et al. 2008). Differences between Palau and Zanzibar may be the result of including different ranges of individual sizes in both areas. *Chl. sordidus* surveyed in SH1 ranged from 5 - 26 cm TL whereas those in Zanzibar sizes ranged from 3 – 39 cm TL.

Bite rate differences observed between IP *Sc. psittacus* and IP *Chl. sordidus* at SH2 may reflect differences between the functional groups these species belong to (i.e. scrapers vs. excavators) and demonstrate that these differences are evident within species at the life phase level. Typically, scrapers take rapid weak bites on the substratum whereas excavators are capable of slow, short and powerful bites and as a result scrapers have higher bite rates than excavating species (Bellwood and Choat 1990). However feeding observations need to be conducted on further species to establish the generality of the difference between scrapers and excavators in Palau.

Bite rate of the small excavator *Chl. sordidus* was significantly higher than that of the larger excavators *Chl. microrhinos* and *Cet. bicolor*. Such differences may result from the differences in their body size, bite area and metabolic rates. Slower bite rates of large-bodied excavators can be explained because their bite area and therefore their food intake per bite are larger (Bruggemann et al. 1994b). Higher feeding rates of the smaller *Chl. sordidus* may occur because the metabolic rate is higher in smaller individuals (von Bertalanffy 1957).

Although in Palau most of the species grazed on a wide variety of substratum types they selected the EAM established on solid substratum. Our results are consistent with previous

findings by Bellwood and Choat (1990) on the GBR who observed that most species of parrotfish grazed on epilithic algae (EA) and Bonaldo and Bellwood (2008) who observed a strong preference for the EAM and rejection of other substratum types. EAM are the preferred and most intensively grazed substrate probably because algal turfs within them are the major primary producing components of the reef benthos (Carpenter and Williams 2007). Turfs also accumulate detritus and organic matter which form an important source of nutrition for roving grazers that target epilithic algae (Purcell and Bellwood 2001). Fleshy macroalgae were neither abundant at the sites nor commonly grazed by the parrotfishes species studied in this paper. However, some of our most recent observations not included in this paper indicate that *Sc. niger*, *Sc. forsteni*, *Sc. rubroviolaceus*, IP *Sc. chameleon*, and (unlike the IP *Sc. psittacus*) TP *Sc. psittacus* fed frequently on *Halimeda* despite its heavy calcification, low productivity, slow growth rate and structural and chemical defences (Hay et al. 1983; Littler et al. 1983). Although *Chl. microrhinos* and *Cet. bicolor* fed on live corals at WBR, no evidence of selective coral predation was found for either of these species. Our results are similar to observations of the Bumphead parrotfish (*B. muricatum*) on the GBR in that it consumed live corals in proportion to their availability rather than exhibiting active selection for live coral (Hoey and Bellwood 2008).

4.3. Area grazed per bite

The indirect bite area estimations obtained in this study have overlooked potential sources of variation such as the substrate density, inclination and curvature, as well as the inclination of the fish when taking a bite. Therefore, comparing the values recorded here with direct measurements of scars provides important information about their accuracy. The individual bite areas observed in Palau for *Chl. microrhinos* and *Chl. sordidus* were similar

to the means registered on the GBR by Bellwood (1995b), Bonaldo and Bellwood (2009) for similar sized individuals of the same species (Table 3).

Table 3 - Comparison of mean bite areas measured directly from scars of *Chl. microrhinos* and *Chl. sordidus* on the GBR with the ranges of bite areas estimated from jaw measurements in Palau.

Species	Size (cm)	Mean B_a (cm²)	Reference
<i>Chl. sordidus</i>	15 – 20 SL (19 – 25 TL)	0.20 – 0.23	Bellwood (1995b)
	17 – 29 TL	0.24 ± 0.03	This study
<i>Chl. microrhinos</i>	35 - 44 SL (46 - 58 TL)	1.45 – 1.94	Bellwood (1995b)
	40 – 45 TL	1.19	Bonaldo and Bellwood (2009)
	24 – 65 TL	1.2 ± 0.2	This study
<i>C. bicolor</i>	24 – 47 TL	1.4 ± 0.1	This study
<i>Sc. rivulatus</i>	5-10 TL	0.03	
	11 – 25 TL	0.28	Fox and Bellwood (2007)
	> 25 TL	0.69	
	35 – 40 TL	0.44	Bonaldo and Bellwood (2009)
<i>Sc. psittacus</i>	18 – 26 TL	0.18 ± 0.02	This study

Bite area, and therefore the amount of epilithic algae ingested by the Caribbean parrotfish *Sparisoma viride*, increased linearly with the fork length of the fish squared (Bruggemann et al. 1994b). An identical relationship was found between the bite area and the total length of *Sc. rivulatus* Bonaldo and Bellwood (2008). Contrastingly, bite area was linearly related with the untransformed TL for four parrotfish species in Palau. Despite this difference bite areas predicted from our models are comparable with direct measurements of the scars of similar sized individuals of the same species (Table 3).

4.4. Is relative biomass a good proxy of relative grazing impact?

Detailed models to predict the grazing impact of the population of a parrotfish species in a specific reef site accounting for the bite rate's diurnal periodicity and variability between life phases, as well as the effect of body size on the individuals' bite area, were generated only for the commonest species *Chl. sordidus*. Results indicate that relative biomass of TP and IP populations (47% vs. 53% respectively) did not reflect their relative contribution to the grazing process (64.5% vs. 35.5% respectively). *Chl. sordidus* is not commonly fished in Palau but is found in the fish markets in other Micronesian countries as a result of non-selective spear-fishing activities (pers. obs.). Our results indicate that although small individuals do not graze a large area per bite, their overall contribution to grazing can be relatively important. Grazing levels could be severely depleted if extraction of *Chl. sordidus* becomes a widespread and uncontrolled practice.

The scope of our study to produce models for populations of parrotfishes including IP's and TP's is limited in SH2 and WBR because only individuals of one of these life phases could be surveyed with adequate replication at these sites. This limitation does not affect the estimated impact of *Chl. microrhinos* because the rarity of IP's of this species seems to be a natural condition across Micronesian reefs (pers. obs.). Further feeding observations of TP *Chl. sordidus* and TP *Sc. psittacus* at SH2, and IP *Chl. sordidus* and IP *Cet. bicolor* at WBR are necessary to produce more inclusive models for these species. However models generated here served to illustrate that a) the differences in bite rate among scrapers and excavators are evident when comparing individuals of the same life phase and b) relative contribution to grazing of excavating species may differ.

Relative biomass of TP *Chl. sordidus*, TP *Chl. microrhinos* and TP *Cet. bicolor* corresponded reasonably to their relative grazing impact at WBR but this was not the case for IP and TP *Chl. sordidus* at SH1 or for IP *Sc. psittacus* and IP *Chl. sordidus* at SH2. Van Rooij et al (1998) found correspondence between the relative biomass and the relative food intake ($\text{kJ ha}^{-1} \text{day}^{-1}$) of several parrotfish species in Bonaire whereas Fox and Bellwood (2007) demonstrated that abundance of a species-size class does not always correspond to its grazing impact on the GBR. The grazing impact of the population of TP *Chl. microrhinos* at WBR ($10 \% \text{m}^2 \text{month}^{-1}$) was comparable to the grazing impact of the same species on the slope habitat of Orpheus Island on the GBR ($13 \% \text{m}^2 \text{month}^{-1}$) but lower than the impact of this species at the GBR reef crest habitats ($40 \% \text{m}^2 \text{month}^{-1}$) (Fox and Bellwood 2007).

Recent studies have estimated the overall grazing impact of parrotfish communities from abundance data on the GBR (see Fox and Bellwood 2007; Hoey and Bellwood 2008). Such predictions have used several sources of data: 1) initial bite rate observations for 17 species by Bellwood and Choat (1990), 2) feeding day-lengths for two species (Bellwood 1995b) and 3) bite rate models incorporating biophysical sources of bite rate variability and scar sizes for *Chl. sordidus* and *Chl. microrhinos* (Bellwood 1995b), *Sc. rivulatus* and *Chl. microrhinos* (Fox and Bellwood 2007) and *B. muricatum* (Bellwood et al. 2003). Predictions yielded relatively realistic estimations of the grazing impact of parrotfish communities on the GBR (Fox and Bellwood 2008), several of which are numerically dominated by two species of parrotfishes (*Sc. rivulatus* and *Chl. microrhinos*) and a rabbitfish (*Siganus doliatus*) (Fox and Bellwood 2007). Unlike communities described by Bellwood (Fox and Bellwood 2007) at some sites on the GBR, parrotfish communities in Palau are relatively diverse which precludes a detailed analysis of the grazing impact of the

entire parrotfish community. Generalising the use of the models obtained here to estimate the impact of other species could result in under or overestimations of bite rates of several species. Similarly, assuming that grazing rates of all species have the same diurnal periodicity could be problematic because the diurnal periodicity can be weaker in some species than in others (Bellwood 1995b). Lastly, assuming that the effect of life phase would be the same for all parrotfish species in Palau may be ignoring the differences in their social organization which can affect the relative amount of time allocated to grazing by IP and TP individuals. It is possible that IP and TP individuals have a more similar grazing behaviour in species that school or do not defend territories.

Models of grazing impact generated here provide useful tools to convert the abundance of important parrotfish species in to a quantitative measure of an essential ecological process: grazing. Such models aim to contribute to two major future goals: 1) to rank Micronesian parrotfish species according to their relative contribution to grazing impact and 2) to aid the generation of maps of grazing. The ranking of species may in future inform the design of fishing regulations by identifying those playing a key role in sustaining resilience. The maps of grazing impact may support management strategies for coral reef areas by highlighting sites that have naturally-high levels of grazing and potentially greater resilience.

In our study TP *Chl. microrhinos* and TP *Cet. bicolor* were major contributors to the grazing impact and bioerosion. On the GBR large species like these were capable of removing algae effectively and opening new colonization sites on the substratum (Bonaldo and Bellwood 2008). Extraction of these species occurs in high volumes in Palau and deserves special attention and careful monitoring in order to establish pertinent regulations.

Further efforts towards defining the functional role of other parrotfish species in Palau as well as to test the applicability of our models across wider spatial scales are being undertaken.

The generation of maps of the grazing impact of populations of *Chl. sordidus*, *Sc. psittacus*, *Cet. bicolor* on Palau reefs requires the coupling of the models of grazing generated here with models that allow the prediction of spatial patterns of abundance of these species across large geographical scales. Such will be the focus of our future research.

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CHAPTER 5
THE EFFECT OF TIDES ON THE BEHAVIOUR OF PARROTFISHES:
BUDGETING TIME BETWEEN GRAZING AND SPAWNING

This chapter comprises of a paper to be submitted to Marine Biology

The effect of tides on the behaviour of parrotfishes: Budgeting time between spawning and feeding

Sonia Bejarano Chavarro¹, Victor Ticzon² and Peter J. Mumby¹

¹Marine Spatial Ecology Lab, University of Exeter, Hatherly Laboratories, Prince of Wales Road, Exeter EX4 4PS, UK.

²Marine Science Institute, University of the Philippines, Manila.

Abstract

Spawning times of most coral reef fish follow a diel periodicity which serves to ensure the best conditions for larval dispersal, survivorship and settlement but also to coordinate the encounter of adults and decrease their own risk of being attacked by predators. In Pacific parrotfishes, spawning periodicity is linked with certain times of day and/or tides. Systematic behavioural observations of terminal males of the commonest species *Chlorurus sordidus* were conducted across a range of tidal conditions in the morning, midday and afternoon in a sheltered barrier reef of Palau, Micronesia. *Chl. sordidus* spawned daily near the reef crest between 8:00 – 16:30 and primarily (but not exclusively) during high tide through to the first hour of ebbing tide. Although more individuals in the population spawned in the afternoon and midday compared to the morning high tides, the spawning intensity was unaffected by the time of day. Spawning lasted 40 minutes to an hour and during this time the feeding of several TP and IP *Chl. sordidus* ceased almost completely, yielding the lowest mean grazing rates during the day (5-10 bites min⁻¹). The effect of tides on feeding of *Chl. sordidus* was different among times of day: bite rates were strongly reduced by tidal condition in the morning and midday but remained unaffected by tides in the afternoon. Tidal conditions, as well as current flow and other factors that may influence the spawning synchrony of grazing fish should be considered when measuring the grazing rates of fish or if predicting spatial and temporal variability of their grazing impact.

Keywords: parrotfish spawning, *Chlorurus sordidus*, tides, grazing rates, Palau.

1. Introduction

Several families of coral reef fish, including parrotfishes, spawn periodically following annual, semi-lunar and diel cycles (Johannes 1978; Ross 1983; Colin and Bell 1991). Diel timing of spawning of several species of labrids, surgeonfishes and parrotfishes occurs in synchronization with the presence of high and ebb tides presumably to utilise the direction and speed of associated currents (Robertson and Hoffman 1977; Robertson et al. 1982; Robertson 1983; Colin and Bell 1991; Hunt von Herbing and Hunte 1991; Sancho et al. 2000; Hamner et al. 2007; Kuwamura et al. 2009). Several hypotheses have been proposed to explain the synchronization of spawning with times of high and outgoing tides (see Shapiro et al. 1988). Some of these explanations focus on the implications of tidal synchrony on the larvae (e.g. Colin and Bell 1991) whereas others also consider certain biological aspects of adults (e.g. Shapiro et al. 1988; Robertson 1991). Tidal synchrony may occur as an adaptation to use tidal currents (a) to maximise larval dispersal outside of the natal reef (Choat and Robertson 1975; Johannes 1978; Colin and Bell 1985) or guarantee the retention of larvae within it (Johannes 1978), or (b) to flush larvae off the reef to avoid predation by planktivores (Johannes 1978; Robertson 1983). Spawning at fixed times of day may also be a strategy of pelagic spawners to reduce the risks of predation on themselves (Robertson and Hoffman 1977). In the case of territorial grazers, the timing of reproduction might be coordinated with their diurnal feeding cycle and the behaviour of their competitors. Food availability for example, was the primary determinant of the seasonality of reproduction in the Caribbean striped parrotfish *Scarus iserti* (Clifton 1995). Moreover, diel spawning rhythms of a strongly territorial surgeonfish seemed to follow variations in competition pressure, and herbivores in general may time their spawning activity to occur on those times that are less suitable for feeding (Robertson 1983).

Parrotfishes are one of the main groups of grazers in Pacific and Caribbean coral reefs (Hiatt and Strasburg 1960; Kiene 1985; Carpenter 1986; Kiene 1988; Bruggemann et al. 1996) and their grazing function is considered critical for the resilience of coral reefs (Bellwood et al. 2004; Mumby et al. 2007). The allocation of time to reproduction and social interactions will hinder the amount of time spent grazing during the day. Therefore, the timing of spawning of important grazers should be identified when attempting to understand the temporal dynamics of their grazing intensity. Moreover, the relative effect of time of day and tidal condition on the spawning intensity, frequency of courtship and aggressive behaviours needs to be quantified.

In this study we aimed to describe the effect of time of day and tidal condition (height and direction) on the spawning periodicity of the territorial bullet-head parrotfish (*Chlorurus sordidus*) in a sheltered barrier reef in Palau. Our main goal was to identify the times allocated by *Chl. sordidus* to spawning and locate them in the context of its overall behavioural budget. In doing so we measured the effects of reproduction on the diel dynamics of *Chl. sordidus* grazing. We conducted systematic behavioural observations of terminal phase (TP) *Chl. sordidus* encompassing a one-month tidal cycle within each time of day (morning, midday and afternoon) to test the following hypotheses:

1. *Spawning behaviour and timing*: Spawning events occur and/or frequency of mating rushes and courtship displays is highest with those specific tidal conditions that can maximise survival of larvae and with those times of day when turf productivity and benefits from grazing are lowest.
2. *Quantitative effects of spawning on grazing rates*: Grazing rates of *Chl. sordidus* are significantly reduced by the spawning timing.

3. *Periodicity and frequency of intra and inter-specific interactions*: the occurrence and the number aggressive interactions increase at or near peak spawning times.

2. Methods

2. 1. Study area

The Palau Archipelago (Republic of Belau, Micronesia) is located in the western Pacific Ocean between 131°-135° E and 2° to 8° N (Kitalong and Dalzell 1994), 740 km east of the Philippines and 1300 km southeast of Guam (PICRC 2003). Data collection took place from mid-April to mid-May 2008 at Ngederrak reef, a sheltered barrier reef located ~4.8 km south from Koror on the west side of the entrance to the Malakal harbour channel (Fig 1). Systematic surveys took place at non-overlapping locations along the shallow forereef (0 and 6 m depth) where the habitat characterized by a gently sloping terrace with high topographic complexity, resulting from abundant live forms of branching corals *Acropora* spp. and *Millepora* spp. mixed with low coral boulders (< 1 m height), high mounds (1-3 m) and piles of consolidated rubble (1-3 m height) colonized by a variety of life forms. The tidal cycle is semidiurnal in Palau and tidal height varied between 0.8 m to 2 m during our study (Tide tables, Palau International Coral Reef Centre). At the Lighthouse reef located adjacent to Ngederrak reef on the east side of the Malakal channel, tidal currents usually flow from the lagoon, through the backreef, over the reef crest and off the reef during ebb tide and in reversed direction during rising tide (Hamner et al. 2007). Local knowledge indicated that the same patterns of current flow occur at Ngederrak reef.

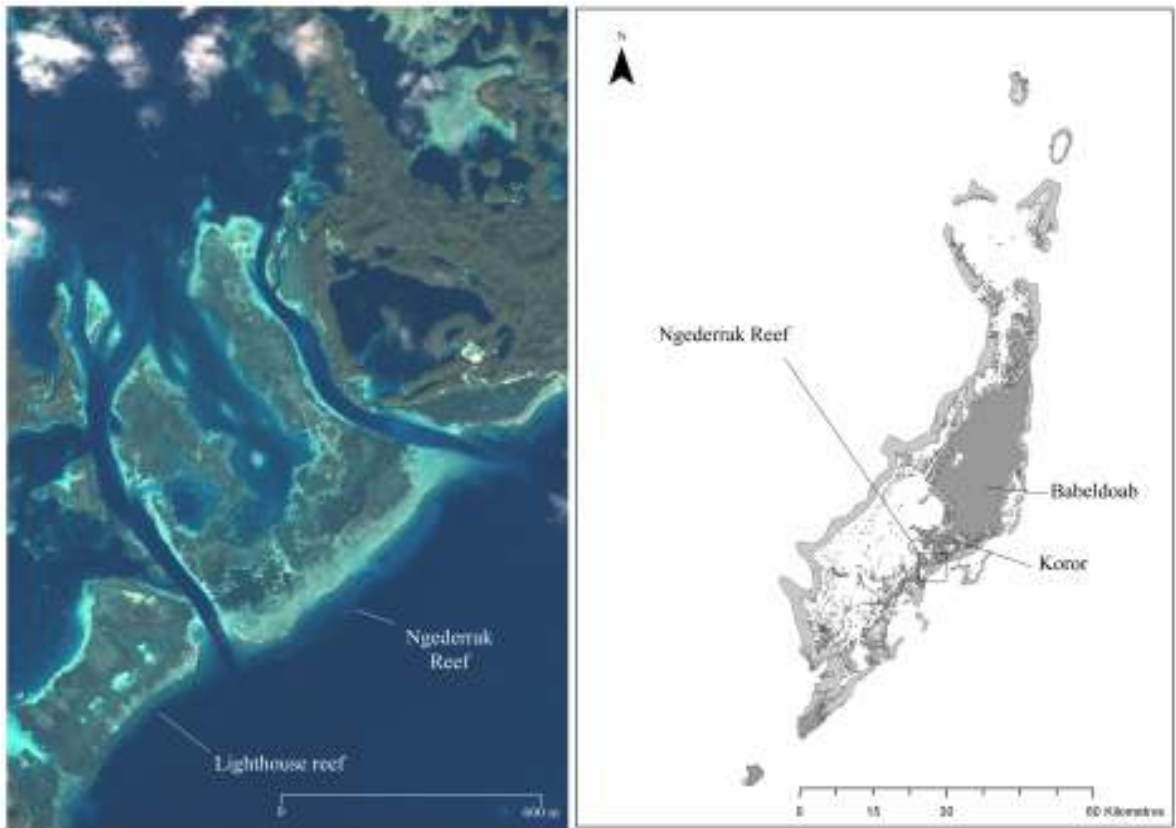


Fig. 1. IKONOS Image of Ngederrak reef near Koror, in the Palau Archipelago.

2.2. Data collection

To test whether spawning events of *Chl. sordidus* were synchronized with specific tidal conditions and/or restricted to the mornings which may be less suitable for feeding (Zemke-White et al. 2002), behavioural surveys were conducted repeatedly throughout an entire month. Observation periods were stratified systematically to include 3 different times of day: morning (9:00 – 11:00), midday (11:30 - 13:30) and afternoon (14:00 – 17:00) and 5 different tidal conditions within each time of day: low outgoing and incoming tides (between 0 - 0.5 m, also referred to as LOW/OUT and LOW/INC), medium outgoing and incoming tides (between 0.6 - 1.5 m, hereafter referred to as MED/OUT and MED/INC) and high tide together with the first hour of outgoing tide (between 1.56 - 2 m, hereafter

referred to as HIG/OUT). As a result, the ranges of tidal heights surveyed at different times of day were similar: 0.56 to 1.99 m in the morning, 0.25 to 1.86 m at midday and 0.12 to 1.44 m in the afternoon.

During each survey period two divers conducted independent feeding and spawning observations on randomly selected TP individuals of *Chl. sordidus* between 20 and 25 cm in total length (TL). Once a target individual was located, the diver followed it for 7 minutes keeping at least a 2 m distance from it and making careful movements to avoid interfering with its normal behaviour. Total number of bites on the substrate, courtship displays, paired spawning rushes, intra and inter-specific interactions, attacks to and from surgeonfishes and damselfishes and (when possible) species involved in the interactions were registered. The two surveyors who conducted these observations compared notes to ensure correct identification of the target species, accurate estimation of an individual's TL and the consistent categorisation of reproductive and aggressive behaviours.

Scuba gear was used to complete the surveys on most cases, except on high tide when snorkelling became necessary to follow the fast movements of the fishes. Normally each surveyor completed observations for at least 6 to 10 individuals per dive. Therefore, a total of 12 to 14 replicate fish ($n = 12$ to 14) were generally obtained within each level of our treatments (tidal condition / time of day). However, because of unfavourable weather a lower number of replicate fish could be surveyed during midday LOW/INC and LOW/OUT tides ($n = 5$).

2. 3. Data analysis

2.3.1. Spawning behaviour and synchrony with the tidal cycle and times of day

To test whether the occurrence of reproductive behaviours was significantly affected by the tidal condition, time of day or the interaction between these variables, a general linear model (GLM), with data treated as proportions with a binomial error structure was used. The response variable comprised a two-column vector containing the number of individuals observed spawning (or displaying any type of courtship behaviour) and the number of individuals displaying no reproductive behaviours within each of the treatment levels. Categorical factors time of day and tidal condition had 3 and 5 levels respectively (time of day: AM, NO, PM; tidal condition: LOW/INC, LOW/OUT, MED/INC, MED/OUT, HIG/OUT). The resulting model was not overdispersed, therefore the significance of each of its parameters was tested through model simplification using chi-square tests (Crawley 2002).

2.3.2. Effect of time of day and tidal height on the spawning frequency

To test whether the time of day affected the number of spawning rushes or courtship displays observed during the peak spawning period (HIG/OUT) we conducted a GLM with data as counts. Because the model assuming Poisson error structures was overdispersed, we specified an estimate of the dispersion parameter (quasi-Poisson) to scale up its standard errors and performed F-tests to test the significance of the factors (Faraway 2006).

2.3.3. Quantitative effects of spawning on grazing rates

To quantify the reduction of grazing intensity caused by the allocation of time to reproduction at different times of day we fitted three linear models. Each model included time of day and one of the following variables considered informative of the tide

fluctuation (a) tidal condition, (b) distance between the time at which each individual fish was surveyed and time at which the nearest daytime HIG/OUT tide occurred, and (c) tidal height. All models included the interaction between factors to test whether the effect of the tidal variation on the grazing rate was different depending on the time of day. To identify the factor's levels that were significantly different from each other we conducted an *a posteriori* Tukey's honestly significant difference (HSD) and assessed the adjusted p-values for significance.

2.3.4. Periodicity and frequency of intra and inter-specific interactions

To test whether the occurrence of inter or intra-specific aggressive interactions in the behavioural budget of *Chl. sordidus* was concentrated on a particular time of day or tidal condition, a GLM was used with data as proportions with a binomial error structure. The response variable comprised a two-column vector containing the number of individuals involved in aggressive interactions and the number of individuals involved in no aggressive interactions within each of the treatment levels.

To test whether aggressive interactions were more closely related with reproduction rather than feeding we used a GLM with Poisson error structure. The model tested whether the number of inter and intra-specific aggressive interactions increased with the proximity of the time when spawning peaked (HIG/OUT tides). Overdispersion was handled as in previous models, specifying an estimate of the dispersion parameter (quasi-Poisson) to scale up its standard errors and performing F-tests to test the significance of the factors (Faraway, 2006).

To test the overall adequacy of all the models fitted in this study we examined (a) the plot of residuals vs. fitted values to look for heteroscedasticity and (b) the normality Q-Q plot to test for the normality of errors (Crawley 2002).

3. Results

3.1. Spawning behaviour and synchrony with the tidal cycle

The occurrence of reproductive behaviours of *Chl. sordidus* was not significantly affected by the time of day but was strongly aligned with the tidal condition. Courtship displays accompanied by spawning events occurred daily regardless of the time of day but almost exclusively during high tide and within the first hour of outgoing tide (HIG/OUT) (Fig 2).

The start of the spawning period at high tide was generally marked by TP individuals swimming fast in an almost straight line from their feeding territories at medium depths (6-9 m) towards the reef crest (0-2 m). When this happened, distance travelled by the fish did not exceed 50 m. Usually, a fish already engaged in spawning or ready to spawn was unmistakably recognised from others because it had risen above the substrate and displayed a distinctive behaviour. Individuals preparing to spawn swam at a faster speed, rapidly beating their pectoral and caudal fins. At times a fish rushed several metres either to chase a conspecific individual or without having an evident purpose. On several occasions a TP male in the proximity of a single female or group of females would swim in small circles directly above them. Spawning always occurred in pairs and group spawning was never observed. Both the male and female rushed to the surface releasing a cloud of eggs and sperm at the end of the ascent and descended to the bottom immediately afterwards.

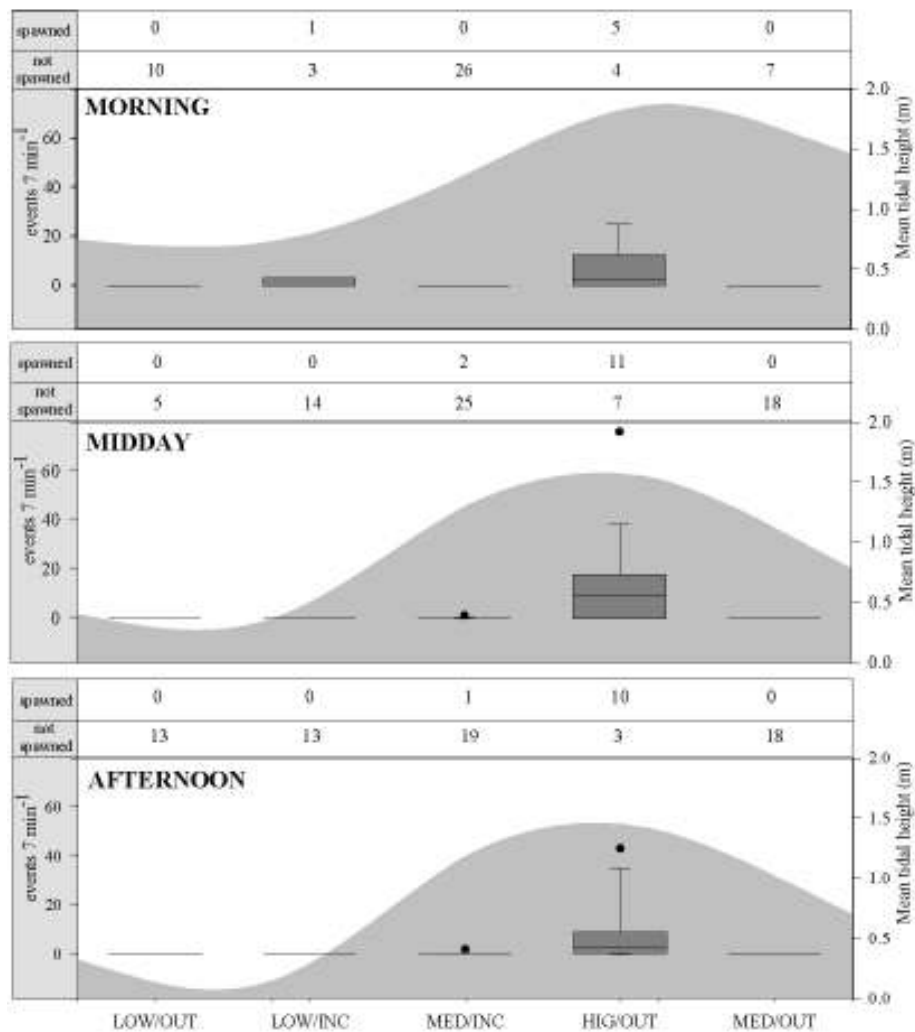


Fig. 2. Box plots indicating the frequency of reproductive events (spawning rushes and courtship displays 7 min⁻¹) at different tidal height and directions in the a) morning, b) midday, and c) afternoon. LOW/OUT: Low outgoing tide, LOW/INC: Low incoming tide, MED/INC: Medium-height incoming tide, HIG/OUT: High tide and first two hours of ebb tide, MED/OUT: medium-height outgoing tide. Low tides ranged from 0 - 0.5 m, medium-height tides ranged from 0.6 – 1.5 m and high tides ranged from 1.6 to 2 m. On top of each graph the number of fish that spawned vs. the number of fish that did not spawn during our observations are indicated.

Several labrids, surgeonfish and other parrotfish species also congregated at the reef crest to spawn during high tide. Forty minutes to an hour after the high tide, *Chl. sordidus* slowly

resumed their ordinary feeding behaviour. Courtship and/or spawning outside of high tide occurred only sporadically during midday MED/INC tide.

3.2. Effect of time of day on reproductive behaviour

The proportion of individuals involved in reproductive behaviours during HIG/OUT tide differed among times of day. A larger proportion of individuals was involved in either spawning rushes or courtship displays in the afternoon and midday high tides (77 and 64% respectively) than in the morning high tide (33%) (Fig 2, $p < 0.001$). However, the number of spawning rushes and courtship displays of individuals during HIG/OUT tide was unaffected by the time of day ($p = 0.34$).

3.3. Quantitative effects of spawning on grazing rates

Grazing rates were significantly affected by time of day and tidal conditions and these effects interacted (Fig 3). In general, rates observed at midday and afternoon were significantly higher than the morning rates ($p = 0.02$ and 0.003 respectively) but not significantly different from each other ($p = 0.70$). Moreover, mean grazing rates observed during HIG/OUT tide were significantly lower than at any other point in the tidal cycle ($p < 0.0001$ in all cases) (Fig 3). In the mornings, grazing rates remained low during most of the tidal cycle. The allocation of time to spawn during the morning HIG/OUT tide reduced feeding so that grazing rates were significantly lower compared to those observed in the morning LOW/OUT tide ($p < 0.01$), midday and afternoon MED/OUT

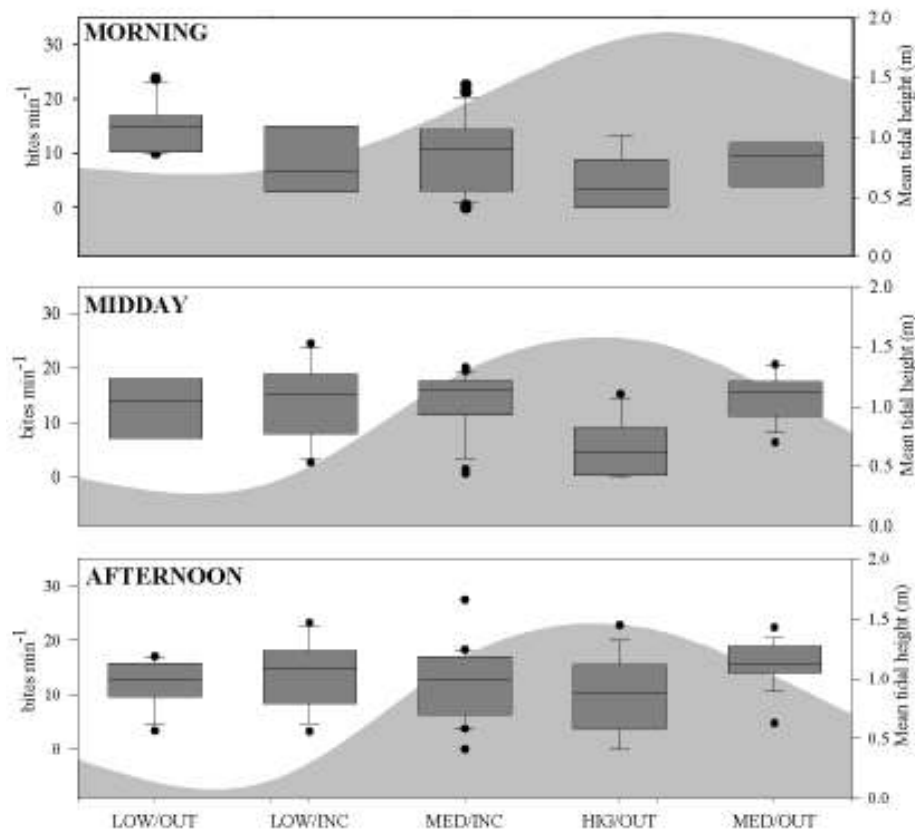


Fig. 3. Box plots indicating the grazing rate (bites min⁻¹) at different tidal height and directions in the a) morning, b) midday, and c) afternoon. LOW/OUT: Low outgoing tide, LOW/INC: Low incoming tide, MED/INC: Medium-height incoming tide, HIG/OUT: High tide and first two hours of ebb tide, MED/OUT: medium-height outgoing tide.

tides, and afternoon LOW/INC tides. Spawning also decreased the feeding activity at midday. During midday HIG/OUT tides, spawning also decreased the feeding activity to rates significantly lower than those observed during midday incoming tides (LOW/INC $p = 0.003$; MED/INC $p = 0.0001$), midday MED/OUT tide ($p = 0.0002$) and morning LOW/OUT tide ($p = 0.0003$). In the afternoon grazing rates remained high especially during the MED/OUT tide and the allocation of time to spawn had no noticeable effect on grazing intensity. Interestingly, the grazing rates at midday and afternoon HIG/OUT tides were not significantly different from the rates observed during most of the tidal cycle in the

mornings. (i.e. the effect of spawning on reducing rate at midday and in the afternoon approximately equalled the reduction in spawning than occurs in the morning compared to the afternoon).

3.4. Periodicity and frequency of intra and inter-specific interactions

Intra-specific interactions occurred when *Chl. sordidus* was both feeding and spawning. These events occurred most commonly as chases from TP to IP individuals but also from TP to other TP individuals, and as localized mouth-to-mouth encounters between pairs of TP individuals.

All intra-specific aggressive interactions appeared to be more energetic during courtship and spawning periods than those occurring during feeding periods. However, a significantly larger proportion of individuals was involved in intra-specific interactions at medium and low tides than at peak spawning times (HIG/OUT tides) (Fig 4. $p = 0.02$). Moreover, the number of observed intra-specific aggressive interactions was unaffected by the time of day or tidal condition (Fig 4). Inter-specific aggressive interactions with other parrotfishes were rarely observed in *Chl. sordidus* (7 cases) and occurred mainly in the mornings.

Terminal phase individuals of *Chl. sordidus* were regularly attacked by damselfishes and by the surgeonfishes *Ctenochaetus striatus*, *Acanthurus lineatus* and *A. nigricans*. The total number of aggressions by these groups of fish was unaffected by time of day but significantly affected by tidal condition. Aggressions from damselfish and surgeonfish to TP *Chl. sordidus* were less frequent during peak spawning times (HIG/OUT tide) and MED/OUT tide compared to MED/INC tide ($p = 0.004, 0.009$).

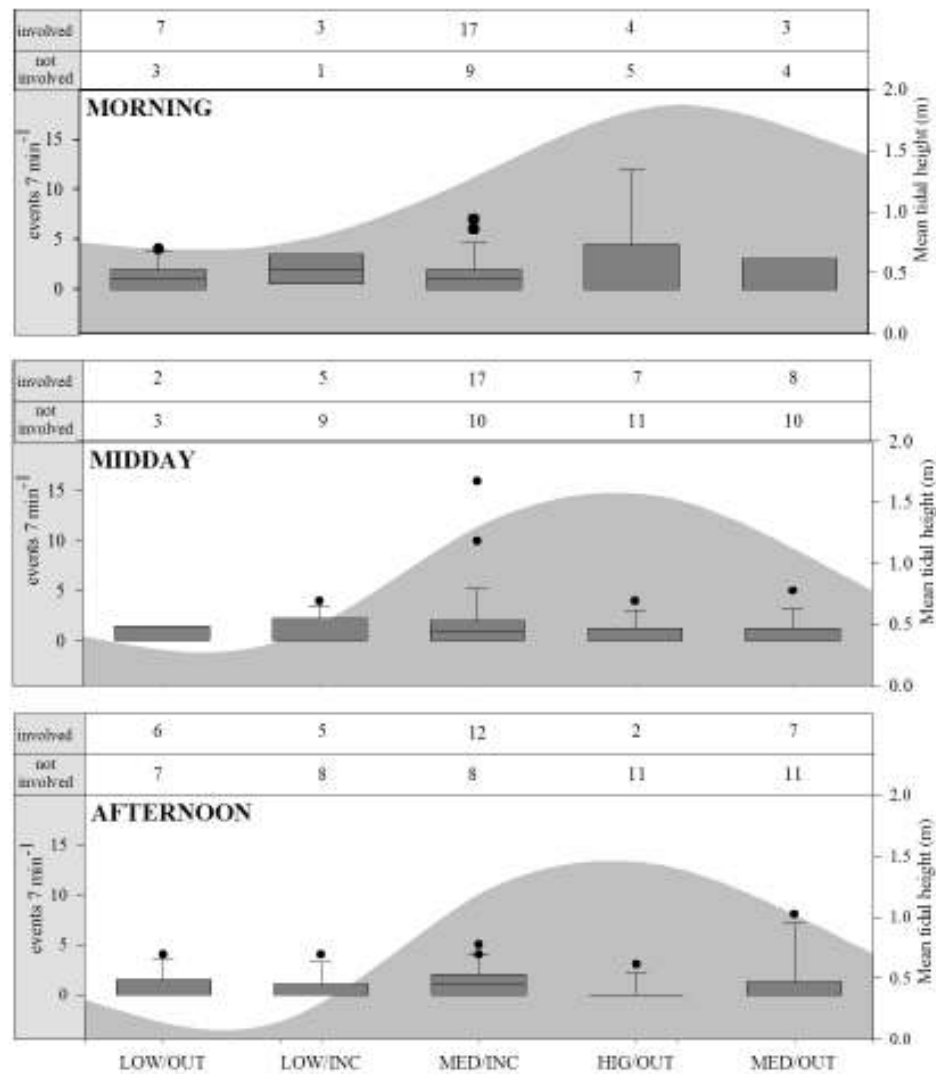


Fig. 4. Box plots indicating the frequency of intra-specific interactions (events 7 min⁻¹) at different tidal height and directions in the a) morning, b) midday, and c) afternoon. LOW/OUT: Low outgoing tide, LOW/INC: Low incoming tide, MED/INC: Medium-height incoming tide, HIG/OUT: High tide and first two hours of ebb tide, MED/OUT: medium-height outgoing tide. On top of each graph the number of fish that were involved in interactions vs. the number of fish were not involved are indicated.

4. Discussion

Chl. sordidus spawned periodically on daytime high tides and during the following hour of ebb tide. Spawning observations were made from 9:00 until 16:30 although additional spawning at high tide was also observed at 6:00–8:00 (PJM unpublished data). Behavioural

observations indicate that grazing rates of TP (and presumably of IP) individuals were significantly reduced when time was allocated to spawning in the morning and at noon. Previous studies of the diurnal dynamics of grazing in *Chl. sordidus* revealed that, as in most herbivores, bite rate is usually lowest in the mornings and highest in the afternoons (Bellwood 1995). However, the present study demonstrates that tidal condition may also have a strong influence on the diel variations of grazing of *Chl. sordidus* through the regulation of the spawning timing of this species.

4.1. *Spawning behaviour and daily synchrony with the tidal cycle*

Several coral reef fish species spawn exclusively or display peaks of spawning activity during particular times of day or tidal conditions. Some parrotfishes on Pacific reefs have been observed spawning either at particular times of day irrespective of the tidal conditions, at particular tidal conditions regardless of the time of day, or within particular times of day at particular tidal conditions (Table 1). However, only few of these records resulted from systematic observations of several individuals of the same species across a range of tidal conditions and times of day (i.e. Sancho et al. 2000; Kuwamura et al. 2009). When *Chl. sordidus* was observed across a wide range of tides within different times of day in Iriomote Island (Japan) it spawned either in the early morning or at high tide but never after 15:00. *Chl. sordidus* displayed different spawning synchrony in Palau. At Ngederrak reef, the spawning of *Chl. sordidus* was determined by the tides rather than by the time of day. Paired spawning occurred on every daytime high tide observed within a month (10 March – 10 April) and during the first 40 min to 1 h of outgoing tide. No spawning was observed during early mornings unless the tide was high or starting to ebb, and spawning also occurred during the late afternoon high tides (16:30). Differences in the spawning

Table 1. Timing of spawning activities of several species of parrotfishes

Species	Location	Spawning timing	Reference
Pacific parrotfishes			
<i>Calotomus carolinus</i>	Aldabra Atoll Iriomote Island, Okinawa	Just after high tide Only during early morning 6:30 – 8:30	Robertson et al (1982) Kuwuamura et al (2009)
<i>Calotomus spinidens</i>	Aldabra Atoll	2 – 3 h after high tide From 8:00 to 10:00	Robertson et al (1982)
<i>Leptoscarus vaigiensis</i>	Aldabra Atoll	2 – 3 h after high tide From 8:00 to 17:00	Robertson (1983)
<i>Scarus rivulatus</i>	Iriomote Island, Okinawa	Only in the early morning irrespective of the tidal phase and moon age	Kuwuamura et al (2009)
<i>Scarus dimidiatus</i>	Iriomote Island, Okinawa	As above	Kuwuamura et al (2009)
<i>Scarus spp.</i> (9 species)	Iriomote Island, Okinawa	Only during early morning 6:30 – 8:30	Kuwuamura et al (2009)
<i>Bolbometopon muricatum</i>	Yonge Reef, GBR	At 7:35 2 h after high tide, on the 20 th day of the lunar month	Gladstone (1986)
<i>Cetoscarus bicolor</i>	Enewetak Atoll, Marshall Islands	Following high tide	Colin and Bell (1991)
<i>Hipposcarus longiceps</i>	Enewetak Atoll, Marshall Islands	Following high tide	Colin and Bell (1991)
<i>Chlorurus bowersi</i>	Iriomote Island, Okinawa	At high tide but never after 16:00	Kuwuamura et al (2009)
<i>Sparisoma viride</i>	Bonaire (Netherlands Antilles)	Between 7:00 – 9:30 without seasonal or lunar variation in spawning frequency	van Rooij et al (1996)
<i>Sparisoma cretense</i>	Lampedusa Island, Italy	Breeding season: (July- Sept) Within a 50 min after dusk	de Girolamo et al (1999)
<i>Chlorurus sordidus</i>	Enewetak Atoll, Marshall Islands	Paired spawning did not appear well timed Site 1: After high tide Site 2: between 10:00 – 12:00 2 - 3 h before high tide	Colin and Bell (1991)
	Johnston Atoll, Central Pacific	14:00 - 15:00 Preferentially in ebb tides. Peak number of spawns during moderate outflowing currents	Sancho (2000)
	Ishigaki Island, Japan	During ebb tides	Moyer (1989)
	Lighthouse reef, Palau	A few hours after high tide throughout the year	Hamner et al (2007)
	Iriomote Island, Okinawa	Either in early morning or at high tide but never after 15:00	Kuwuamura et al (2009)
	Ngederrak reef Palau	From 9:00 – 16:30 but only at high tide and during the first hour of ebb tide.	This study

behaviour among individuals of the same species at different sites are not unusual or unexpected and may be related to inter-site variability of the prevailing winds and currents (Johannes 1978). *Chl. sordidus* spawned after high tide at a passage on the rim of Enewetak Atoll where tidal currents were consistently strong whereas it occurred 2-3 h before high tide in the lagoon where currents were not as clearly influenced by the tides (Colin and Bell 1991).

Although speed and direction of tidal currents were not measured directly at our study site, our observations indicate that these are similar if not identical to those observed by Hamner et al (2007) at a similar reef located just 1 km southwest of our study site across the Malakal Channel (Lighthouse reef) (Fig 1). During flood tides water flowed from the ocean towards the lagoon and during ebb tides the water moved from the lagoon onto the reef crest and off the reef. At the times when *Chl. sordidus* spawned in Ngederrak, current speed was likely to have been similar to the average measured at the Lighthouse reef at the same tidal conditions (14 cm s^{-1} Hamner et al. 2007).

Both the synchronization of spawning to coincide with ebbing tides and the occurrence of highest spawning intensities at spring tides may be strategies of reef fishes to maximise offshore tidal transport of the eggs (Johannes 1978; Robertson 1983). However, few studies have conducted surveys with the appropriate level of detail to test this (Shapiro et al. 1988), and some observations suggest that reef fish may not benefit from their eggs being rapidly flushed away from the natal reef (Ross 1983; Sancho et al. 2000).

Because current speed and direction were not measured directly during our study it is difficult to determine the fate of the eggs spawned by *Chl. sordidus* or to establish if larvae

are exported outside the natal reef. However, some hypotheses can be drawn, based on the patterns of current flow observed at the Lighthouse reef (Hamner et al, 2007).

Firstly if current patterns at Ngederrak are similar to those observed at the Lighthouse reef (Hamner et al. 2007), during the first 2 hours after high tide the current would move outside the reef at a faster speed (14 cm sec^{-1}) than during flood tide when water would move towards the lagoon at 1.1 cm sec^{-1} . Moreover, the ebbing tide current would move fastest three days after the new moon (spring tide) and slowest during the last quarter of the moon (neap tides) (Hamner et al. 2007). Our observations indicate that *Chl. sordidus* selected that moment of the day in which transport of eggs outside the reef could be maximised (1 hour after high tide). However, the fact that significantly more individuals spawned at the afternoon and midday high tides (neap tides) compared to the morning high tide (spring tide) indicated that spawning did not occur preferentially at the time of the month when ebbing current reached maximum speeds. It is possible that, at least some of the eggs spawned at high tide at Ngederrak forereef, may return to the reef and re-enter the lagoon with the flood tide. This was observed at the Lighthouse reef 10 - 12 h after they were spawned, during the night when rates of piscivory are reduced (Hamner et al. 2007).

4.2. *Quantitative effects of spawning on grazing rates*

Grazing rates were significantly reduced when individuals engaged in courtship and spawning events at high tide and during the hour following ebb tide. Since spawning occurred at high tides between 8:30 – 16:30, several TP and IP individuals ceased feeding activities almost completely for at least 40 min - 1 h regardless of the time of day. However, substantial reduction of individuals' bite rate due to reproduction occurred both in the morning and midday but not in the afternoon. Although previous studies revealed

that the feeding behaviour of *Chl. sordidus* is strongly affected by time of day with highest grazing intensities occurring in the afternoons (Bellwood 1995), our study indicates that at least at those sites where predictable tidal currents occur, the effect of time of day may interact strongly with tides. At certain states of the tide, morning grazing rates can be significantly higher than (or similar to) midday and afternoons grazing rates.

The loss of feeding time has been suggested to play a role in the timing of spawning activities of herbivores such that spawning takes place exclusively in the early mornings because these are less adequate for feeding (Robertson 1983). This was clearly not the case for *Chl. sordidus* since individuals spawned throughout the day including at times when turf algae are likely to have a higher nutritional quality (Polunin and Klumpp 1989). The fact that afternoon bite rates were the less affected by the allocation of time to spawning indicates that spawning may occur at the most suitable times for feeding but that feeding losses are minimised during afternoon periods.

The effects of tidal fluctuations on the grazing behaviour of tropical reef fish have rarely been studied. Tidal height was found to be negatively correlated with the frequency of forays in *Scarus ghobban* in Panama but positively correlated with the number of bites per foray of *Scarus ghobban* (Smith 2008). Unfortunately no explanations for such relationships were offered.

4.3. Periodicity and frequency of intra and inter-specific interactions

Intra-specific aggressive interactions are common behavioural displays of reef fish territoriality. Territories are defended by Caribbean parrotfishes mainly from conspecifics and the defended resources may include mates, spawning sites and/or food resources

(Buckman and Ogden 1973; van Rooij et al. 1996; Mumby and Wabnitz 2002). Aggressions observed in TP *Chl. sordidus* were mainly directed towards other TP or IP conspecifics and interspecific interactions with other parrotfish species were rare. Although attacks observed during *Chl. sordidus* spawning times seemed more energetic than those observed during feeding times, the number of territorial aggressions was similar when defending spawning or feeding territories. Tidal condition seemed to affect the frequency of attacks from surgeonfish and damselfish and likely resulted from the effects of tides on parrotfish foraging behaviour. For example, aggression from other families of herbivores was minimal during HIG/OUT tides when *Chl. sordidus* was feeding less often. Thus the parrotfishes likely undertook fewer intrusions into the territories of *Acanthurus lineatus*, *Ctenochaetus striatus* and *A. nigricans* and experienced fewer agonistic interactions as a result.

Although some of the factors causing spatial variability of territorial behaviours have been explored, they are still poorly understood. Territorial aggressions occur only when the benefits of defending resources exceed the costs involved in defending them (Mumby and Wabnitz 2002). Parrotfish territorial behaviour may change or disappear if population densities are high (van Rooij et al. 1996) and surgeonfish territory sizes may change in response to variations of topographic complexity (Semmens et al. 2005). Accounts of temporal fluctuations in the frequency of parrotfish territorial interactions are even rarer in the literature. Buckman and Ogden (1973) found intra-specific interactions of *Scarus iserti* varied with the time of day because of the diurnal migrations of the fish to and from feeding areas to sleeping sites. And *Sparisoma aurofrenatum* was involved in more conspecific aggressions when in found in groups than when found alone (Overholtzer and Motta 2000). Our study demonstrates that tidal fluctuations can also be responsible for

short-term temporal changes in the feeding behaviour of parrotfishes and therefore, can cause indirect changes in their interactions with other herbivores. The magnitude and significance of these changes will depend on the strength of the tidal regime and the duration of the changes caused.

This study highlights the importance of tidal fluctuations as a source of spatial and temporal variations in the grazing impact of herbivorous reef fish on Pacific reefs. Tides can affect grazing impact of herbivores not only by altering the feeding behaviour of individual fish and the time allocated to courtship and spawning behaviours as observed here, but can also cause short term fluctuations in the abundance fish (Sancho et al. 2000). At Ngederrak *Chl. sordidus* feeding sites and spawning sites overlapped, so that feeding could be resumed instantly after spawning. However, in some species, tides can act as cues for migrations between feeding and spawning grounds (Gladstone 1986, 1996; Mazeroll and Montgomery 1998; Kuwamura et al. 2009) and can have a more profound effect on feeding behaviour and the location of feeding.

Lastly, tidal patterns differ among sites and may affect species differently. Observations of the spawning behaviour of other species or in common species across larger spatial scales are necessary to determine the generality of our conclusions.

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CHAPTER 6: GENERAL DISCUSSION

6. GENERAL DISCUSSION

The research summarized in the preceding chapters takes important steps in constructing key tools to support management practises aiming to enhance coral reef resilience: i.e., maps of fish grazing. By focusing on improving the accuracy with which reef fish habitats can be mapped in the Caribbean and mapping the patterns of reef fish abundance in response to topographic complexity Chapters 2 and 3 provided useful tools to protect functionally and commercially important species and their habitats. By improving the understanding of the process of grazing on Micronesian reefs from a biophysical perspective, Chapters 4 and 5 provided tools to predict the grazing impact of populations of parrotfishes from abundance data incorporating sources of spatio-temporal variability in their feeding behaviour. This study will be taken a step forward throughout the author's Post-doctoral research by generating spatial predictions of the abundance and the grazing impact of fish for the same geographic location.

The chapters of this thesis focused on coral reef fish not only because their stocks comprise an essential resource for the subsistence of tens of millions of people (Munro 1983) but also because some fish families seem to play a crucial role in sustaining the reefs' resilience (Bellwood et al. 2004; Mumby and Steneck 2008).

Although the positive relationship between the topographic complexity and species richness, diversity, total biomass and abundance of reef fish was widely documented (Luckhurst and Luckhurst 1978; Carpenter et al. 1981; Sale and Douglas 1984; Caley and St John 1996; Rooker et al. 1997; Friedlander and Parrish 1998a,b; Ohman and Rajasuriya 1998; Nanami and Nishihira 2002; Friedlander et al. 2003; Gratwicke and Speight 2005a,b)

the response of individual species to changes in reef rugosity had rarely been described comprehensively (but see Ebersole 1985; Mumby and Wabnitz 2002). Understanding the abundance-rugosity relationships at a species level would not only allow spatial patterns across natural gradients of topographic complexity to be predicted, but also to quantify the temporal changes that are likely to occur if topographic complexity is lost.

6.1. Combining optical and acoustic data to enhance the accuracy of coral reef habitat maps

From a management perspective, mapping the distribution of those habitats that favour the occurrence or abundance of functionally or commercially important fish species may be as necessary as predicting the patterns of abundance of those species. A range of optical remote sensing products have been used to map the distribution of coral reef habitats in the Caribbean (Mumby et al. 1997; Mumby et al. 1998; Mumby and Edwards 2002; Andréfouët et al. 2003; Call et al. 2003) and Pacific reefs (Capolsini et al. 2003; Isoun et al. 2003; Bertels et al. 2008). Discriminating structurally complex habitats from flatter ones could provide a valuable insight into their inhabiting fish fauna (see Chapter 3), yet can prove challenging because many of these habitats have similar spectral reflectance signatures (Hedley and Mumby 2002). Fundamentally, acoustic instruments provide benthic data that may complement optical data (Malthus and Mumby 2003; Riegl and Purkis 2005) thus facilitating the discrimination of habitats with different topographic complexity. In fact, acoustic depth had been used to depth-correct optical layers of an IKONOS image yielding highly accurate discrimination of 8 coral reef habitats in the Arabian Gulf (Purkis and Riegl 2005). While it seems reasonable to expect that the combination of good quality optical data and the different axis of acoustic information (roughness, hardness and depth) will work complementarily to enhance the accuracy of

Caribbean habitat maps, the magnitude of such enhancement had not been yet been quantified. In this thesis the results of combining high-resolution optical data (IKONOS) and data derived from the single-beam acoustic system (RoxAnn) were examined for the first time, mapping 4 typical Caribbean forereef habitats at Glovers Atoll. By comparing 12 pairs of habitat maps constructed with different data layers in Chapter 2, not only were moderate improvements of accuracy obtained by combining optical and acoustic data, but the role of each data layer in determining the accuracy was quantified. Therefore, useful information was made available for practitioners in Chapter 2, to assist their choice of an appropriate set of acoustic and optical data layers to be used in order to match their particular objectives.

The depth-correction of IKONOS spectral bands using RoxAnn's depth data was highlighted in Chapter 2 as the approach yielding the highest possible accuracy for habitat maps of the forereef of Glovers Atoll. Therefore, this thesis demonstrated the capacity of RoxAnn-derived depth to complement optical data through depth-correction to aid the discrimination of Caribbean habitats, which had only been demonstrated for the QTCView processor in the Red Sea (Purkis and Riegl 2005).

It is not unreasonable to expect that the combination of optical and acoustic data could also facilitate habitat discrimination on Indo-Pacific coral reefs. First, the inherent optical properties of many Indo-Pacific reefs are similar to those at Glovers Atoll (Mumby and Hedley, unpublished data) and the limitations of optical data appear to be comparable between regions (Andréfouët et al. 2002). Second, the morphological diversity of corals is much greater in the Indo-Pacific (Veron 2000) which is likely to favour the discrimination of coral communities by acoustic sensors (White et al. 2003; Riegl and Purkis 2005).

The cost-effectiveness of RoxAnn in comparison with other sensors, as well as that of the combination of acoustic and optical data relative to other analytical approaches, is an important issue that could not be examined in Chapter 2. In future, further data will be collected to allow a detailed cost-effectiveness assessment that can provide further guidance to practitioners on the choice of adequate instruments.

6.2. Predicting the structural complexity of reefs and fish abundance using RoxAnn

By examining the relationship between *in situ* rugosity and the abundance of 46 Caribbean reef fish species, we constructed models to predict the spatial patterns of density and biomass of 10 common Caribbean fish species as well as the occurrence and/or abundance when present of 10 rare species. The relevance of obtaining abundance predictions for grazers (i.e. parrotfishes and surgeonfishes) for example, lies in the role that these families have in sustaining reefs' resilience. Obtaining biomass predictions for certain snappers, groupers and grunts is also relevant due to the importance of such species as fishing targets. The species-level models that have been generated in this thesis will allow practitioners to focus management decisions on species that may contribute more intensively to the process of grazing, and therefore have a more fundamental contribution to resilience of Caribbean reefs than others, or on those that may be more susceptible to overfishing than others.

Having models to predict the abundance of certain reef fish species as a function of topographic complexity is therefore useful from a management perspective. However, the application of such models in the design of effective conservation practises will largely depend on the scale at which their predictions can be generated. Widely-available techniques (e.g. the chain and tape method) serve to measure the topographic complexity of reefs at the scale of a few metres, involve a considerable underwater effort and are therefore

impractical across large extensions of reefs. Acoustic remote sensing instruments measure parameters that, albeit acquired within a large footprint of the bottom (tens of centimetres), reflect the topographic complexity of reefs. Habitat complexity at a scale relevant to fish can be predicted using certain satellite remote sensing products (Purkis et al. 2008). In some areas of the Caribbean, the rugosity generated from Experimental Advanced Airborne Research Lidar (EAARL) data were weakly correlated with fish species richness (Kuffner et al. 2007) whereas in other areas, sites of high fish species richness were predicted using GIS and a spatial layer representing fine-scale topographic complexity patterns (Pittman et al. 2007). At the Chagos Archipelago, digital elevation models (DEMs) derived from an IKONOS image were used to predict fish species richness and abundance (Purkis et al. 2008). By demonstrating a relatively strong relationship between the RoxAnn's roughness (E1) and the smaller scale *in situ* rugosity measurement, our study expanded the number of remote sensing instruments available to predict reef complexity at a scale relevant to fish. Furthermore, by finding relatively strong relationships between the acoustic roughness and the occurrence, density and/or biomass of 21 species of reef fish, our study extended the scope of large-scale measurements of topographic complexity, previously limited to the prediction of fish community attributes (i.e. total abundance and species richness), to the spatial patterns of abundance of different species and life-phases (in the case of parrotfishes).

The magnitude of the difference in topographic complexity between two sites which a) could be predicted and b) would reflect in these sites harbouring different fish communities was unknown. Importantly, our study found that small differences in acoustic roughness between sites resulted in subtle but significant differences in the abundance of a species of parrotfish strongly affected by topographic complexity (see Chapter 3). Furthermore, our

study provided a measure of the sampling effort needed to achieve meaningful spatial predictions. It is necessary to acquire a minimum of 70 RoxAnn echoes per site to detect significant differences in the biomass of species that are highly sensitive to topographic complexity, whereas a minimum of 37 echoes are enough to detect significant differences in density. Detecting subtle differences for species that do not hold a strong relationship with E1 may prove more challenging. Given that the quality of the RoxAnn's signal is affected by the movements of the boat during data acquisition and several echoes need to be eliminated during the filtration of data, a larger number of echoes (100 per site) should be collected.

In the Chapters 2 and 3 of this thesis I demonstrated that in Caribbean reefs, the discrimination of habitats with different topographic complexity and the prediction of rugosity-driven spatial patterns of density and biomass of reef fish is possible at a relatively large scale, within the same geomorphological zone (forereef).

6.3. Predicting parrotfish grazing impact in Palau, Micronesia

Within coral reef fish communities families of grazers play a key role in the resilience of Caribbean and Pacific reefs. Parrotfishes in particular are the dominant grazers of Caribbean reefs (Carpenter 1986; Bruggemann et al. 1996) and one of the main groups on Pacific reefs along with surgeonfish and rabbitfishes (Hiatt and Strasburg 1960; Kiene 1985,1988; Bellwood 1995). Parrotfish grazing has not only been associated with the reduction of macroalgal biomass (Williams and Polunin 2001; Mumby et al. 2006) but has also been linked to the reduction of coral mortality (Hughes et al. 2007) and increase in coral recruitment (Mumby et al. 2007). By mapping the spatial patterns of biomass of parrotfish populations across a particular geographic area, for example, an insight into the

area's spatial patterns of resilience can be gained. However, it is necessary to quantify to what extent is biomass of a population proportional to its grazing impact (i.e. area of reef grazed by the population per month). A major component of the grazing impact of a population is determined by the grazing behaviour of individual fish which in turn is determined by the species or functional group (Bellwood and Choat 1990; Bonaldo et al. 2006; Fox and Bellwood 2007; Alwany et al. 2009; Cardoso et al. 2009), life phase (Bonaldo et al. 2006; Lokrantz et al. 2008) and body size (Lokrantz et al. 2008; Cardoso et al. 2009) of the fish and may vary temporally and spatially under the influence of a number of environmental factors. Parrotfish communities are particularly diverse on western Pacific reefs. The complexities of their grazing behaviour are well understood for certain species on the Great Barrier Reef (Bellwood and Choat 1990; Bellwood 1995; Bellwood et al. 2003; Fox and Bellwood 2007; Bonaldo and Bellwood 2008; Fox and Bellwood 2008; Hoey and Bellwood 2008). As a result, the grazing impact of the populations of *Scarus rivulatus*, *Chlorurus microrhinos* and *Bolbometopon muricatum* on natural reef environments, across different spatial scales and including certain sources of variability of feeding behaviour has been quantified (Fox and Bellwood 2007; Hoey and Bellwood 2008). In Chapter 4 I quantified the effects of several biophysical factors on the bite rate of Micronesian parrotfishes and created models to convert fish body size into a direct metric of grazing. Therefore, not only does this thesis extend the grazing impact calculations to 3 more parrotfish species (i.e. *Chl. sordidus*, *Cetoscarus bicolor* and *Sc. psittacus*), but it also tests the generality of the results found on the GBR on some Micronesian reefs which have an even higher diversity of parrotfish species. Importantly, models generated here serve to predict the relative grazing impact of some of the most important targets of spear-fishing activities in Palau and other Micronesian countries (*Chl. microrhinos* and *Cet. bicolor*), and for some of the commonest grazers of Pacific reefs (*Chl. sordidus* and *Sc. psittacus*).

Our grazing impact estimates are a first step towards assessing the relative contribution of different species of fish to the process of grazing and the maintenance of resilience of Micronesian reefs. Such a contribution provides initial-stage policy guidance to help prioritise the conservation of key herbivorous species and identify physical conditions that favour high rates of grazing. Small species with relatively high bite rates (i.e. *Sc. psittacus* *Chl. sordidus*) are among the most abundant in several reefs in Micronesia (pers. obs.) and may play an important role in maintaining algae in a cropped state. Although these small parrotfish species are not commonly fished in Palau, they are found in the fish markets in other Micronesian countries as a result of non-selective spear-fishing activities (pers. obs.). Our results indicate that although small individuals do not graze a large area per bite, their overall contribution to grazing can be relatively important. Grazing levels could be severely depleted if extraction of *Chl. sordidus* becomes a widespread and uncontrolled practice. Moreover, TP *Chl. microrhinos* and TP *Cet. bicolor* were major contributors to the grazing impact and bioerosion in our study. On the GBR large species like these were capable of removing algae effectively and opening new colonization sites on the substratum (Bonaldo and Bellwood 2008). Extraction of these species occurs in high volumes in Palau (pers. obs.) and deserves special attention and careful monitoring in order to establish pertinent regulations. Further efforts towards defining the functional role of other parrotfish species in Palau as well as to test the applicability of our models across wider spatial scales are being undertaken.

Further efforts should be directed towards extending the predictions of grazing impact to a larger number of species of grazers on Micronesian reefs. These species should include parrotfishes, herbivorous surgeonfishes and rabbitfishes. Combining models of the grazing impact with the fish abundance data collected by the Palau International Coral Reef Center

(PICRC) as part of their annual monitoring program, could potentially aid the mapping of spatial patterns of resilience of Palauan reefs.

6.4. *The effect of tides on the behaviour of parrotfishes: Budgeting time between spawning and feeding*

Although parrotfishes feed continuously during the day, grazing must cease temporarily when time is allocated to reproduction. Parrotfishes spawn periodically following annual, semi-lunar and diel cycles (Johannes 1978; Ross 1983; Colin and Bell 1991). Diel cycles may occur in synchronization with the presence of high and ebb tides presumably to utilise the direction and speed of tidal currents (Robertson and Hoffman 1977; Robertson et al. 1982; Robertson 1983; Colin and Bell 1991; Hunt von Herbing and Hunte 1991; Sancho 2000; Hamner et al. 2007; Kuwamura et al. 2009). Few studies designed to observe parrotfish behaviour systematically and predict the timing of spawning on Pacific reefs have been undertaken (Sancho et al. 2000a; Kuwamura et al. 2009). Furthermore, no previous study of the temporal variability of grazing has accounted for the effect that tides may have on parrotfish behaviour. Chapter 5 summarises the results of systematic behavioural observations conducted on the commonest parrotfish species in Palau (*Chl. sordidus*) in a sheltered barrier reef in Palau (Ngederrak) encompassing a one-month tidal cycle within each time of day (morning, midday and afternoon). *Chl. sordidus* spawned at high tide and during the first hour of ebbing tide, from 8:00 until 16:30.

When our data on the spawning timing and frequency are interpreted in the context of the current speed and direction of an adjacent and comparable reef (see Hamner et al. 2007), a preliminary insight into the fate of the spawned parrotfish eggs and larvae could be gained

(see Chapter 5). It is possible that, at least some of the eggs spawned at high tide at Ngederrak forereef, may return to the reef and re-enter the lagoon with the flood tide.

Tidal condition had a strong effect on the diel variation of parrotfish bite rate through the regulation of their spawning periodicity, and such effects interacted with the time of day. Spawning decreased the feeding activity in the morning and at midday, but remained unaffected in the afternoon. By describing the effect of spawning on parrotfish grazing behaviour, Chapter 5 demonstrated that at least in some species of parrotfishes, the diurnal foraging periodicity may be more complex than previously thought. Although previous studies revealed that grazing intensities of *Chl. sordidus* peaked in the afternoons (Bellwood 1995), our results indicate that at certain tidal conditions, morning grazing rates can be significantly higher than (or similar to) midday and afternoons grazing rates.

Communities of herbivorous reef fish are species rich on Pacific reefs and the behavioural interactions amongst them are highly complex and rarely studied in detail (but see Choat and Bellwood 1985). The occurrence of aggressive interactions from territorial surgeonfishes towards intruding parrotfishes has been found to depend on the size of the intruder and to vary spatially (Choat and Bellwood 1985). Further, our study demonstrated that tidal fluctuations may be indirectly responsible for short-term temporal changes in the interactions between parrotfishes and other groups of herbivores. Parrotfishes elicited significantly fewer aggressive reactions from surgeonfish and damselfishes when they were spawning, most likely because they undertook fewer intrusions into their territories. The magnitude and significance of these temporal changes is likely to vary among reefs, depending on the strength of the tidal regime and the duration of the changes caused.

Chapter 5 highlighted the importance of tidal fluctuations as regulators of the timing of *Chl. sordidus* spawning and as sources of spatial and temporal variation in its grazing rates and social interactions. Therefore, more accurate predictions of the temporal dynamics of parrotfish grazing impact are possible.

Tides can affect the grazing impact of herbivores not only by altering the feeding behaviour of individual fish and the time allocated to courtship and spawning behaviours as observed here, but can also cause short term fluctuations in the abundance fish (Sancho et al. 2000b). At Ngederrak *Chl. sordidus* feeding sites and spawning sites overlapped, so that feeding could be resumed instantly after spawning. However, in some species, tides can act as cues for migrations between feeding and spawning grounds (Gladstone 1986,1996; Mazeroll and Montgomery 1998; Kuwamura et al. 2009) and can have a more profound effect on feeding behaviour and the location of feeding. Lastly, tidal patterns differ among sites and may affect species differently. Observations of the spawning behaviour of other species or in common species across larger spatial scales are necessary to determine the generality of our conclusions.

This thesis combines studies of remote sensing and fish behaviour as part of a strategic plan to enhance the use of remote sensing for mapping ecological processes and ultimately, reef resilience. Future studies will combine the maps of predicted parrotfish density in Belize with existing models of fish grazing behaviour (Mumby 2006) though the effects of physical factors such as tides on grazing rates have yet to be investigated in the Caribbean.

In Palau, further efforts are required to understand the rugosity-abundance relationships of several species of grazing fish and to map their density. However, the research undertaken

here took steps towards the prediction of the grazing impact of different populations of Pacific parrotfishes. Specifically, fish census data from sites in Palau (and likely elsewhere in the region) can be converted to grazing impact using the allometric scaling relationships described in Chapter 4 and used to identify sites of relatively high grazing or changes in grazing over time, perhaps as a result of fishing or conservation.

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