2009

The Development of Communities on Large-scale Breakwater Reefs with a Comparison to Natural Reefs

John Burt
University of Windsor

Recommended Citation
Burt, John, "The Development of Communities on Large-scale Breakwater Reefs with a Comparison to Natural Reefs" (2009). *Electronic Theses and Dissertations*. 381.
https://scholar.uwindsor.ca/etd/381

THE DEVELOPMENT OF COMMUNITIES ON LARGE-SCALE BREAKWATER REEFS WITH A COMPARISON TO NATURAL REEFS

by

John A. Burt

A Dissertation
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfilment of the Requirements for
the Degree of Doctor of Philosophy at the
University of Windsor

Windsor, Ontario, Canada

2009

The Development of Communities on Large-scale Breakwater Reefs with a Comparison to Natural Reefs

by

John A. Burt

APPROVED BY:

Dr. Bernhard Riegl, External Examiner
Nova Southeastern University

Dr. Brian Fryer
Department of Geology

Dr. Kenneth Drouillard
Department of Biological Sciences

Dr. Douglas Haffner
Department of Biological Sciences

Dr. Peter Sale, Advisor
Department of Biological Sciences

Dr. William McConkey, Chair of Defense
Department of Physics

30 April 2009

DECLARATION OF CO-AUTHORSHIP / PREVIOUS PUBLICATION

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is result of joint research, as follows: This dissertation also incorporates the outcome of joint research conducted with Dr. Aaron Bartholomew (American University of Sharjah) and Mr. Paolo Usseglio (United Nations University). The collaboration is covered in Chapter 2 of the thesis. In all cases, the key ideas, primary contributions, sampling design, data analysis, and interpretation were performed by the author, and the contribution of the co-authors was primarily the provision of field assistance and manuscript reviewing and editing.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above material in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

II. Declaration of Previous Publication

This thesis includes one original paper that has been previously published in a peer reviewed journal, as follows:

Thesis Chapter	Publication citation	Status
Chapter 2	Burt J, Bartholomew A, Usseglio P (2008) Recovery of corals a decade after bleaching in Dubai, United Arab Emirates. Marine Biology 154: 27-36	Published

I certify that I have obtained a written permission from the copyright owner to include the above published material(s) in my thesis. I certify that the above material describes work completed during my registration as graduate student at the University of Windsor.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone’s copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owner(s) to include such material(s) in my thesis.

I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

ABSTRACT

Coastal defense structures currently make up more than half of the coastline in many regions, yet their ecological role is poorly understood. These structures represent novel habitat open to colonization and provide opportunity to investigate the various stochastic and deterministic processes driving community development on hard substrata in the marine environment. To investigate these processes, a series of breakwaters were studied in Dubai, UAE, where the addition of >65 km of breakwater has substantially increased the amount of hard-bottom habitat in the area. These were compared with those of natural reefs to determine whether processes structuring community development were comparable between reef types. Breakwater benthic communities appeared to follow a predictable sequence of successional development, becoming more similar to natural reefs with time. However, even the oldest breakwater community (31 yr) remained distinct from that of natural reefs. Breakwaters older than 25 yr had higher coral cover than natural reefs, but had lower coral diversity. Fish abundance, composition, and community structure was seasonally dynamic on >25 yr old breakwaters, resulting in divergence from natural reefs in the summer and fall, mainly as a result of adult migration and/or predation on breakwaters. Early benthic communities were comparable among tiles made of different breakwater materials. However, in areas of high coral recruitment, corals recruited preferentially to gabbro stone compared with concrete and sandstone. Wave exposure was an important determinant of coral community structure on breakwaters, with high post-settlement mortality resulting in a low cover coral community composed of few small colonies at sheltered sites. However, overall coral recruitment, mortality, and growth rates were comparable among leeward and windward sites and natural reefs. A manipulative caging experiment indicated few biologically significant effects from fish or urchin grazing on benthic community development. Overall, this study indicates that breakwaters can develop diverse and abundant communities, but that they are not direct surrogates for communities on natural reefs. The results also suggest that the breakwater communities examined in this study are mainly structured by stochastic processes, although deterministic processes can play a role to a lesser extent.

ACKNOWLEDGEMENTS

Thanks go to A. Bartholomew, A. Bauman, M. Bernardo, G. Cavalcante, D. Feary, E. Marquis, and P. Usseglio for assistance in the field, and K. Jenahi and M.A. Shakankiri for assistance in the laboratory. Logistics support was provided by Nakheel PJSC and Emirates Marine Environmental Group, and early sampling permits were provided by Dubai Municipality. Financial support from this research was provided by Zayed University, Nakheel PJSC, United Nations University, and an NSERC grant to P. Sale. V. Burt is thanked for her patience and support.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 6: Coral community dynamics on a breakwater and natural reef 121

Chapter 7: The influence of fish and sea-urchin grazing on early benthic community development 145

LIST OF FIGURES

Chapter 1 - Introduction 1

Chapter 2: Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates 19

Chapter 3: Long-term changes in benthic assemblages on large breakwater reefs and a comparison to natural reefs 46

Chapter 4: A comparison of natural reefs with large, mature artificial reefs 67

Chapter 5: Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs 99

LIST OF APPENDICES

Chapter 1 - Introduction

Urban development along the world's coastlines is increasing as populations grow and infrastructure is developed for human use (Svane and Peterson 2001; UNEP 2002). Large-scale structures such as breakwaters, sea-walls, and groynes, among others, can dominate the near-shore environment in many areas, making up more than half of the coastline in many regions (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005). These structures are increasingly thought of as artificial reefs in reference to the ecological role that they play in urban marine ecosystems (Svane and Peterson 2001; Airoldi et al. 2005; Bulleri 2005b). They are rapidly colonized and often develop communities with comparable or higher abundance and diversity than in surrounding natural habitats (Bohnsack et al. 1994; Lincoln-Smith et al. 1994; Stephens et al. 1994; Pickering and Whitmarsh 1997; Rilov and Benayahu 2000; Pondella et al. 2002; Perkol-Finkel and Benayahu 2004). Despite their ecological importance in coastal ecosystems, the processes structuring community development on coastal defense structures are poorly understood (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Moschella et al. 2005). Given that these structures represent 'natural experiments', they provide ample opportunity to investigate the relative importance of stochastic and deterministic processes structuring marine colonization and succession.

This dissertation explores these processes. The process of community colonization and development is the result of both stochastic processes resulting from variable larval dispersal and settlement success (Fager 1971; Talbot et al. 1978; Gaines and

Roughgarden 1985; Prince 1995; Bortone et al. 1997; Sandin and Pacala 2005; D'Alessandro et al. 2007; Briones-Fourzan et al. 2008), as well as deterministic processes relating to habitat availability and preference (Schmitt and Holbrook 1999; Schmitt and Holbrook 2000; Garpe and Ohman 2007), competition with resident organisms (Buss and Jackson 1979; Ebersole 1985; Robertson 1996), and predation (Steele and Forrester 2002; Almany 2004; Osman and Whitlatch 2004; Nydam and Stachowicz 2007). In this thesis I will examine how communities develop on these breakwaters and explore the processes that underlie community development through time. Breakwaters are an ideal means to approach such questions, as new breakwaters provide an opportunity to investigate the processes involved in initial colonization and development, while breakwaters constructed at staggered times in the same area allow an understanding of possible long-term trends in community development.

Colonization of new substrates in marine environments occurs rapidly (Lecchini 2003; Chapman and Clynick 2006; Jang et al. 2006). This is due to the two-phase life cycle of most marine organisms, where adults are generally sedentary, but their propogules can travel considerable distances (Shanks et al. 2003; Kinlan et al. 2005; Paulay and Meyer 2006; Graham et al. 2008). Algal spores and animal larvae disperse from native reefs through hydrodynamic processes, as well as behavior in the case of animals (Leis 2002; Grantham et al. 2003; Reed et al. 2004; Hogan and Mora 2005; Thiel and Gutow 2005; North et al. 2008). However, mortality and offshore advection of propogules is thought to be quite high, sometimes resulting in the occurrence of recruitment limitation where there is a shortage of individuals capable of recruiting into open space (Menge 1991; Doherty and Fowler 1994; Reed et al. 2004). Additionally, those organisms that do encounter substrates often exhibit habitat preference and will settle only if the habitat is suitable. Substrate characteristics are important for colonization of algal species (Diaz-Pulido and McCook 2004; Lee et al. 2004), and both vertebrate and invertebrate animals are known to preferentially select habitats based on characteristics such as depth, complexity, and substrate type (Rilov and Beniyahu 2002; Bulleri 2005a; Petersen et al. 2005; Adjeroud et al. 2007; Creed and DePaula 2007; Field et al. 2007). This chance supply of propogules and their differential settlement to substrates, in part, determines the final community composition.

As the colonization process continues, the influence of the deterministic process of biotic interaction will become more important in development of these communities. Residents can affect colonizers through facilitation or inhibition, and these processes transcend taxonomic boundaries (Connell and Slatyer 1977). For example, turf algae can directly facilitate the settlement of sea-grass and kelp species by providing a habitat which entrains the propogules of later arrivals (Turner 1983; Bulleri and Benedetti-Cecchi 2008), while urchins can provide protective biogenic habitat that directly facilitates the settlement of fish and invertebrates (Day and Branch 2002; Hartney and Grorud 2002). The grazing action of consumers such as fish, sea urchins, and gastropods can also indirectly facilitate settlement by clearing substrates of early successional species that inhibit later colonists (Anderson and Underwood 1997; Cebrian and Uriz 2006; Zabin and Altieri 2007). Inhibition is also commonly observed in marine systems. For example, algae can trap sediments that inhibit colonization by corals and other benthos (Hata et al. 2002; Birrell et al. 2005), territorial fish are known to directly inhibit settlement of competitors (Bay et al. 2001; Almany 2003; 2004), and direct and indirect effects of predation are known to affect settlement patterns of a variety of marine organisms (Steele 1997; Osman and Whitlatch 2004; Nydam and Stachowicz 2007). The order of settlement is also important. Settlement of one space-limited species can prevent recruitment of its competitors (Sale 1978; Benedetti-Cecchi 2000; Dürr and Wahl 2004; Munday 2004) and initial settlement of consumers can inhibit recruitment of prey species (Sutherland 1974; Shulman et al. 1983; Almany 2003). These priority effects can significantly affect the composition of the communities that develop even with species recruited from the same pool (Drake 1990), and set communities off on divergent successional trajectories. Thus, species interactions also play a role in structuring communities in addition to recruitment supply and habitat selection.

Thus, marine communities are structured by a combination of stochastic and deterministic processes. The relative role that these processes play is unknown, and likely varies in time and space and in the context of community composition (Menge 1991; Syms and Jones 2000; Lecchini and Galzin 2003). This is evident in the contrasting observations in marine systems worldwide, where there are examples of communities structured mainly by recruitment (Fager 1971; Talbot et al. 1978; Gaines and Roughgarden 1985; Prince 1995; Martin and Bortone 1997; McClanahan 1999), mainly by deterministic processes (Buss and Jackson 1979; Ebersole 1985; Fletcher and Underwood 1987; Robertson 1996; Steele 1998; Bertness et al. 2004; Dürr and Wahl 2004; Osman and Whitlatch 2004; Almany and Webster 2006; Kuffner et al. 2006; Nydam and Stachowicz 2007), or some mix of the two (Sutherland 1974; Menge and Sutherland 1987; Connolly and Roughgarden 1999; Munday et al. 2001; Webster 2003; Moore et al. 2004; Sams and Keough 2007).

Artificial habitats could play a critical role in investigating the relative influence of these processes, and how they affect successional dynamics. While such research is beginning on traditional small-scale modular artificial reefs, it is important that these investigations are expanded to include such structures as quays, jetties, breakwaters, sea-walls and piers (Baine 2001). Such structures are ubiquitous in coastal urban areas and represent substantially more habitat upon which marine communities can develop. Given that many of these structures are engineered using standard construction techniques, their composition, orientation, relief, complexity, and other characteristics will be highly consistent both within and among sites, making them ideal candidates for comparative studies.

While coastal defense structures do represent natural experiments that provide opportunity to understand community development processes, it is important that they are also compared with natural reefs. Artificial habitats are frequently promoted as surrogates for natural reefs on the assumption that they will enhance production of exploited species or offset natural or anthropogenic damage to natural reefs (Baine 2001; Svane and Peterson 2001; Miller 2002; Seaman 2002; Bulleri 2005c). While there is debate regarding these underlying assumptions, particular with reference to the attraction-production controversy (see Bohnsack 1989 for review), comparisons between these systems are ecologically relevant. Empirical comparisons of natural and artificial reefs are few (Carr and Hixon 1997; Bulleri 2005b), and are generally confounded by comparing natural reefs to artificial structures that are small and/or young (Bohnsack et al. 1994; Carr and Hixon 1997; Connell 1997; Tupper and Hunte 1998; Abelson and Shlesinger 2002; Chapman and Clynick 2006). Given that the size and age of a reef can influence community structure and function (Bohnsack et al. 1994; Connell 1997; Tupper and Hunte 1998), the results from analysis of small-scale, young artificial structures are not likely to apply to much larger coastal defense structures. As such, it is important that investigations of community development on large-scale artificial structures also includes comparison to natural reef systems to determine whether similar processes operate across these different habitats.

The objective of this dissertation was to investigate the processes structuring community development on large-scale breakwater reefs using a series of observational and manipulative studies, and to compare these communities with those on natural reefs. These studies were conducted from 2006 through 2008 in the Persian/Arabian Gulf, an area that has been relatively understudied ecologically. Marine communities in this area are represented by a relatively simple subset of species from the Indian Ocean (Sheppard

1987; Sheppard et al. 1992; Coles 2003; Rezai et al. 2004), rendering them ideal for the exploration of the factors structuring community development. These studies will be important in developing our understanding of the marine system in this area, particularly given the extensive past, present, and future coastal development projects occurring throughout the Gulf (Price 1993; Rezai et al. 2004; Al-Jamali et al. 2005; Hansen 2005; Khan 2007).

The Arabian Gulf is characterized by environmental extremes, mainly due to its shallow depths (averaging 35 m) and relatively enclosed nature (Sheppard et al. 1992; Carpenter et al. 1997). Water temperatures in this area regularly range over 20 °C, with recorded summer highs exceeding 37 °C and winter lows below 12 °C (Coles and Fadlallah 1991; Sheppard and Loughland 2002). Salinity values are also severe, with salinities exceeding 45 ppt being recorded on various reefs in the southern basin of the Gulf (Coles 2003). As a result, coral species diversity in the Arabian Gulf is only about a tenth of the species diversity in the Indo-Pacific and less than half of that of the Red Sea, and is compositionally different with higher representation of taxa considered tolerant of environmental extremes (Sheppard and Sheppard 1991; Coles 2003). Fish diversity is also low compared with other biogeographic subsets of the Indian Ocean such as the Gulf of Oman and the Red Sea as a result of these environmental conditions (Randall 1995; Krupp and AlMarri 1996). Because the majority of coral reef ecosystems lie in the shallow southern basin of the Gulf where waters are generally less than 20 m depth and experience the most extreme environmental conditions (Sheppard et al. 1992; Coles

2003), coral reefs in this area experience recurrent mass mortality as a result of high and low water temperatures (Coles and Fadlallah 1991; Riegl 1999; Riegl 2001; Riegl 2002b; Riegl and Purkis 2009). As a result, most reefs in this area are not true reefs but a relatively discontinuous low-relief coral veneer overlaying exposed limestone caprock (Sheppard and Sheppard 1991; Riegl 1999; Purkis and Riegl 2005).

The studies described in this dissertation were conducted in Dubai, United Arab Emirates, in the southern basin of the Arabian Gulf. Water depths in this area are shallow, with water depths of less than 15 m extending out more than 10 km from shore. The natural substrate in this area is almost entirely dominated by fine to coarse sands, and natural reefs are restricted to a discontinuous series of small (< 1000 m^2) patch reefs associated with exposed caprock along a 10 km near-shore band in the vicinity of the Jebel Ali district to the southwest of the city. The near-shore environment in this area has been heavily developed for real-estate, shipping, and industrial purposes, adding more than 65 km of rocky breakwaters to the natural sand coastline (Hansen 2005). The construction of these breakwaters began in the late 1970s and continues today, providing opportunity for the comparison of community development on structures across a range of ages.

The first data chapter of this dissertation (Ch. 2) describes the coral community associated with the natural reefs in the Jebel Ali area of Dubai. These natural reefs were substantially impacted by mass coral mortality events in both 1996 and 1998, and a lesser event in 2002, as a result of elevated sea surface temperatures (Riegl 1999; Riegl 2002a; Rezai et al. 2004). These events modified community composition by reducing species richness and shifting dominance towards faviids and poritids, eventually resulting in the loss of over 90% of the framework building corals from the area (Riegl 1999; Riegl 2002a). These reefs were further modified by the construction of a large near-shore residential development in the area commencing in 2002 (Rezai et al. 2004). However, there were signs of active coral recruitment by *Acropora* in the area in 1999 (Riegl 2002a; Riegl 2002b), suggesting that coral cover and species dominance for the community described in the late 1990s was in a state of change. The purpose of Chapter 2 was to document the contemporary community structure on the natural reefs in this area to gain an understanding of how these communities compare to those that were reported prior to the natural and anthropogenic impacts of the past decade. This information is essential for providing a natural reef baseline against which breakwater reef communities can be compared.

There is little understanding of how benthic communities on artificial structures develop through time, or if and when these communities begin to resemble those on natural reefs. Those studies that have been performed have tended to focus on structures only in the early stages of colonization (Osman and Whitlatch 2004; Bulleri 2005a; Bulleri 2005c), or on those that have developed mature communities (Moschella et al. 2005). Few have compared these with communities on natural reefs (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005). To gain an understanding of changes in community structure over time, Chapter 3 describes a comparative study in which benthic communities associated with breakwaters ranging from 1 to 31 years of age were compared with each other, and to a natural reef community. Although not a true longitudinal study of community development, the use of breakwaters of differing age provides a ‘natural experiment’ in which temporal patterns of development can be inferred from contemporary communities. Information from this study is important for understanding the types of communities and the sequence of development to expect as breakwater reefs mature. This may have implications for coastal management.

Given the widespread construction of breakwaters around the globe, it is important that we understand the ecological role that these structures play in marine ecosystems as they mature. Coral and fish abundance are often higher on breakwaters than in surrounding natural habitats (Lincoln-Smith et al. 1994; Stephens et al. 1994; Pondella et al. 2002; Wen et al. 2007), and these structures have the potential to increase regional biomass and production in areas where hard-bottom habitat is limiting (Bohnsack et al. 1997; Carr and Hixon 1997). However, comparisons to natural reefs are few, and most have been confounded by focusing on small, immature artificial structures (Bohnsack et al. 1994; Carr and Hixon 1997; Connell 1997; Tupper and Hunte 1998). The purpose of Chapter 4 was to compare coral and fish communities on several large, mature breakwater reefs with those on natural reefs to determine whether coastal defenses act as surrogates for natural reefs. In addition, fish abundance, recruitment, and age-class structure on breakwaters and natural reefs were compared to determine whether there is comparable community functions between reef types, and whether breakwaters may be enhancing fish production.

Differences in benthic community development among breakwaters and natural reefs may be the result of propogule supply, larval substratum preferences, or post-settlement processes. To assess the relative importance of substrate material in influencing early community development, in Chapter 5, coral abundance and overall benthic community structure were compared on tiles constructed from materials commonly used in the construction of breakwaters and artificial reefs (concrete, gabbro, and granite) as well as those from the natural reef (sandstone caprock), with terra-cotta included for comparison to other locations. An understanding of how substrate materials influences community development would inform the design of future breakwaters and artificial reefs to maximize coral cover and/or avoid development of communities dominated by nuisance species.

The influence of design features on breakwater community development is poorly understood. In addition to material, the amount of wave exposure is likely to be one of the most important features affecting community development on breakwaters. Most coastal defense structures are constructed with a windward face designed to absorb the predominant wind-driven swell, with a leeward face in the shadow. Hydrodynamic changes along the length of a structure may result in differences in sedimentation rates (Purcell 2000; Walker 2007) as well as differences in larval supply (Roughgarden et al.

1988; Wilding and Sayer 2002; Arthur et al. 2006), presumably resulting in spatially distinct community development processes. In Chapter 6 coral community composition, cover, size structure, recruitment, mortality, and growth rates were examined on a breakwater with differing levels of exposure to wave action, and these were compared with that of a natural reef. An understanding of how wave exposure influences coral community dynamics on breakwaters, and how these dynamics compare to those on natural reefs, can guide the appropriate design of coastal defense structures.

Chapter 7 examines the role of grazing in structuring early benthic community development. Fish and sea urchins are widely recognized to alter the succession of algal communities through their grazing, but less is known about how they influence the development of the wider epifaunal assemblage. Even nominally herbivorous fish and urchins are known to consume fauna while grazing, occasionally having diets dominated by animal tissue (Choat et al. 2002; Cobb and Lawrence 2005; Crossman et al. 2005; Endo et al. 2007). Such grazing has the potential to strongly alter the benthic assemblage, perhaps influencing the successional trajectory of community development. A manipulative study was performed to assess the relative influence of grazing by fish and sea urchins on initial community development using a series of exclusion cages. An understanding of how these grazers influence community development on novel substrates will be of importance to marine management, particularly in areas where fishing pressure may be altering the abundance of these grazers.

Chapter 8 concludes this dissertation with a discussion of the results of these comparative and manipulative studies. These results will be discussed in the context of how these communities compare structurally and functionally to those on natural reefs, and the role that breakwaters are likely to play in coastal urban areas here and elsewhere with increasing development of the world's coastlines.

References

Abelson A, Shlesinger Y (2002) Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. Journal of Marine Science 59: 122-126

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. Journal of Experimental Marine Biology and Ecology 341: 204-218

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Al-Jamali F, Bishop JM, Osment J, Jones DA, LeVay L (2005) A review of the impacts of aquaculture and artificial waterways upon coastal ecosystems in the Gulf (Arabian/Persian) including a case study demonstrating how future management may resolve these impacts. Aquatic Ecosystem Health & Management 8: 81-94

Almany G (2003) Priority effects in coral reef fish communities. Ecology 84: 1920-1935

Almany G (2004) Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology 85: 2872-2880

Almany G, Webster M (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25: 19-22

Anderson M, Underwood A (1997) Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. Oecologia 109: 442-453

Arthur R, Done TJ, Marsh H, Harriott V (2006) Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. Coral Reefs 25: 427-440

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Baine M (2001) Artificial reefs: A review of their design, application, management and performance. Ocean & Coastal Management 44: 241-259

Bay LK, Jones GP, McCormick MI (2001) Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. Coral Reefs 20: 289-298

Benedetti-Cecchi L (2000) Priority effects, taxonomic resolution, and the prediction of variable patterns of colonisation of algae in littoral rock pools. Oecologia 123: 265-274

Bertness M, Trussel G, Ewanchuk P, Sillman B, Crain C (2004) Consumer-controlled community states on Gulf of Maine rocky shores. Ecology 85: 1321-1331

Birrell C, McCook L, Willis B (2005) Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin 51: 408-414

Bohnsack J (1989) Are high densities of fishes at artificial reefs the result of habitat limitation of behavioral preference? Bulletin of Marine Science 44: 631-645

Bohnsack J, Harper D, McClellan D, Hulsbeck M (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bulletin of Marine Science 55: 796-823

Bohnsack JA, Ecklund AM, Szmant AM (1997) Artificial reef research: is there more than the attraction-production issue? Fisheries 22: 14-16

Bortone S, Turpin R, Cody R, Bundrick C, R.Hill (1997) Factors associated with artificial-reef fish assemblages. Gulf of Mexico Science: 17-34

Briones-Fourzan P, Candela J, Lozano-Alvarez E (2008) Postlarval settlement of the spiny lobster Panulirus argus along the Caribbean coast of Mexico: Patterns, influence of physical factors, and possible sources of origin. Limnology and Oceanography 53: 970-985

Bulleri F (2005a) Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. Marine Environmental Research 60: 355-374

Bulleri F (2005b) The introduction of artificial structures on marine soft- and hard-bottoms: Ecological implications of epibiota. Environmental Conservation 32: 101-102

Bulleri F (2005c) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Marine Ecology-Progress Series 287: 53-65

Bulleri F, Benedetti-Cecchi L (2008) Facilitation of the introduced green alga Caulerpa racemosa by resident algal turfs: experimental evaluation of underlying mechanisms. Marine Ecology-Progress Series 364: 77-86

Buss W, Jackson J (1979) Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. American Naturalist 113: 223-234

Carpenter KE, Krupp F, Jones D, Zajonz U (1997) FAO Species Guide for Fishery Purposes: The Living Marine Resources of Kuwait, Eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates. Food and Agriculture Organization of the United Nations, Rome

Carr M, Hixon M (1997) Artificial reefs: The importance of comparisons with natural reefs. Fisheries 22: 28-33

Cebrian E, Uriz MJ (2006) Grazing on fleshy seaweeds by sea urchins facilitates sponge *Cliona viridis* growth. Marine Ecology-Progress Series 323: 83-89

Chapman MG, Clynick BG (2006) Experiments testing the use of waste material in estuaries as habitat for subtidal organisms. Journal of Experimental Marine Biology and Ecology 338: 164-178

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs - I: Dietary analyses. Marine Biology 140: 613-623

Cobb J, Lawrence J (2005) Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. Marine Ecology-Progress Series 295: 171-182

Coles S (2003) Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific region. Atoll Research Bulletin 507: 1-19

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low-temperatures in the Arabian Gulf - new species-specific lower temperature limits. Coral Reefs 9: 231-237

Connell J, Slatyer R (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. The American Naturalist 111: 1199-1144

Connell SD (1997) The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. Journal of Experimental Marine Biology and Ecology 209: 261-278

Connolly S, Roughgarden J (1999) Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. Ecological Monographs 69: 277-296

Creed J, DePaula A (2007) Substratum preference during recruitment of two invasive alien corals onto shallow-subtidal tropical rocky shores. Marine Ecology-Progress Series 330: 101-111

Crossman D, Choat J, Clements K (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. Marine Ecology-Progress Series 296: 129-142

D'Alessandro E, Sponaugle S, Lee T (2007) Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. Marine Ecology-Progress Series 331: 85-100

Day E, Branch G (2002) Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). Ecological Monographs 72: 133-149

Diaz-Pulido G, McCook L (2004) Effects of live coral, epilithic algal communities and substrate type on algal recruitment. Coral Reefs 23: 225-233

Doherty P, Fowler T (1994) An empirical test of recruitment limitation in a coral reef fish. Science 263: 935-939

Drake J (1990) The mechanics of community assembly and succession. Journal of Theoretical Biology 147: 213-233

Dürr S, Wahl M (2004) Isolated and combined impacts of blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) on structure and diversity of a fouling community. Journal of Experimental Marine Biology and Ecology 306: 181-195

Ebersole J (1985) Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66: 14-20

Endo H, Nakabayashi N, Agatsuma Y, Taniguchi K (2007) Food of the sea urchins Strongylocentrotus nudus and Hemicentrotus pulcherrimus associated with vertical distributions in fucoid beds and crustose coralline flats in northern Honshu, Japan. Marine Ecology-Progress Series 352: 125-135

Fager E (1971) Pattern in the development of a marine community. Limnology and Oceanography 16: 241-253

Field S, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs 26: 279-289

Fletcher W, Underwood A (1987) Interspecific competition among subtidal limpets: Effect of substratum heterogeneity. Ecology 68: 387-400

Gaines S, Roughgarden J (1985) Larval settlement rate: A leading determinant of structure in an ecological community of the intertidal zone. Proceedings of the National Academy of Sciences 82: 3707-3711

Garpe KC, Ohman MC (2007) Non-random habitat use by coral reef fish recruits in Mafia Island Marine Park, Tanzania. African Journal of Marine Science 29: 187-199

Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27: 529-539

Grantham B, Eckert G, Shanks A (2003) Dispersal potential of marine invertebrates in diverse habitats. Ecological Applications 13: S108-S116

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75: 12-13

Hartney K, Grorud K (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia 131: 506-513

Hata H, Nishihira M, Kamura S (2002) Effects of habitat-conditioning by the damselfish *Stegates nigricans* (Lacepede) on the community structure of benthic algae. Journal of Experimental Marine Biology and Ecology 280: 95-116

Hogan JD, Mora C (2005) Experimental analysis of the contribution of swimming and drifting to the displacement of reef fish larvae. Marine Biology 147: 1213-1220

Jang SH, Lee JJ, Lee JH (2006) Colonization and succession of epilithic diatoms on artificial substrata. Algae 21: 295-304

Khan NY (2007) Multiple stressors and ecosystem-based management in the Gulf. Aquatic Ecosystem Health & Management 10: 259-267

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Diversity and Distributions 11: 139-148

Krupp F, AlMarri M (1996) Fishes and fish assemblages of the Jubail marine wildlife sanctuary. In: Krupp F, Abu Zinada A, Nader I (eds) A marine wildlife sanctuary for the Arabian Gulf: Environmental research and wildlife conservation following the 1991 gulf war oil spill. NCWCD, Riyadh and Senkenberg Research Institute, Frankfurt, Germany

Kuffner I, Walters L, Becerro M, Paul V, Ritson-Williams R, Beach K (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology-Progress Series 323: 107-117

Lecchini D (2003) Ecological characteristics of fishes colonizing artificial reefs in a coral garden at Moorea, French Polynesia. Bulletin of Marine Science 73: 763-769

Lecchini D, Galzin R (2003) Influence of pelagic and benthic, biotic and abiotic, stochastic and deterministic processes on the dynamics of auto-recruitment of coral reef fish: A review. Cybium 27: 167-184

Lee K, Yoon S, Ki J, Han M (2004) Ecological studies on Togyo Reservoir in Chulwon, Korea. VII. The colonization of epilithic algae on artificial substrata (tiles) at mesocosm. Algae 19: 107-114

Leis J (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. Environmental Biology of Fishes 65: 199-208

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bulletin of Marine Science 55

Martin T, Bortone S (1997) Development of an epifaunal assemblage on an estuarine artificial reef. Gulf of Mexico Science 15: 55-70

McClanahan T (1999) Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. Ecosystems 2: 511-523

Menge B (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. Journal of Experimental Marine Biology and Ecology 146: 69-100

Menge B, Sutherland J (1987) Community regulation: Variation in disturbance, competition and predation in relation to environmental stress and recruitment. American Naturalist 130: 730-757

Miller M (2002) Using ecological processes to advance artificial reef goals. ICES Journal of Marine Science 59: S27-S31

Moore J, Ruesink J, McDonald K (2004) Impact of supply-side ecology on consumer-mediated coexistence: Evidence from a meta-analysis. American Naturalist 163: 480-487

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52: 1053-1071

Munday P (2004) Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology 85: 623-628

Munday P, Jones G, Caley M (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology 82: 2177-2189

North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS (2008) Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Marine Ecology-Progress Series 359: 99-115

Nydam M, Stachowicz JJ (2007) Predator effects on fouling community development. Marine Ecology-Progress Series 337: 93-101

Osman R, Whitlatch R (2004) The control of the development of a marine benthic community by predation on recruits. Journal of Experimental Marine Biology and Ecology 311: 117-145

Paulay G, Meyer C (2006) Dispersal and divergence across the greatest ocean region: Do larvae matter? Integrative and Comparative Biology 46: 269-281

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23: 195-205

Petersen D, Laterveer M, Schuhmacher H (2005) Innovative substrate tiles to spatially control larval settlement in coral culture. Marine Biology 146: 937-942

Pickering H, Whitmarsh D (1997) Artificial reefs and fisheries exploitation: A review of the 'attraction versus production' debate, the influence of design and its significance for policy. Fisheries Research 31: 39-59

Pondella D, Stephens J, Craig M (2002) Fish production of a temperate artificial reef based on the density of embiotocids. Journal of Marine Science 59: S88-S93

Price ARG (1993) The Gulf - human impacts and management initiatives. Marine Pollution Bulletin 27: 17-27

Prince J (1995) Limited effects of the sea urchin *Echinometra mathaei* (de Blainville) on the recruitment of benthic algae and macroinvertebrates into intertidal rock platforms at Rottnest Island, Western Australia. Journal of Experimental Marine Biology and Ecology 186: 137-158

Purcell SW (2000) Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. Bulletin of Marine Science 66: 199-214

Purkis S, Riegl B (2005) Spatial and temporal dynamics of Arabian Gulf coral assemblages quantified from remote-sensing and *in situ* monitoring data. Marine Ecology-Progress Series 287: 99-113

Randall J (1995) Coastal Fishes of Oman. University of Hawaii Press, Honolulu

Reed D, Schroeter S, Raimondi P (2004) Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). Journal of Phycology 40: 275-284

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson C (ed) Status of coral reefs of the World: 2004. Australian Institute of Marine Science, Townsville, pp 155-169

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18: 63-73

Riegl B (2001) Inhibition of reef framework by frequent disturbance: examples from the Arabian Gulf, South Africa, and the Cayman Islands. Paleo 175: 79-101

Riegl B (2002a) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Marine Biology 140: 29-40

Riegl B (2002b) Phoenix from the ashes? Repetitive mass mortality and the biogeology of southern Arabian Gulf (United Arab Emirates) coral systems. The Vienna School of Marine Biology: 137-159

Riegl B, Purkis S (2009) Model of coral population response to accelerated bleaching and mass mortality in a changing climate. Ecological Modelling 220: 192-208

Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Marine Biology 136: 931-942

Rilov G, Beniyahu Y (2002) Rehabilitation of coral reef-fish communities: the importance of artificial-reef relief to recruitment rates. Bulletin of Marine Science 70: 185-197

Robertson DR (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77: 885-899

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Sale P (1978) Coexistence of coral reef fishes - a lottery for living space. Environmental Biology of Fishes 3: 85-102

Sams MA, Keough MJ (2007) Predation during early post-settlement varies in importance for shaping marine sessile communities. Marine Ecology-Progress Series 348: 85-101

Sandin S, Pacala S (2005) Demographic theory of coral reef fish populations with stochastic recruitment: Comparing sources of population regulation. American Naturalist 165: 107-119.

Schmitt R, Holbrook S (2000) Habitat-limited recruitment of coral reef damselfish. Ecology 81

Schmitt RJ, Holbrook SJ (1999) Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia 118: 76-86

Seaman J, W. (2002) Unifying trends and opportunities in global artificial reef research, including evaluation. Journal of Marine Science 59: S14-S16

Shanks A, Grantham B, Carr M (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13: S159-S169

Sheppard C, Loughland R (2002) Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. Aquatic Ecosystem Health & Management 5: 395-402

Sheppard C, Price A, Roberts C (1992) Marine ecology of the Arabian region: patterns and processes in extreme tropical environments. Academic Press, Toronto

Sheppard C, Sheppard A (1991) Corals and coral communities of Arabia. Fauna of Arabia 12: 3-170

Sheppard CRC (1987) Coral species of the Indian Ocean and adjacent seas: A synonymized compilation and some regional distribution patterns. Atoll Research Bulletin 307: 1-32

Shulman M, Ogden J, Ebersole J, McFarland W, Miller S, Wolf N (1983) Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64: 1508-1513

Steele M (1998) The relative importance of predation and competition in two reef fishes. Oecologia 115: 222-232

Steele M, Forrester G (2002) Early postsettlement predation on three reef fishes: Effects on spatial patterns of recruitment. Ecology 83: 1076-1091

Steele MA (1997) Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112: 64-74

Stephens J, Morris P, Pondella D, Koonce T, Jordan G (1994) Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California, USA, 1974-1991: A recruitment driven system. Bulletin of Marine Science 55: 1224-1239

Sutherland J (1974) Multiple stable points in natural communities. American Naturalist 108: 859-873

Svane I, Peterson J (2001) On the problems of epibioses, fouling and artificial reefs, a review. Marine Ecology 22: 169-188

Syms C, Jones G (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81: 2714-2729

Talbot F, Russell B, Anderson G (1978) Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs 48: 425-440

Thiel M, Gutow L (2005) The ecology of rafting in the marine environmment. II. The rafting organisms and community. Oceanography and Marine Biology: An Annual Review 43: 279-418

Tupper M, Hunte W (1998) Predictability of fish assemblages on artificial and natural reefs in Barbados. Bulletin of Marine Science 62: 919-935

Turner T (1983) Facilitation as a successional mechanisms in a rocky intertidal communities. American Naturalist 121: 729-738

UNEP (2002) Percent of the population living within 100 kilometers from the coast. Retrieved 21 Feb 2005, from http://geocompendium.grid.unep.ch/data_sets/coastal/document/pop_100km_coast_MD.htm

Walker JW (2007) Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. Marine Ecology-Progress Series 331: 109-118

Webster M (2003) Temporal density dependence and population regulation in a marine fish. Ecology 84: 623-628

Wen K, Hsu C, Chen K, Liao M, Chen C, Chen C (2007) Unexpected coral diversity on the breakwaters: potential refuges for depleting coral reefs. Coral Reefs 26: 127

Wilding T, Sayer M (2002) Evaluating artificial reef performance: approaches to pre- and post-deployment research. Marine Science 59: S222-S230

Zabin CJ, Altieri A (2007) A Hawaiian limpet facilitates recruitment of a competitively dominant invasive barnacle. Marine Ecology-Progress Series 337: 175-185

Chapter 2: Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates

Introduction

Elevated sea surface temperatures (SST's) resulting from El Ninõ events in the late 1990s were associated with mass coral bleaching throughout the world (Bruno et al. 2001; Mumby et al. 2001; Carriquiry et al. 2001; Aronson et al. 2002; Bena and van Woesik 2004). Indian Ocean reefs were the most severely impacted, with bleaching resulting in regional loss of 50 to 90% of coral cover (Obura 2001; Stobart et al. 2005; Sheppard and Obura 2005; Arthur et al. 2006). As a biogeographic subset of the Indian Ocean, the Arabian Gulf was also impacted by these increased sea surface temperatures.

The Arabian Gulf is characterized by environmental extremes. Salinity regularly exceeds 45 ppt, and sea surface temperatures annually fluctuate from winter lows less than 12 °C to summer highs above 36 °C (Coles and Fadlallah 1991; Sheppard et al. 1992). These environmental conditions are selective for corals adapted to these extremes, with corals surviving in summer temperatures that would normally cause mortality in other areas (Coles 2003). As a result, dominant taxa in Arabian Gulf Reefs differ from those in the Indo-Pacific, where Gulf fauna are over-represented by more tolerant taxa such as faviids and siderastreids while more sensitive acroporids are under-represented (Coles 2003). Despite housing a relatively more tolerant sub-set of the Indo-Pacific fauna, extreme thermal events do occasionally result in bleaching and mortality. These events generally result in differential mortality of *Acropora* species, while faviids and poritids are often negligibly impacted (Coles and Fadlallah 1991; Riegl 2002a; Sheppard and Loughland 2002).

Coral reefs in the Arabian Gulf were severely affected by thermal bleaching in both 1996 and 1998 (Riegl 2002a). Summer conditions are the most extreme in the shallow southern basin of the Arabian Gulf (Sheppard et al. 1992), where sea surface temperatures reached 37.7 °C during the 1998 bleaching event (Sheppard and Loughland 2002), a 4 to 8 °C increase over temperatures associated with bleaching elsewhere (Bruno et al. 2001; Mumby et al. 2001; Aronson et al. 2002; Sheppard 2003). These high temperatures caused extensive loss of coral cover from patch reefs located along the coastline in the United Arab Emirates (UAE) (Riegl 1999; George and John 1999; Sheppard and Loughland 2002; Sheppard and Loughland 2002). Dense coral patch reefs in the Saih Al-Shaib and Jebel Ali areas of Dubai, UAE, were heavily impacted by a 2°C positive sea surface temperature anomaly in the summer of both 1996 and 1998 (Riegl 2002a). Bleaching virtually eliminated *Acropora* species that had constituted over 98.7% of the reef building coral in the area (Riegl 1999), and resulted in a complete loss of corals from a 7.8 km^2 area in Jebel Ali alone (Riegl 2002a).

Recovery from mass bleaching events can take a number of years to occur, if it happens at all. Recruitment levels are typically depressed for several years following bleaching (Aronson et al. 2002; Tamelander 2002; Sheppard and Obura 2005), due to the high mortality in the reproductive population and the reduced fecundity of partially bleached survivors (Baird and Marshall 2002). Subsequent to thermal bleaching events, a shift in dominance can occur as a result of space preemption by opportunistic algal and invertebrate competitors (Carriquiry et al. 2001; Aronson et al. 2002; McClanahan et al. 2002), or the coral community composition can change due to differential reproductive success in species less affected by bleaching (Tamelander 2002; Sheppard and Loughland 2002; Sheppard and Obura 2005). Alternatively, assemblages may progressively recover to their pre-bleaching state due to the rapid growth rates of taxa that were most affected by bleaching (Baird and Marshall 2002; Arthur et al. 2005). Coral recovery can be highly site specific as a result of differences in proximity to seeding reefs, hydrodynamic conditions, and the extent of damage (Arthur et al. 2006), making it difficult to predict the extent and direction of recovery.

This study describes the coral assemblages in Saih Al-Shaib nearly a decade after mass coral bleaching, and compares the present coral communities with those described in the area both before and soon after the mass mortality event to determine the extent to which these assemblages have changed since bleaching. Surveys performed through 2002 indicated that coral cover remained low compared with pre-bleaching levels and was composed mainly of bleaching resistant *Porites* and faviid species (Riegl 1999; Purkis and Riegl 2005). However, recruitment of rapidly growing *Acropora* juveniles was also observed in the two years after the bleaching event (Riegl 2002). This indicated a potential return to *Acropora* dominance in the area and associated recovery of coral cover to pre-bleaching levels within a matter of years. This study examined both the adult assemblage and patterns of juvenile recruitment to determine whether community composition is stable or if species dominance appears to be shifting. Coral communities in the Arabian Gulf are exposed to rapid and extreme sea-surface temperature elevations. It is important to understand whether the composition and condition of coral assemblages here are resilient to the bleaching that is likely to occur with increasing frequency in the coming decades. Information on these assemblages and their recovery from bleaching may be useful in predicting changes to coral community composition and potential recovery processes in other regions that are likely to be impacted by future increases in sea-surface temperatures.

Methods

The Dubai reef is composed of discontinuous coral patches associated with areas of exposed cap-rock approximately 0.5 – 1 km from shore, and are interspersed between areas of unconsolidated sands and mixed algal assemblages. The size of coral patches differs, but each generally exceeded 1,000 m^2. This series of patch reefs extends approximately 12 km along western Dubai from the Saih Al-Shaib through Jebel Ali areas (Figure 1). Pre-bleaching communities have been described for the entire area by Riegl (1999). Following the elevated sea surface temperatures of 1998, extensive loss of *Acropora* was reported on patch reefs sampled in the Jebel Ali area, while massive corals were negligibly impacted (Purkis and Riegl 2005; Riegl 2002). Similar bleaching response was observed in patch reefs in Saih Al-Shaib (Riegl, pers. comm.). To compare current communities with those that had been described for Dubai before and after the 1998 bleaching event, six sites in Saih Al-Shaib were selected for detailed evaluation of coral communities (Figure 1), and were sampled between 04 September and 23 October 2006. The patch reefs described by Riegl (2002) for the Jebel Ali area could not be re-sampled as they lie in a restricted area that is the site of extensive land reclamation activities.

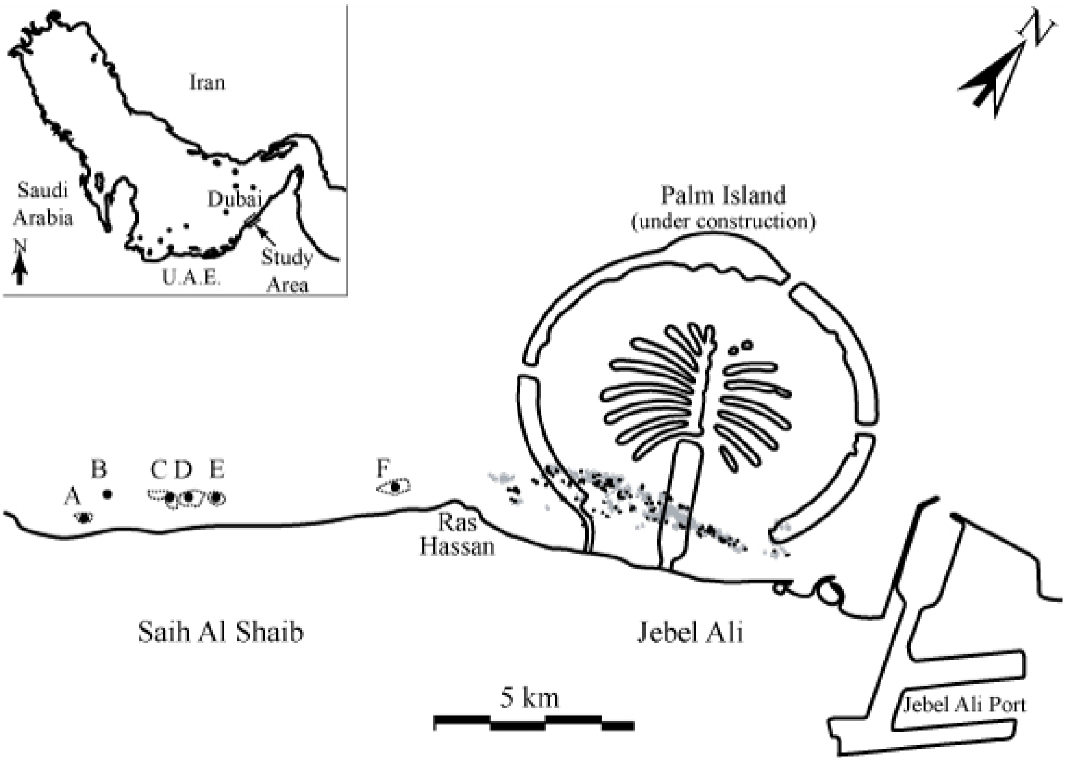

Figure 1: Map of study area in Dubai, United Arab Emirates. Sampling sites for the current study are marked with a black circle and labeled. Areas identified as containing dense live corals during preliminary surveys in Saih Al-Shaib are enclosed by a dashed line, but should not be considered exhaustive. In Jebel Ali, areas containing dense live corals (black) and dense dead corals (grey) following 1996/1998 thermal bleaching are indicated as classified from satellite imagery captured in 2001 (adapted from Purkis and Riegl 2005). Palm Island construction began in 2002 and is in progress.

Within each site six 30 m fibreglass tapes were placed approximately 5 m apart and laid parallel to the coastline. This length is representative of the scale of coral patches in these discontinuous habitats, and is appropriate based upon patch descriptions from earlier studies in the area (Riegl 1999). Depth varied negligibly (<0.5 m) among transects due to the low substrate relief in this area. A total of 21 quadrats were photographed on each transect at 1.5 m intervals, resulting in a total of 126 quadrats per site. Each quadrat enclosed an area of 0.25 m^2. Photographs were taken digitally using a SeaLife DC500 5.0 mega-pixel camera mounted on a PVC frame demarcating the photoquadrat area.

Photoquadrats were analyzed using CPCe software, version 3.4 (Kohler and Gill 2006). Each 0.25 m^2 quadrat was examined using 50 randomly placed points, and the fauna underlying each point were identified to the lowest possible taxa (Veron 2000). Identification from photographs was confirmed visually in the field on subsequent surveys, and microscopically in the laboratory through examination of corallite structure. Specimens were cleaned using 5% sodium hypochlorite immersion for 4 hrs at 30° C (Clode and Marshall 2003). Juvenile corals were categorized as those with a maximum diameter of ≤4 cm, and were identified to the lowest taxonomic level possible.

Quadrat data were pooled within each transect. Coral percent cover data was transformed using arcsine square root prior to analysis to normalize the data. Preliminary analysis indicated that one transect was an outlier (Transect B6: Ave Sørensen distance = 0.797, SD = 3.98), and was excluded from subsequent analysis (Tabachnick and Fidell 2001).

Species occurring in less than 5% of samples were removed prior to multivariate analyses as recommended by McCune and Grace (2002).

Transects were grouped using hierarchical agglomerative cluster analysis. The flexible beta linkage method (β = -0.25) was applied, using a Sørensen (i.e. Bray-Curtis) distance matrix. Sørensen distance is generally preferred for analysis of community data, and is compatible with this linkage method (McCune and Grace 2002). The resulting dendrogram was scaled by Wishart's objective function converted to a percentage of information remaining (McCune and Mefford 1999).

Indicator species analysis was used to determine the number of ecologically meaningful groups resulting from cluster analysis (Dufrene and Legendre 1997). This method combines information on both the fidelity and the relative abundance of species in a group, such that a species' indicator value is maximum (IV = 100%) when all transects in a group are occupied by that species and it is only found in that group. Indicator values for each species were calculated for 2 to 20 possible groups resulting from the cluster analysis using PC-ORD (McCune and Mefford 1999), and statistical significance was evaluated using a randomly seeded Monte Carlo test with 1,000 iterations. The optimum number of groups was selected as that which provided the maximum number of significant indicator species, as well as the lowest average *p*-value compared with all other possible grouping combinations (Dufrene and Legendre 1997). The species with significant indicator values were also subsequently used to characterize the coral communities in these groups.

Univariate comparisons of substrate coverage employed the non-parametric Kruskal-Wallis ANOVA and post-hoc Mann-Whitney *U*-tests. The diversity of each group identified from cluster analysis was examined by calculating the Shannon-Wiener diversity index, inclusive of rare species. Pair-wise comparisons between group indices were performed using the Shannon *t*-test (Zar 1996). To assess the adequacy of sampling, species-area curves were generated in PC-ORD (McCune and Mefford 1999), where the curve represents the mean number of species from 500 sub-samples for each possible sample size and associated estimates of standard deviation. The abundance of juvenile corals was compared among assemblages using a Kruskal-Wallis ANOVA and post-hoc Mann-Whitney *U*-tests.

Results

A total of 25 coral species were found in Saih Al-Shaib, with a mean richness of 12.8 ± 2.1 species per transect (mean ± SD). The most common species were *Porites harrisoni* (23.5% of living coral), *Porites lutea* (22.2%), *Cyphastrea microphthalma* (13.4%), *Acropora downingi* (9.1%), *Acropora clathrata* (7.9%), and *Platygyra daedalea* (5.7%), with remaining species each representing less than 5% of coral cover. Overall coral cover in Saih Al-Shaib was 35.0 ± 1.6 % (mean ± SE).A species area curve was generated to assess the adequacy of sampling. Species accumulation was asymptotic with ten transects capturing 90% of the maximum richness, indicating that the sampling design was sufficient to catalogue diversity in this area.

Cluster analysis was used to group transects, and species indicator analysis was applied to optimize the number of biologically meaningful groups from cluster analysis. Five groups (clusters) yielded the lowest average *p*-value from Monte Carlo significance tests (average $p = 0.091$ for all species) and maximized the number of significant indicator species (17 of the 26 species) compared with all other grouping combinations examined. Trimming the dendrogram from cluster analysis at five groups provided a good compromise between information loss (approximately 53% retained) and summarizing affinities among groups (Figure 2). The biological characteristics of the five community groups are summarized in Table 1 and described below.

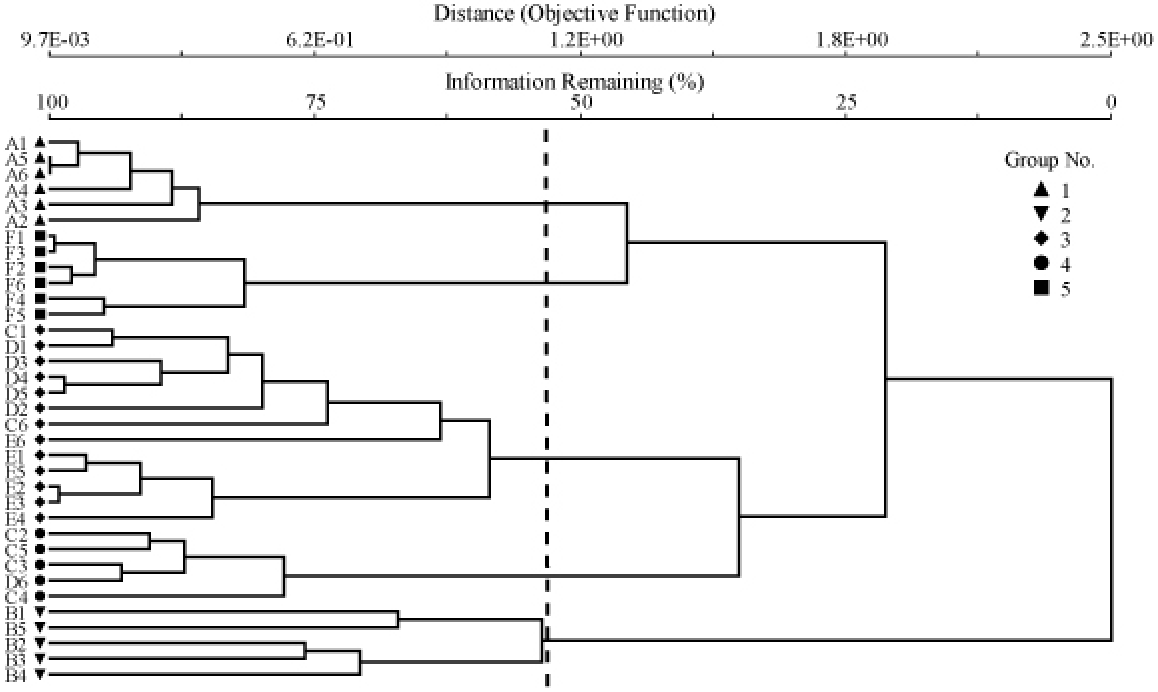

Figure 2: Dendrogram of transect groups generated from cluster analysis. Symbols correspond with community groups described in Table 1. The cut point is indicated by the dashed line, which represents the grouping combination with the highest number of significant species and lowest average p-value from indicator species analysis. Transects are indicated by the letter-number code (site-replicate).

Table 1: Biological characteristics of coral community groups identified from cluster analysis and ordination (Fig. 3 and 4). Assemblage description summarizes the ecologically and spatially dominant taxa associated with each group, along with their growth form. Indicator species are those which had significant indicator values (given in parentheses) compared with randomized values from Monte Carlo tests ($p < 0.05$). Indicator species are listed in descending order of each species' indictor value to a group, not taxonomic affinity.

Group	Coral Cover (% ± SE)	Assemblage Description	Indicator Species	Richness	Shannon-Wiener *H*
Group 1	26.0 ± 1.6	Small massive *Porites* with extensive *Acropora* rubble	*Acanthastraea echinata* (50)	16	1.83
Group 2	7.6 ± 0.6	Sparse small massive *Porites lutea*	None	16	1.69
Group 3	41.9 ± 2.5	Dense tabular *Acropora*	*Acropora valenciennesi* (60) *Acropora clathrata* (57) *Acropora downingi* (40) *Leptastrea transversa* (38) *Platygyra daedalea* (35)	24	2.34
Group 4	37.3 ± 2.4	Dense columnar *Porites harrisoni*	*P. harrisoni* (49)	19	1.51
Group 5	34.7 ± 2.1	Small massive faviids and *Porites*	*Coscinaraea monile* (57) *Favia pallida* (56) *Cyphastrea serailia* (51) *Platygyra lamellina* (41) *Psammocora contigua* (41) *Favia rotumana* (38) *Pseudosiderastrea tayamai* (35) *Turbinaria reniformis* (32) *P. lutea* (31)	18	1.91

Group 1: This community was characterized by small massive corals and extensive *Acropora* rubble. Live coral cover in this group was 26.0 ± 1.6%, mainly dominated by *P. lutea* (42.1 ± 5.4% of living coral cover), *C. microphthalma* (16.8 ± 0.8%), and *P. daedalea* (7.7 ± 1.1%). One species, *Acanthastraea echinata*, was characteristic of this assemblage having a species indicator value of 50 in this group, and was absent from all other groups (Table 1). This assemblage was distinct to Site A, a shallow (approx. 4 m depth) near-shore site where *Acropora* rubble was significantly more frequent (20.4 ± 0.7% of space) than at any other site (overall mean: 4.6 ± 0.6%) (Kruskal-Wallis ANOVA: $H_{(4, N=35)} = 23.1$, $p < 0.001$; Post-hoc Mann-Whitney U-tests: $p < 0.001$ for each).

Group 2: This assemblage is characterized by sparse massive corals separated by large areas of pavement and sand. Overall coral cover was significantly lower in this group (7.6 ± 0.8% of substratum) than in any other groups (overall mean: 36.5 ± 1.7%; Kruskal-Wallis ANOVA: $H_{(4, N=35)} = 23.0$, $p < 0.001$; Post-hoc Mann-Whitney U-tests: $p < 0.01$ for each.). *P. lutea* made up almost half of the live coral observed in this site (48.7 ± 5.2 % of live coral cover). No species had significant indicator values in this group (Table 1), indicating that no species had high fidelity for this assemblage and/or none were common among transects representing this group. Bare pavement was significantly more common here (40.1 ± 5.7% of total substratum) than in other groups (overall mean: 5.9 ± 1.5%; Kruskal-Wallis ANOVA: $H_{(5, N=35)} = 22.4$, $p < 0.001$; Post-hoc Mann-Whitney U-tests: *p*

< 0.001 for each.). Although this group included only transects from Site B, this community was observed to be the most widespread in the area.

Group 3: Large tabular *Acropora* dominated this community, making up 32% of the 41.9 ± 2.5% live coral cover in this assemblage. Coral cover was significantly more abundant in this group than in groups 1 and 2 (Mann-Whitney U-tests: Z = -3.24, $p < 0.01$ and Z = -3.20, $p < 0.01$, respectively). Tabular *Acropora* spp. dominated this assemblage, with significantly higher coverage here than in any other group (Overall mean of other groups: 2.1 ± 0.6; Kruskal-Wallis ANOVA: $H_{(4, N=35)} = 30.1$, $p < 0.001$; Post-hoc Mann-Whitney U-tests: $p < 0.01$ for each). *Acropora* colonies were generally larger than 1 – 1.5 m in maximum diameter. Three *Acropora* species were significant indicators of Group 3 (Table 1), including *A. clathrata* (IV = 57), *A. downingi* (40), *Acropora valenciennesi* (60). In addition *P. daedalea* (IV=35), and *Leptastrea transversa* (38) were also common to this assemblage. This community included 24 of the 25 species observed in this study, with a Shannon-Wiener diversity index significantly higher than any other group (Table 1; Pair-wise Shannon *t*-tests, $p < 0.05$ for each). This assemblage was generally associated with low relief areas of sand covered limestone found at sites C, D and E, and it graded into the group 2 and group 4 assemblages. Coral rubble occupied 6.0 ± 1.1% of total space in this assemblage.

Group 4: The columnar *P. harrisoni* dominated the Group 4 assemblage, making up two-thirds of live coral cover (24.6 ± 1.2 of 37.3 ± 2.4%). This species had an indicattor value of 49%, and was significantly more abundant in this group than in any other group (Overall mean of other groups: 3.8 ± 0.7%; Kruskal-Wallis ANOVA: $H_{(4, N=35)} = 27.7$, $p < 0.001$; Post-hoc Mann-Whitney U-tests: $p < 0.01$ for each). Despite having 19 of the 25 species observed in this study, Shannon-Wiener diversity was significantly lower in this group than in any other group (Table 1; Pair-wise Shannon *t*-tests, $p < 0.05$ for each), reflecting low species evenness because of the dominance of *P. harrisoni* in this assemblage. This assemblage was generally associated with elevated limestone ridges found at Site C and Site D, and was usually located at the periphery of the *Acropora* dominated Group 3 assemblage. Surrounding substrate was mainly coarse sand with occasional limestone pavement outcrops. Coral rubble occupied 4.5 ± 1.0% of space.

Group 5: This assemblage was characterized by shared dominance of faviids and poritids. Ten significant indicator species characterized this community: *Coscinaraea monile* (IV = 57), *C. microphthalma* (31), *Cyphastrea serailia* (51), *Favia pallida* (56), *Favia rotumana* (38), *Platygyra lamellina* (41*), P. lutea* (31), *Psammocora contigua* (41), *Pseudosiderastrea tayamai* (35), and *Turbinaria reniformis* (32) (Table 1). *Acropora* comprised 0.3 ± 0.1% of substrate cover. This assemblage was spatially distinct, with representation occurring only at Site F, where corals were associated with low relief limestone outcrops surrounded by pockets of sand. Although this assemblage was observed to be widely distributed in the area immediately surrounding Site F, it was not observed elsewhere in the survey area. Here, coral rubble occupied 5.5 ± 0.6% of substrates.

Mean density of juvenile corals across all assemblages was 0.8 ± 0.2 recruits m^{-2}, and differed significantly among the assemblages described above (Kruskal-Wallis ANOVA: $H_{(4,\ N=35)} = 21.1$, $p < 0.001$). Groups 2 and 5 had the highest juvenile density, and did not differ significantly from each other (Mann-Whitney *U*-test). Group 1 had significantly fewer juveniles than Group 5, while Groups 3 and 4 had significantly lower density than all other groups based on post-hoc Mann-Whitney *U*-tests ($p < 0.05$; Figure 3a). Most juveniles were either *Porites* or faviids (59.4% and 16.7% of recruits, respectively). *Acropora* made up less than 2% of all juvenile corals observed. The relative composition of coral recruits generally reflected that of the current adult composition within each assemblage, with the exception of the *Acropora* dominated group 3 (Figure 3b). Here, *Acropora* recruits represented 12.5% of juvenile corals, despite representing almost a third of the live coral cover, and *Porites* represented 62.5% of juveniles compared with an adult population representing just over a third of live cover.

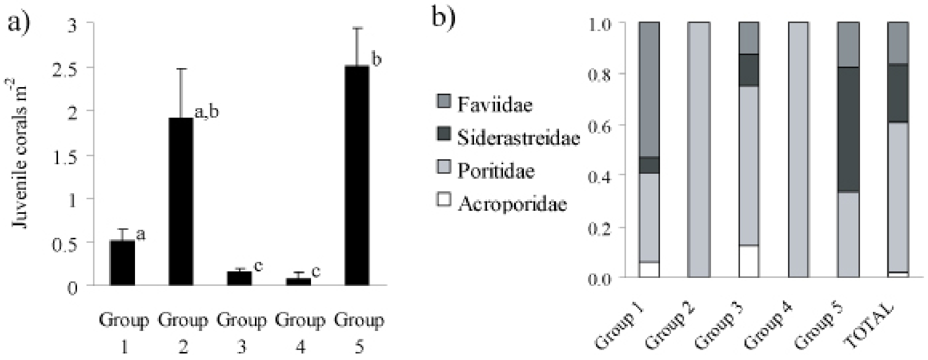

Figure 3: Density and composition of coral juveniles in the five assemblages identified from cluster analysis. (a) Density of coral juveniles for each group (mean ± SE m^{-2}). Letters indicate significant differences based on Mann-Whitney *U*-tests ($p < 0.05$) (b) Relative abundance of juveniles by family for each assemblage group, and the overall total.

Discussion

Elevated sea surface temperatures during the summers of 1996 and 1998 resulted in extensive loss of corals from patch reefs along hundreds of kilometres of coastline of the United Arab Emirates (Riegl 1999; George and John 1999; Sheppard and Loughland 2002). Similar to bleached reefs in other regions (Loya et al. 2001; Sheppard and Obura 2005; Arthur et al. 2006), some coral species were more vulnerable to bleaching than others. In the Arabian Gulf, dominant *Acropora* species were virtually eliminated, resulting in stands of dead coral skeletons extending over large areas of patch reefs (Sheppard and Loughland 2002; Riegl 2002a). Faviids and *Porites* were less affected by mortality (Riegl 1999; Sheppard and Loughland 2002), and recovery of partially bleached colonies was common (George and John 1999). In the decade since the mass bleaching event, there are signs of extensive recovery of *Acropora* cover in parts of Saih Al-Shaib, and there is little evidence of a phase-shift in coral dominance in the area to those less affected by bleaching, except at site F (see below).

Prior to the mass mortality event, coral cover in *Acropora* dominated assemblages in the Saih Al-Shaib area was 62 ± 24 %, and *Acropora* was represented by six species (Riegl 2002a). Following the 1998 bleaching event, live coral cover fell to 22 ± 10% (Riegl 2002a), and *Acropora* was virtually eliminated with only five partially bleached surviving *A. clathrata* colonies observed in the entire 37.7 km^2 study area (Riegl 1999). Overall species richness fell from 34 to 27 species (Riegl 2002a). In the current study *Acropora* were observed in five of the six sites examined and dominated assemblages at three of these sites. Coral cover in the *Acropora* dominated assemblage (Group 3) is now 41.9 ± 2.5 %, nearly double that observed after the mass mortality event. This *Acropora* dominated assemblage is found in sites C, D, and E, areas formerly dominated by *Acropora* that had suffered substantial loss during the bleaching event (Riegl 1999). Although coral cover remains lower than pre-bleaching levels it is likely that recovery will continue barring any additional disturbances. Many *Acropora* colonies in this assemblage are approximately 1 m in diameter, supporting earlier growth rate estimates of 10 cm yr^{-1} for this genus in the Arabian Gulf (Coles and Fadlallah 1991). Coral cover will likely continue to increase for the next few years as the common *A. clathrata* and *A. downingi* colonies approach the 1.5 m size typical of these species (Fadlallah 1996). Similar recovery of coral cover through rapid re-growth of new *Acropora* colonies has been observed on bleached reefs elsewhere (Loya et al. 2001; Arthur et al. 2005; Arthur et al. 2006), even in cases where juvenile recruitment is depressed (Tamelander 2002). Rapid *Acropora* growth rates appear to compensate for the low recruitment levels observed in this assemblage in Saih Al-Shaib, allowing coral cover to recover quickly. Although coral cover is increasing, species richness remains depressed in this assemblage. Several *Acropora* species previously reported as common to Dubai (Riegl 1999) were absent from the present study, including *A. arabensis*, *A. horrida*, *A. florida*, *A. valida*, and *A. tenuis*, and *A. pharaonis* is now uncommon. Similar diversity loss has followed bleaching in other areas (Loya et al. 2001; Sheppard and Loughland 2002; Tamelander 2002), with richness remaining depressed for years afterwards despite improvements in coral cover (Sheppard and Obura 2005; Lambo and Ormond 2006). Despite the loss of these species, over 85% of *Acropora* cover remains occupied by the same species which had dominated *Acropora* assemblages in the Arabian Gulf prior to the bleaching event, *A. clathrata* and *A. downingi* (Fadlallah 1996; Riegl 2002a). The recovery of these dominant species indicates that although there has been a loss of species richness, long-term ecosystem function may not be substantially impaired as a result of the bleaching event.

In this study the faviid/*Porites* dominated assemblage (Group 5) occupies an area that was dominated by *Acropora* before the mass bleaching events of the late 1990s (Site F; see map in Riegl 2002). *Acropora* now contributes less than one percent of coral cover in this area. Faviids and *Porites* have been widely reported to be among the most resistant taxa on reefs affected by thermal bleaching throughout the world (Loya et al. 2001; Obura 2001; Baird and Marshall 2002; Sheppard and Obura 2005). This was also true in Dubai, where the elevated sea surface temperatures in both 1996 and 1998 had negligible impact on the live coral coverage and species richness of faviids and *Porites* (Riegl 1999; Riegl 2002a). The differential survival and subsequent reproductive success of such bleaching resistant taxa has been suggested to contribute to shifts in coral dominance in an area (Tamelander 2002; Sheppard and Loughland 2002). This appeared to be occurring at site F. This site is now dominated by bleaching resistant taxa, and current coral cover of these bleaching resistant taxa (34.7 ± 2.1 %) is double that observed following the bleaching event in areas that were formerly *Acropora* dominated (mean: 17 %, Riegl 1999), and in compositionally similar faviid dominated assemblages in the area both before and after the bleaching event (16 ± 4 %, Riegl 1999). This site also contained the highest densities of coral juveniles in all of Saih Al-Shaib, and the composition of juveniles reflected the composition of adults with faviids, siderastreids, and poritids dominating recruitment. *Acropora* juveniles were not observed. These patterns of recruitment coupled with the increased coral cover compared with similar assemblages in 1998 indicate that there has been a shift in coral dominance at this site in the decade following the mass bleaching event, and that it is unlikely that *Acropora* will regain dominance in the near future.

The assemblage dominated by small massive corals and *Acropora* rubble (Group 1) appears to have experienced *Acropora* bleaching in recent years. Similar to the *Acropora* dominated Group 3 assemblage, the presence of several large (1 – 1.5 m) *Acropora* colonies indicate that this assemblage was recovering from the 1996 and 1998 bleaching event. However, extensive *Acropora* rubble covering approximately a fifth of the substratum compared with less than 5% in other assemblages, and the lack of standing dead *Acropora* skeletons known to persist for several years after bleaching (Riegl 1999, 2002a; Sheppard and Loughland 2002) suggest that many *Acropora* were killed in the years since the 1998 bleaching event, most likely in 2002. Elevated sea-surface temperatures in the summer of 2002 were associated with coral bleaching events in the Arabian Gulf and surroundings (Dodge 2002; Wilkinson 2004), and coral bleaching was also observed on near-shore reefs in the Jebel Ali area, 10 km west of Saih Al-Shaib (Dodge 2002; B. Riegl, pers. comm.). It is likely that this 2002 bleaching event also reset recovery of *Acropora* on the patch reef at site A due to its shallow depth. This assemblage occurs at a 3 - 4 m depth, while intact *Acropora* assemblages elsewhere in Saih Al-Shaib (Group 3) occur at approximately 6 m depth. Shallow depth has been related to increased levels of coral bleaching (Mumby et al. 2001; Sheppard and Loughland 2002; Bena and van Woesik 2004; Stobart et al. 2005), and this assemblage lies within the 3 – 5 m 'critical depth' associated with severe bleaching in the Arabian Gulf (Sheppard and Obura 2005), making it more susceptible to elevated sea-surface temperatures. This assemblage may recover *Acropora* dominance over time unless interrupted by future bleaching events or anthropogenic disturbance. Currently, there are several large *Acropora* colonies that appear to have survived the 2002 bleaching event, as well as a number of young colonies 30 – 40 cm in diameter which have likely recruited in the years since. Although *Acropora* juveniles are currently a minor component of the recruiting assemblage, we predict that *Acropora* recruitment will increase in the next few years as young colonies become reproductive, generally occurring at approximately 50 cm (Hall and Hughes 1996). The rapid growth rates and increasing fecundity with size should contribute to the rapid recovery of *Acropora* in this assemblage, provided that there are no further disturbances.

The recovery of the formerly dominant *Acropora* is highly site specific. In general, recovery is highest in western Saih Al-Shaib. This may be a reflection of either natural settlement processes or the influence of coastal development in the area. Early post-bleaching *Acropora* recruitment in 1999 was observed to decline from west to east in Dubai (Riegl 2002a). This pattern of recruitment follows the direction of prevailing coastal currents in the area (Wilkinson 2004; Smit et al. 2005), and suggests that this area is being seeded by reefs 30 km upstream which had *Acropora* survive the 1998 bleaching event (Riegl 2002a). However, it is also possible that large scale coastal development extending several kilometers east of Saih Al-Shaib may have affected recovery. The patch reef closest to this development is currently dominated by sediment tolerant faviids and poritids, and the more sensitive *Acropora* now account for less than 1% of the live coral cover a that site. Because this area was not sampled between 2002 and 2006, it is unknown to what extent either propogule supply or human influence has affected this recovery. Continued monitoring of the area is warranted.

The remaining assemblages in Saih Al-Shaib are dominated by *Porites*. *Porites* are generally tolerant of elevated sea surface temperatures (Obura 2001; Loya et al. 2001; Baird and Marshall 2002; Sheppard and Loughland 2002; Sheppard and Obura 2005), and the sparse *P. lutea* and the dense *P. harrisoni* dominated assemblages in the Saih Al-Shaib area were negligibly impacted by the 1996 and 1998 bleaching event (Riegl 1999; Riegl 2002a). In the intervening years, these assemblages have changed little in Saih Al-Shaib. Coral cover has not increased in either of the *Porites* dominated assemblages (Groups 2 and 4) compared with pre-bleaching coverage. It is also unlikely that there will be substantial increases in coral cover for these assemblages in the near future due to the slow growth rate known for both *Porites* adults (Yap et al. 1998; Baird and Marshall 2002; Flora and Ely 2003) and juveniles (Tamelander 2002). This is particularly true in the dense *P. harrisoni* assemblage which had the lowest recruit density of all assemblages, indicating that any increases in coral cover will result mainly from vegetative growth of adult colonies. Like coral cover, composition and diversity in these *Porites* dominated assemblages remains comparable to that observed prior to the bleaching event (Riegl 1999; Riegl 2002a). Because the current juvenile composition in each assemblage reflects that of the adult population it is likely that the community composition is stable. Thus, coral coverage and composition in the sparse *P. lutea* assemblage (Group 2) and the dense *P. harrisoni* (Group 4) assemblages remain comparable to pre-bleaching levels.

In the first five years following the 1998 bleaching event most impacted reefs worldwide showed little recovery of coral cover compared with pre-bleaching levels (Aronson et al. 2002; Riegl 2002a; McClanahan et al. 2005; Stobart et al. 2005; Sheppard and Obura 2005). However, the presence of abundant juvenile recruits (Tamelander 2002; Stobart et al. 2005; Sheppard and Obura 2005), with densities increasing through time (Aronson et al. 2002; Sheppard and Obura 2005), suggested that recovery was beginning in many areas. Ten years after the 1996 mass mortality of *Acropora* in Dubai (Riegl 1999; Riegl 2002a), *Acropora* cover shows strong signs of recovery in parts of Saih Al-Shaib, and despite the loss of several species *A. clathrata* and *A. downingi* have recovered their former dominance. The resilience of this assemblage appears due, in part, to the rapid growth rates of the species dominating this assemblage. Other assemblages in Saih Al-Shaib, dominated by more temperature-tolerant taxa such as faviids, *P. harrisoni*, and *P. lutea*, were negligibly impacted by the bleaching events of the late 1990s (Riegl 1999;

Riegl 2002a). The differential survival of taxa in these assemblages has not resulted in the predicted phase-shift in coral dominance in the area (Sheppard and Loughland 2002; Sheppard and Obura 2005), most likely because localized coral recruitment has resulted in self-seeding assemblages and because the slow growth rates of most bleaching resistant taxa inhibits competitive overgrowth of available substrates. There has also not been a phase-shift to dominance by macro-algae. Similar observations have been made in other areas recovering from bleaching (Arthur et al. 2005, 2006; Stobart et al. 2005), and macro-algae cannot achieve long-term dominance in this region due to seasonal die-offs (Ateweberhan et al. 2006).

The patterns of resilience and resistance observed in Saih Al-Shaib have important implications both regionally and globally. The southern Arabian Gulf experiences repeated mass coral mortality on a 10 -15 year cycle due to recurrent thermal anomalies (Riegl 1999; Riegl 2001; Riegl 2002b; Purkis and Riegl 2005). This has resulted in corals which are acclimatized and adapted to extreme environmental conditions (Coles and Fadlallah 1991; Coles and Brown 2003; Coles 2003), capable of both enhanced survival through both high and low temperature extremes as well as relatively rapid recovery from bleaching events. The comparatively minimal loss of species richness in the Saih Al-Shaib (11%) compared with other areas (>50%; Loya et al. 2001; Sheppard and Obura 2005; Lambo and Ormond 2006), during the most extreme bleaching event on record (West and Salm 2003; McClanahan et al. 2005) provides further evidence of tolerance to temperature extremes. This is particularly true given that temperatures here were 4 – 10

°C higher than associated with bleaching elsewhere (Bruno et al. 2001; Wellington et al. 2001; Mumby et al. 2001; Aronson et al. 2002; Sheppard 2003). Given that elevated sea-surface temperatures are predicted to continue increase in both magnitude and frequency in the coming decades (Sheppard 2003; Coles and Brown 2003), such patterns of resistance and resilience may approximate what will occur in more stable reef environments in the tropics in the future. Those taxa more tolerant of high temperatures or more capable of rapid re-colonization and growth may come to dominate in areas affected by increasing sea-surface temperatures, while those less tolerant and slower growing species may eventually become regionally extinct. Like Saih Al-Shaib, reefs experiencing repeated bleaching may recover coral cover to pre-bleaching levels, but diversity will likely decline through time eventually becoming dominated by a low-diversity subset of the original fauna which is more adapted to extreme conditions. The ability of species to acclimatize to increasing temperatures will also be important (Coles and Brown 2003). The predicted 5-year cycle of bleaching events expected to affect low latitude reefs may be too frequent to allow many populations to adapt (Sheppard 2003). However, the rapid recovery of corals following major stress events 2 to 4 years apart observed in this study does indicate that regional pockets of resilient taxa can withstand these perturbations.

Coral patch reefs in the Saih Al-Shaib area exhibit both resistance and resilience to the impacts of high sea-surface temperatures, and are among the richest assemblages in the Arabian Gulf (Riegl 1999; Coles 2003). Such areas are considered a priority for coral reef conservation and management efforts because they are likely to support recovery of regional reefs more affected by bleaching in the coming decades (West and Salm 2003). However, large-scale coastal development, land reclamation projects, and development of desalination facilities throughout Dubai are a threat to these patch reefs (Wilkinson 2004). A number of these current and proposed developments are within several hundred meters of reefs surveyed in this study and are likely to directly affect these coral communities through burial or sedimentation, or indirectly through modification of near-shore water movement and large-scale changes in coastal currents with related changes in accretion or erosion zones. It is possible that these direct and indirect impacts may inhibit or even eliminate the natural recovery and resilience capacity of even these hardy corals and coral reef communities. The immediate protection and conservation of surviving coral communities in this area is warranted.

References

Aronson R, Precht WF, Toscano MA, Koltes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. Mar Biol 141: 435-447

Arthur R, Done TJ, Marsh H, Harriott V (2006) Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. Coral Reefs 25: 427-440

Arthur R, Done TJ, Marsh H (2005) Benthic recovery four years after an El Nino-induced coral mass mortality in the Lakshadweep Atolls. Curr Sci 89: 694-699

Ateweberhan M, Bruggemann J, Breeman A (2006) Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). Coral Reefs 25: 391-406

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol-Prog Ser 237: 133-141

Bena C, van Woesik R (2004) The impact of two bleaching events on the survival of small coral colonies (Okinawa, Japan). Bull Mar Sci 75: 115-125

Bruno J, Siddon C, Witman J, Colin P, Toscano M (2001) El Nino related coral bleaching in Palau, western Caroline Islands. Coral Reefs 20: 127-136

Carriquiry J, Cupul-Magana A, Rodriguez-Zaragoza F, Medina-Rosas P (2001) Coral bleaching and mortality in the Mexican Pacific during the 1997-98 El Nino and prediction from a remote sensing approach. Bull Mar Sci 69: 237-249

Clode P, Marshall A (2003) Variation in skeletal microstructure of the coral *Galaxea fascicularis*: effects of an aquarium environment and preparatory techniques. Biol Bull 204: 138-145

Coles S, Tarr A (1990) Reef fish assemblages in the western Arabian Gulf: A geographically isolated population in an extreme enviroment. Bull Mar Sci 47: 696-720

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low-temperatures in the Arabian Gulf - new species-specific lower temperature limits. Coral Reefs 9: 231-237

Coles S (2003) Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific region. Atoll Res Bull 507: 1-19

Coles S, Brown B (2003) Coral bleaching - capacity for acclimatization and adaptation. Advances in Mar Biol 46: 183-223

Dodge R (2002) Bleaching in the southern Arabian Gulf NOAA Coral Reef Watch Program: NOAA National Environmental Satellite Data and Information Service, Maryland. Accessed 8-Apr.-2007 from http://coralreefwatch.noaa.gov/satellite/bleachingreports/als_bleaching.9.27.2002

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67: 345-366

EWS-WWF (2006) Coral reef investigations in Abu Dhabi and eastern Qatar: Biannual report. Emirates Wildlife Society-World Wildlife Fund, Dubai, UAE

Fadlallah YH (1996) Synchronous spawning of *Acropora clathrata* coral colonies from the western Arabian Gulf (Saudi Arabia). Bull Mar Sci 59: 209-216

Flora CJ, Ely PS (2003) Surface growth rings of *Porites lutea* microatolls accurately track their annual growth. Northwest Sci 77: 237-245

George J, John D (1999) High sea temperatures along the coast of Abu Dhabi (UAE), Arabian Gulf - their impact upon corals and macroalgae. Reef Encounter 25: 21-23

Hall V, Hughes T (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77: 950-963

Kinlan B, Gaines S (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84: 2007-2020

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32: 1259-1269

Lambo A, Ormond R (2006) Continued post-bleaching decline and changed benthic community of a Kenyan coral reef . Mar Poll Bull 52: 1617-1624

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4: 122-131

McClanahan T, Maina J, Soede L (2002) Effects of the 1998 coral morality event on Kenyan coral reefs and fisheries. Ambio 31:

McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005) Detriments to post-bleaching recovery of corals. Coral Reefs 24: 230-246

McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR

McCune B, Mefford M (1999) Multivariate analysis of ecological data (Version 4.14) . MjM Software: Gleneden Beach, OR

Mumby P, Chisholm J, Edwards A, Clark C, Roark E, Andrefouet S, Jaubert J (2001) Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. Mar Biol 139: 183-189

Obura D (2001) Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress? Bull Mar Sci 69: 421-442

Purkis S, Riegl B (2005) Spatial and temporal dynamics of Arabian Gulf coral assemblages quantified from remote-sensing and *in situ* monitoring data. Mar Ecol Prog Ser 287: 99-113

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18: 63-73

Riegl B (2001) Inhibition of reef framework by frequent disturbance: examples from the Arabian Gulf, South Africa, and the Cayman Islands. Paleo 175: 79-101

Riegl B (2002a) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Mar Biol 140: 29-40

Riegl B (2002b) Phoenix from the Ashes? Repetitive mass mortality and the Biogeology of Southern

Arabian Gulf (United Arab Emirates) Coral Systems. Vienna School of Mar Biol: 137-159

Shanks A, Grantham B, Carr M (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13: S159-S69

Sheppard C (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425: 294-297

Sheppard C, Loughland R (2002) Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. Aquat Ecosyst Health & Manag 5: 395-402

Sheppard C, Obura D (2005) Corals and reefs of Cosmoledo and Aldabra atolls: extent of damage, assemblage shifts and recovery following the severe mortality of 1998. J Nat Hist 39: 103-121

Sheppard C, Price A, Roberts C (1992) Marine ecology of the Arabian region: patterns and processes in extreme tropical environments. Academic Press, Toronto

Smit, F, Mocke, G, and Al-Zahed, K (2005) Quantifying and managing the coastal response to major offshore developments in Dubai. Proceedings of the 14th Biennial Coastal Zone Conference New Orleans, Louisiana. NOAA Coastal Services Center, Charleston SC

Stobart B, Teleki K, Buckley R, Downing N, Callow M (2005) Coral recovery at Aldabra Atoll, Seychelles: five years after the 1998 bleaching event. Phil Trans Roy Soc Lond, Ser A 363: 251-255

Tabachnick B, Fidell L (2001) Using multivariate statistics. Allyn and Bacon, Needham Heights MA

Tamelander J (2002) Coral recruitment following a mass mortality event. Ambio 31: 551-557

Veron J (2000) Corals of the world. Australian Institute of Marine Science, Townsville

Wellington G, Glynn P, Strong A, Navarette S, Wieters E, Hubbard D (2001) Crisis on coral reefs linked to climate change. Eos 82: 1-7

West J, Salm R (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Cons Biol 17: 956-967

Wilkinson C (2004) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville

Yap HT, Alvarez RM, Custodio HM, Dizon RM (1998) Physiological and ecological aspects of coral transplantation. J Exper Mar Biol Ecol 229: 69-84

Zar J (1996) Biostatistical analysis. Prentice Hall, Upper Saddle River NJ

Chapter 3: Long-term changes in benthic assemblages on large breakwater reefs and a comparison to natural reefs

Introduction

There has been increased urbanization of marine ecosystems as a result of growing human populations in coastal areas. Man-made coastal defense structures such as breakwaters, jetties, and groynes now dominate the near-shore environment in many areas, in some cases more than doubling the length of the natural coastline (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005). Such structures represent large-scale unplanned artificial reefs in that they provide substantial hard-bottom habitat capable of developing diverse and abundant marine communities (Baine 2001; Svane and Peterson 2001; Airoldi et al. 2005). Although not designed for ecological purposes, the relatively large size and ubiquity of such structures suggests that they are likely to play an increasingly important ecological role in coastal marine ecosystems as human populations continue to grow.

Most investigations of community development on coastal structures have focused on fish (Lincoln-Smith et al. 1994; Pondella et al. 2002; Stephens and Pondella 2002; Guidetti et al. 2005b; Clynick 2006; Clynick et al. 2008), and have largely ignored the benthic assemblage. However, benthos is of particular ecological importance in providing food, settlement habitat, and shelter for most reef associated organisms, including fish (Elliott et al. 1995; Qian 1999; Crossman et al. 2001; Hartney and Grorud 2002;

Nishizaki and Ackerman 2004). The benthic community also contains many of the species considered important for their aesthetic or nuisance value to marine management (Airoldi et al. 2005). Despite this importance, relatively little is known about how benthic communities develop on these large-scale breakwater reefs or how they compare to assemblages on natural reefs.

Studies of benthic community development on coastal defense structures has typically focused either on the very early stages of recruitment and colonization (Chapter 5; Osman and Whitlatch 2004; Bulleri 2005c; Bulleri 2005a) or on mature communities (Chapter 4; Moschella et al. 2005). There is little knowledge of how these communities develop over time, or if and when these structures begin to resemble benthic communities on natural reefs or rocky shores (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005). An understanding of the types of communities to expect and the sequence of development is essential for addressing the ecological and management implications of these large-scale artificial reefs.

Coastal defense structures can be viewed as ‘natural experiments’ on which to observe the development of communities through time. Adjacent structures are often designed with standardized materials, relief, and medium-scale complexity, and are generally deployed in comparable near-shore environments. Their staggered construction also results in structures immersed for different lengths of time, providing an opportunity to infer temporal patterns of community development by comparing assemblages on structures of different known ages. Such natural experiments cannot account for confounding factors to the extent that is possible with true manipulative experiments, but they do allow examination of ecological processes at scales that would not be possible with a more controlled approach (Diamond 1986). In this study, the benthic communities on six breakwater reefs ranging from one to 31 years of age were compared to provide an understanding of community development on large-scale artificial structures over time. They were also compared to benthic communities on natural reefs to gain an understanding of how communities develop on these structures relative to natural habitats.

Methods

This study was conducted in Dubai, United Arab Emirates, in the south-eastern basin of the Persian Gulf. Six rocky-reef breakwaters ranging from 1 to 31 years of age were selected for study, with two sites sampled on each (Figure 1). All breakwaters were constructed of 1 – 3 m^3 quarried rock blocks, with the exception of the Jebel Ali Port breakwater which was made of interlocked concrete jacks of comparable size. Six natural reef sites were also sampled for comparison to communities on breakwaters. Natural patch reefs exist only in areas south-west of the Palm Jebel Ali, with the remainder of the area dominated by course to fine mobile sands. Maximum depth to the natural substratum at all sites did not exceed 11 m.

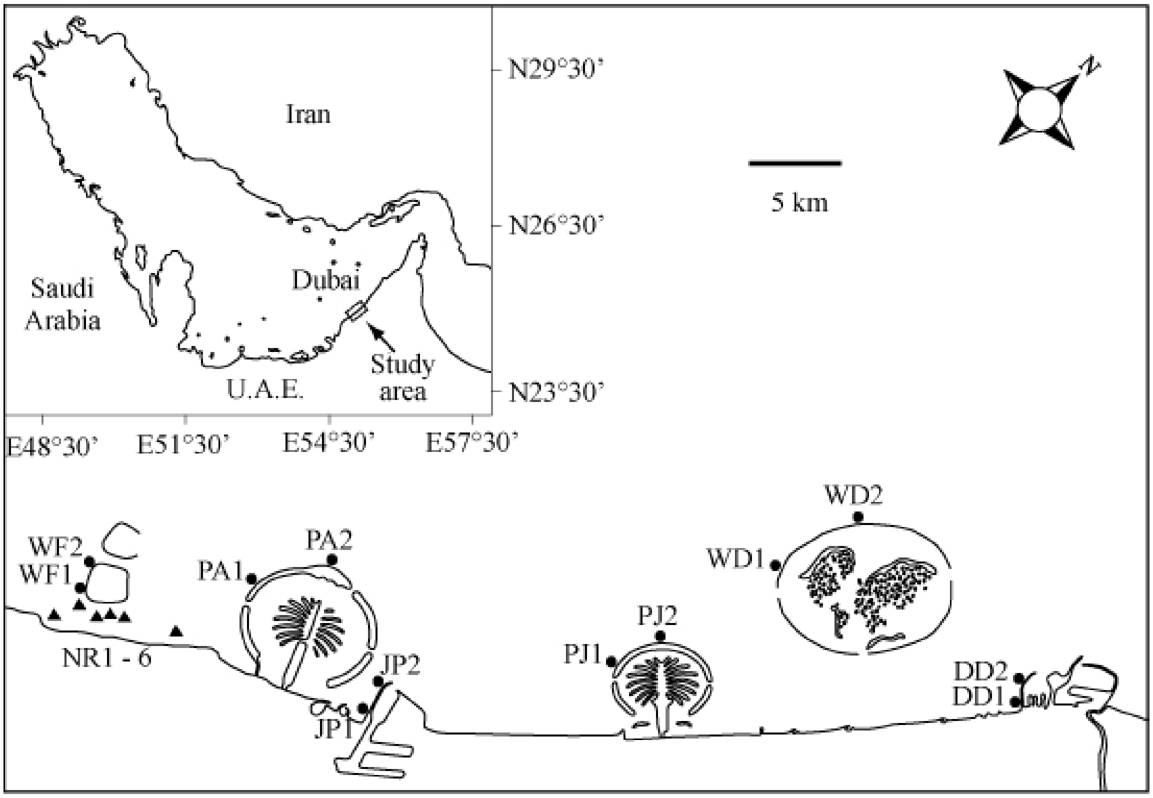

Figure 1: Map of breakwater (●) and natural reef (▲) sampling sites. Site names and age: NR = natural reefs; WF = Dubai Waterfront (1.5 yr); PA = Palm Jebel Ali (3.5 yr); JP = Jebel Ali port (31 yr); PJ – Palm Jumeirah (5.5 yr); WD = The World (1 yr); DD = Dubai dry docks (25 yr).

Composition of benthic communities was estimated using photo-quadrats. Six replicate 30 m line transects were photographed at 3 m intervals using a Nikon D80 10 mega-pixel digital camera mounted on a PVC frame enclosing a 0.25 m^2 area, for a total of 66 photo-quadrats per site. Sampling was standardized to approximately 5 - 6 m depth on each structure. Benthic coverage from each photograph was estimated using 50 random point intercepts in CPCe image analysis software, version 3.5 (Kohler and Gill 2006).

Analyses were performed on substrate categories occurring in more than 5% of samples (McCune and Grace 2002), including coverage of scleractinian corals, turf algae, coralline algae, porifera, solitary ascidians, bivalves, gastropods, the echinoids *Diadema setosum* and *Echinometra mathaei*, as well as the amount of bare pavement. Preliminary analysis indicated that one natural reef site was an extreme outlier (NR2: Mean Bray-Curtis distance = 0.77, SD = 2.62), and it was excluded from further analysis (Tabachnick and Fidell 2001). All data were pre-treated with arc-sine square-root transformations prior to multivariate analyses.

Non-metric multidimensional scaling (NMS) on Bray-Curtis distances was used to ordinate benthic data for each site. The NMS autopilot mode of PC-ORD (McCune and Mefford 1999) performed a Monte Carlo significance test on the best of 40 runs of real data with 50 runs of randomized data to optimize the number of axes. To ease interpretation, ordinations were rotated to load the age of breakwaters on the first axis. Joint plots were superimposed on the ordination to illustrate the strength and direction of correlation of benthic members with ordination axes. Only benthos with a Pearson's $r > 0.5$ were included in the joint plot.

To test for differences in benthic communities among breakwaters of different age and natural reefs, a one-way analysis of similarity (ANOSIM) was performed on benthic data from transects. ANOSIM is a multivariate randomization test analogous to a standard one-way ANOVA being performed on a distance matrix, but with a minimum of assumptions (Clarke and Gorley 2006), and is appropriate for assessing groups that have been assigned a priori. ANOSIM produces a test statistic, R, that assesses the null hypothesis that there are no differences among groups. $R \approx 0$ when there are no significant differences among groups, with greater differences among groups indicated as R approaches -1 or 1. The significance of the R statistic is generated from randomization tests on the distance matrix. This was augmented with a one-way similarity percentage analysis (SIMPER) to determine the percent dissimilarity in benthic communities between reefs, and to identify benthic members which were driving these differences, where differences between groups had been shown to exist in ANOSIM.

To further explore patterns of change in benthic variables among structures of different age, and with the natural reef, one-way ANOVA with post-hoc Tukey's HSD tests were used to identify significant differences in benthic members that were related to community differences in multivariate analysis.

Results

Differences in benthic communities were indicated by separation of sites in NMS ordination (Figure 2), where a two-dimensional representation reduced stress significantly compared with randomized data (Real 2-D stress: 3.8, Stress in randomized data: 15.6; $p < 0.05$), with no significant further reduction in stress in a third dimension. The first axis represented 88% of variation and was aligned with differences in benthic communities related to the age of breakwaters. There was a relatively tight clustering of breakwaters less than 5.5 years old to the left on this first axis, while breakwaters more than 25 years old and the natural reef sites were clustered to the right. In general, the distribution of sites on this axis changes sequentially with the age of breakwaters, becoming more similar to natural reefs with increased age. Pearson's *r* indicated that younger breakwaters were strongly associated with turf algae (r = -0.90), bivalves (r = -0.61), and sponges (r = -0.55), while older breakwaters and the natural reefs were strongly correlated with higher coverage of corals (r = 0.76) and coralline algae (r = 0.51) in the ordination. The second axis represented 9% of the variation, with sites spread across this axis based on the relative abundance of bare pavement (Pearson's r = 0.95), bivalves (r = 0.58), and the urchin *D. setosum* (r = 0.58). The three sites most strongly associated with this axis (Site 1 of PA, PJ, and WD) represent the section of breakwater most exposed to the predominant wind-driven wave action on each of these structures (Sheppard et al. 1992; Smit et al. 2005), and this wave action may explain the increased bare pavement at these sites. In addition, differences in the relative abundance of *D. setosum* among sites was also associated with this axis, and its grazing action may have also contributed to the abundance of bare pavement that is the primary determinant of community divergence.

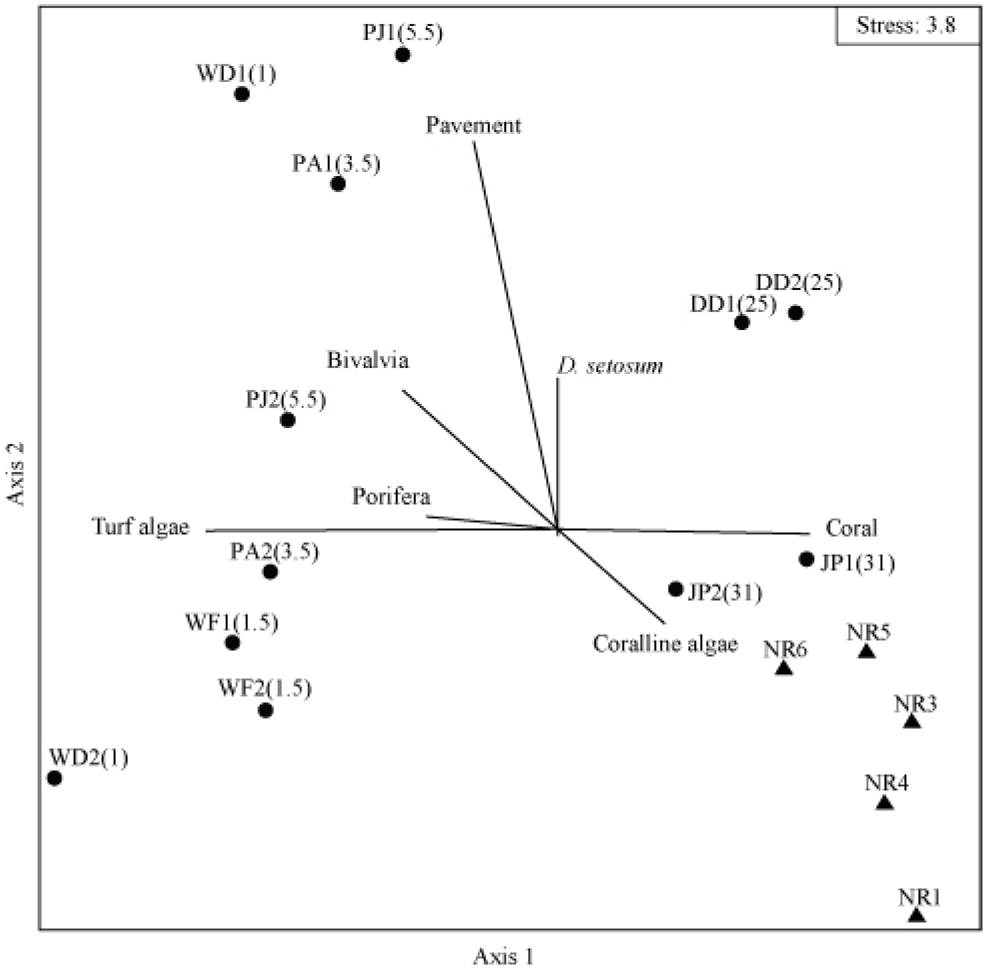

Figure 2: Ordination of benthic communities at sampling sites on breakwaters (●) and natural reefs (▲), with a joint plot of benthic components that were strongly associated with either axis. Site name-number is given in capital letters, with age since construction (years) provided in parentheses for breakwaters.

Benthic communities on breakwaters of consecutive age generally differed from one another, and the oldest artificial structure also differed from the natural reef (Table 1). Of all pair-wise comparisons, only reefs of 3.5 and 5.5 years (PA and PJ) had a non-significant *R*-value; benthic communities on all other reefs compared differed significantly. Average percent dissimilarity values indicated that the youngest reefs (1.0

to 1.5 yr) had dissimilar communities, but that benthos became more similar through 5.5 yr, where 3.5 and 5.5 yr reef communities did not differ from one another. The 5.5 and 25 yr breakwaters, however, had highly dissimilar communities, likely as a result of the 20 year difference in immersion time. Dissimilarity between the mature 25 and 31 yr reefs was lowest of all significantly different groups. The oldest artificial reef (31 yr) had a benthic community that differed significantly from that on natural reefs, with a dissimilarity value that ranked third behind reefs that were 20 yr apart in construction (5.5 and 25 yr) or were just recently built (1.0 and 1.5 yr).

Table 1: Results of comparisons between benthic communities on breakwater sites of consecutive age and natural reefs, pooled for each location/age. The *R*-statistic and its *p*-value for overall comparisons between groups is shown, with average percent dissimilarity (Mean δ (%)) where differences are significant. Percent cover of benthos discriminating these groups with their respective percent and cumulative percent contribution to the mean dissimilarity are shown for significantly different groups. Percent cover is based on raw data for ease of interpretation; all other results are based on arc-sine square-root transformed data. Only benthic variables with >10% contribution are shown. Calculations based on mean benthic cover across sites for each location.

Groups Compared	*R*	*p*	Mean δ (%)	Benthic variable	Group 1 Cover (%)	Group 2 Cover (%)	Contribution δ (%)	Cumulative δ (%)
1.0 & 1.5 yr	0.57	$p < 0.001$	33.9	Pavement	36.0	21.9	28.5	28.5
				Turf algae	50.5	66.8	24.3	52.6
				Porifera	4.3	0.3	12.0	64.8
				Coral	0.03	2.6	11.3	76.2
1.5 & 3.5 yr	0.50	$p < 0.001$	25.5	Turf algae	66.8	44.0	28.1	28.1
				Pavement	21.9	39.9	25.8	53.9
				Bivalves	1.7	7.5	15.8	69.7
3.5 & 5.5 yr	0.11	$p > 0.05$	23.4	n. a.				
5.5 & 25 yr	0.92	$p < 0.001$	42.2	Coral	6.8	45.8	29.6	29.6
				Turf algae	33.8	4.8	25.4	55.0
				Bivalves	7.9	0.2	14.1	69.1
				Pavement	44.2	34.5	12.1	81.2
25 & 31 yr	0.75	$p < 0.001$	25.1	Pavement	34.5	13.8	26.7	26.7
				Turf algae	4.8	10.1	20.6	47.3
				Coral	45.8	56.0	12.3	56.7
31 yr & NR	0.66	$p < 0.001$	25.6	Turf algae	10.1	1.0	25.8	25.8
				Coral	56.0	36.5	25.3	51.1
				Pavement	13.8	7.6	20.8	71.9

In terms of specific benthic members which discriminated community groups, the results of SIMPER analyses augmented the patterns indicated by joint plot in the NMS (Table 2;

Figure 2). Dissimilarity among reefs less than 3.5 yr result mainly from differences in the relative abundance of bare pavement and turf, together contributing more than 50% of the cumulative dissimilarity. Because no difference was identified between reefs aged 3.5 and 5.5 yr, no attempt was made to identify discriminating taxa. An increase in coral cover and a decline in turf algae with age were primarily responsible for the high dissimilarity shown between the 5.5 and 25 yr reefs. On 25 and 31 yr reefs, dissimilarity was caused mainly by differences in the relative abundance of pavement, turf, and coral. However, overall dissimilarity, as stated above, was lower here than in all other groups. Lastly, benthic differences between the oldest artificial reef (31 yr) and the natural reefs were mainly driven by lower cover of coral, turf, and bare pavement on natural reefs compared with the mature artificial reef.

Changes in the cover of the benthic variables that were identified as discriminating reefs of different age are illustrated in Figure 3. One-way ANOVAs indicated significant difference in the cover of each benthic variable among reefs (ANOVA $F_{(6,94)}$: Turf = 59.5, Pavement = 15.1, Porifera = 8.4, Bivalves = 44.5, Coral = 295.7; $p < 0.001$ for each). Post hoc comparisons between reefs used Tukey's unequal-N HSD tests.

Turf algae generally declined with the age of breakwaters (Figure 3 a). There was no significant difference in turf on 1 and 1.5 year old reefs, but turf coverage declined significantly from 1.5 to 5.5 year old reefs (Tukey's unequal N HSD test: $p < 0.01$) and again on reefs 25 years of age ($p < 0.001$). The oldest breakwaters (25 and 31 yr) and the natural reefs did not differ in turf cover. The highest turf coverage occurred on 1.5 yr old reefs, with an average of almost 20% more cover than the temporally adjacent 1 yr and 3.5 yr reefs. This increased turf cover corresponds with a proportional decline in the total of bare pavement, porifera, and bivalve cover on the same reef (Figure 3 b, c, d), suggesting that their decline in percent cover is a function of turf dominance on this artificial reef rather than age.

The cover of bare pavement did not differ significantly between any of the five reefs aged 1 to 25 yr, with the exception of the 1.5 yr old reef discussed above having less pavement than the 5.5 yr reef (Figure 3 b; $p < 0.05$). The oldest reef (31 yr) had the lowest bare pavement of all artificial structures, and this was significant compared with reefs aged 3.5 to 25 yr ($p < 0.05$ each). Only this oldest reef (31 yr) had comparable bare pavement to the natural reef; all younger artificial structures had significantly more bare pavement than natural reefs ($p < 0.05$ for all).

Porifera cover was highest on the youngest reef (1 yr), which had significantly more sponge than any other reef ($p < 0.05$ for all). However, porifera was not a dominant member of the benthos, with maximum coverage of only 4.3 ± 0.8%. There were no significant differences among any other reefs, with the exception that the 1.5 yr reef that was dominated by turf had less porifera cover than the 5.5 yr reef ($p < 0.05$). This explains the relatively weak, single appearance of porifera as a discriminating taxon in the SIMPER analysis (Table 1).

The cover of bivalves was low on the 1 yr reef and declined significantly on the 1.5 yr reef ($p < 0.05$), where the benthos was dominated by turf. Bivalve cover increased and peaked on the 3.5 and 5.5 yr reefs, which had significantly more bivalves than all other reefs examined ($p < 0.05$ for all). The lowest bivalve cover was on the mature 25 yr old reef, which did not differ from the 31 yr artificial reef nor the natural reef.

In contrast to all other benthic variables which tended to decline with age, coral cover increased with the age of breakwaters. Coral coverage was virtually absent on 1 year old reefs with only one juvenile coral observed, but increased significantly on reefs 1.5 years old where they occupied 2.4 ± 0.4% of substrate ($p < 0.001$). Coverage increased significantly again on 5.5 year old reefs, as well as at each successive age ($p < 0.001$ for each). Coral cover was highest on the oldest reef (31 years of age), at 56.0 ± 1.4 %, and the rate of coral cover increase showed no indications of becoming asymptotic on older breakwaters. Natural reefs had 36.5 ± 1.7% cover, which was significantly higher than reefs ages 5.5 yr or less ($p < 0.001$), but was lower than the coral cover on mature 25 and 31 yr breakwaters.

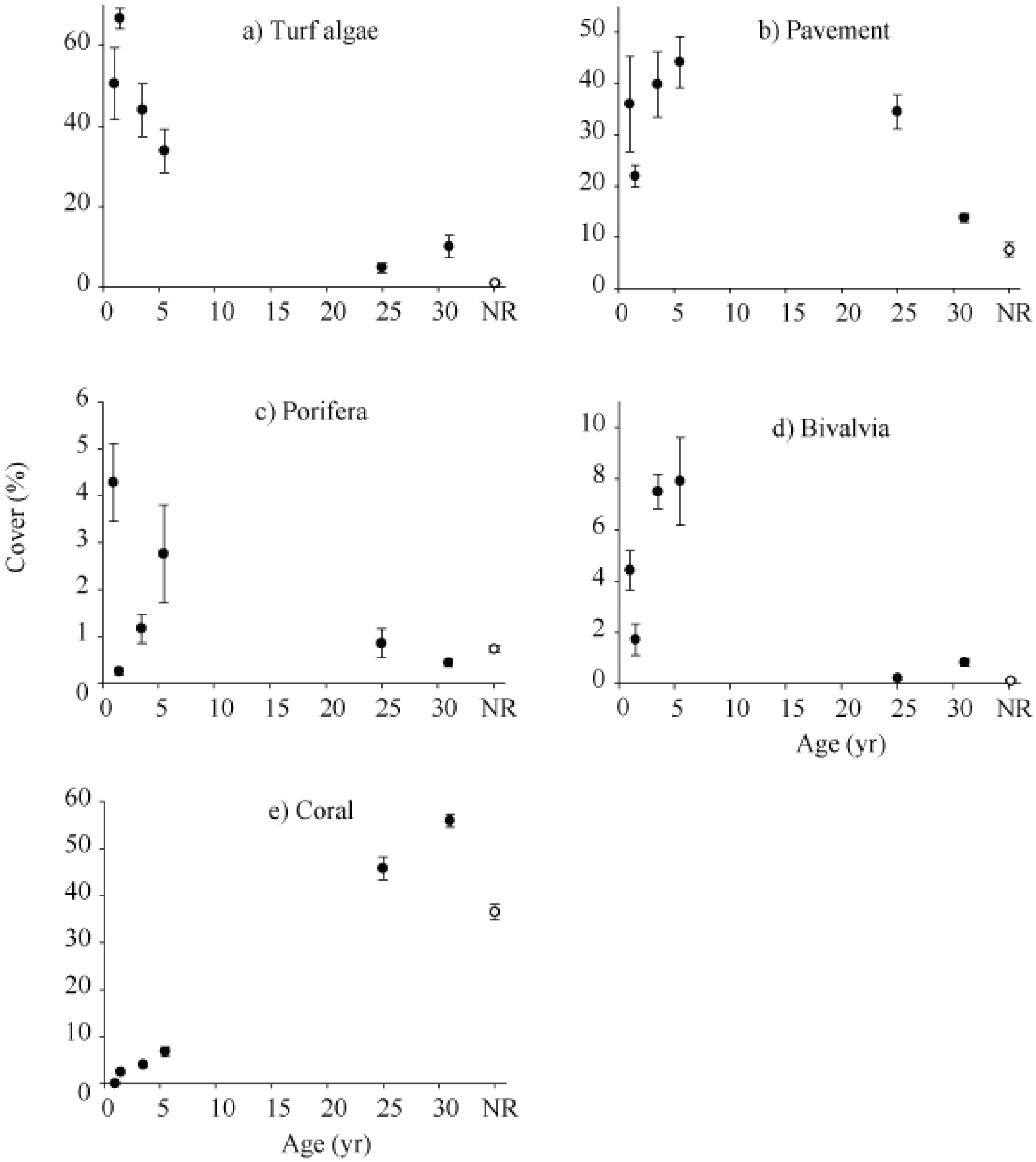

Figure 3: Mean percent cover (± SE) of benthic variables associated with breakwaters of different age (closed circles) and natural reefs (open circle; NR). Note difference in scale on vertical axis.

Discussion

The long-term development of benthic communities on the large-scale breakwaters is poorly understood, and is likely to be of increasing importance with urbanization of coastal marine ecosystems worldwide. Although early benthic development on recently submerged structures has been relatively well studied, there is inadequate knowledge of how benthic assemblages develop over the long-term and how they compare with natural reefs over time. The results of this study suggest that benthic communities associated with breakwaters continue to change over periods exceeding 31 years, and that while there is a general convergence in community structure towards that on natural reefs with increasing breakwater age, the overall benthic community remains distinct. However, like all natural experiments the results of this study are qualified. This is not a longitudinally temporal study but a one-time comparison of breakwaters that were constructed at different times in different physical and biological conditions. Although there appears to be general trends in community development among structures of different age in this study, long-term monitoring of community development on each breakwater would be necessary to determine the temporal and spatial consistency of these patterns.

The youngest artificial structures examined here were dominated by fouling organisms such as turf algae, bivalves, and sponges. Turf algae are among the earliest colonists on artificial structures, and are often dominant members of the benthos during the first few years (McClanahan 1997; Aseltine-Neilson et al. 1999; McClanahan et al. 2002). Here, turf algae cover was greater on 1.5 year old reefs, where it occupied over two-thirds of the substratum, than on 1.0 year old reefs or on reefs of greater age. This might suggest a temporal pattern in which algal abundance increases through at least the first 1.5 years of age, before declining. It is unlikely, however, that the spike in abundance on 1.5 yr reefs is related to age as much as differences in environmental conditions. Cover of turf algae is usually highest shortly after immersion, and cover generally declines within a few months and remains relatively stable for several years thereafter (McClanahan 1997; Bacchiocchi and Airoldi 2003). Instead, the high coverage of turf algae on the 1.5 yr reef was likely due to coastal reclamation occurring within several hundred meters of this location during sampling. The suspension of sediments during dredging is known to increase nutrient loads in the water column (Lohrer and Wetz 2003; Cao et al. 2007), and such nutrient pulses are associated with increased turf algae cover (McClanahan et al. 2002; McClanahan et al. 2003). The spike in turf algae was associated with a decrease in the amount of bare pavement available for colonization, and it is likely that competitive interference for settlement space explains the concomitant decrease in the abundance of sponges and bivalves on this 1.5 year old reef. Overall on the reefs younger than 5.5 years as a whole, changes in the abundance of bivalves generally reflect patterns of bivalve development on artificial structures elsewhere. Bivalves are often common members of the early benthic community (Perkol-Finkel and Benayahu 2005), and generally increase in dominance over the first several years on artificial structures (Hirata 1987; Aseltine-Neilson et al. 1999; Nicoletti et al. 2007). Bivalve cover peaked on the 3.5 and 5.5 year old reefs examined here, and then declined on older reefs. Similarly, sponge abundance was highest on the youngest artificial reef, and declined thereafter.

The decline in turf, bivalves, and sponges on the oldest breakwaters coincided with an increase in coral cover. Corals were virtually absent on the 1 yr old artificial reef with only a single juvenile observed, but increased to 2.4 ± 0.4% cover on a reef just six months older. This relatively rapid increase in coral cover on young breakwaters is not unusual. Although coral recruits are known to settle to artificial materials within a matter of months (Glassom et al. 2004; Abelson et al. 2005), they are rarely observed in situ on artificial structures during their first year likely as a result of their small size and cryptic habitat preference (Abelson and Shlesinger 2002; Lam 2003). However, observed densities generally increase rapidly within the first few months of the second year, as increased recruitment balances loss to mortality and the surviving juveniles grow to sufficient size for observation (Abelson and Shlesinger 2002; Lam 2003). Coral cover showed a near linear pattern of increase on reefs of subsequent age, with no indication of asymptote through 31 years in this study. Abelson and Shlesinger (2002) observed a similar linear increase in coral colonies over an eight year period on artificial reefs in the Red Sea. However, a series of studies of other artificial reefs in the Red Sea indicate that hard coral cover does tend to plateau over time. There, hard coral cover was 5.7% on 10 year old reefs (Perkol-Finkel and Benayahu 2005), increasing to 16.6% on 14 year old reefs (Perkol-Finkel and Benayahu 2004), but stabilizing on seven reefs ranging from approximately 20 to over 100 years of age (mean: 33.4%; Perkol-Finkel et al. 2005). The lack of such an asymptote on reefs studied here may be due to reduced competition for space. In the Red Sea, soft corals preferentially recruit to artificial structures (Perkol-Finkel and Benayahu 2007), and their cover increases significantly with age (Perkol-

Finkel et al. 2005), frequently resulting in soft coral dominance on these man-made structures (Perkol-Finkel and Benayahu 2004). The competition for space between soft and hard corals may explain the asymptotic cover of hard corals on older artificial structures in the Red Sea. However, soft corals do not exists in the study area examined here (Riegl 1999), and the absence of these competitive interactions may have allowed the continued increase in hard coral cover on older breakwaters examined here. However, a variety of other mechanisms could also be involved in developing these patterns, and ascribing cause and effect would be speculative. Regardless of cause, there has been no plateau in coral cover up to 31 years on breakwaters, and coral cover on the 31 year old breakwater is higher than on the nearby natural reef suggesting that it may continue to increase on more mature breakwaters.

Overall, the change in benthic communities on reefs of different age suggests a progressive convergence towards assemblages on natural reefs. It has been suggested that at least ten years are required for artificial structures to develop communities comparable to natural reefs (Aseltine-Neilson et al. 1999; Abelson and Shlesinger 2002; Perkol-Finkel and Benayahu 2005). However, even the oldest 31 year old reef had a community distinct from those on natural reefs in this study. Although cover of turf, bivalves, sponges and bare pavement were comparable between the oldest artificial reef and the natural reefs, there was significantly higher coral cover on the mature artificial reef and this is driving multivariate differences between communities on these reef types. It is unknown whether coral cover will ever be comparable among these types of reef. These natural reefs are in a low-relief area with substrates dominated by mobile sands and silts (Chapter 2; Riegl 1999) while the high-relief rocky breakwaters provide substantial opportunity for coral settlement, presumably with lower impacts from sedimentation stress. These habitat associated differences may result in continued divergence of natural reef and mature breakwater coral communities in this area as corals develop higher cover on breakwaters. In addition, the planned development of coastal real estate, ports, and desalination facilities near the natural reefs (Rezai et al. 2004) are likely to contribute to further divergence of these communities.

The results of this study must be interpreted with caution. Although it appears that successional changes in benthic communities on breakwaters are resulting in a convergence towards those on natural reefs, the results are based on a single point in time. While it is possible that there is a spatially and temporally consistent sequence of community change taking place on these breakwaters, it is also possible that large-scale changes in hydrodynamics, nutrient loads, and other environmental parameters resulting from the extensive coastal developments in this area will result in divergent successional trajectories for benthic communities on reefs constructed at different points in time. Long-term monitoring of each artificial reef would be required to fully understand the dynamics of community change over time, with manipulations required to identify causal processes driving community development. Our continuing study of these communities will begin that these analyses.

References

Abelson A, Shlesinger Y (2002) Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. ICES J Mar Sci 59:122-126

Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: Temporal and spatial variation, and possible effects of anthropogenic disturbances. Mar Pollut Bull 50:576-582

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52:1073-1087

Aseltine-Neilson D, Bernstein B, Palmer-Zwahlen M, Riege L, Smith R (1999) Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. Bull Mar Sci 65:37-57

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuar Coast Shelf Sci 56:1157-1166

Baine M (2001) Artificial reefs: A review of their design, application, management and performance. Ocean & Coastal Management 44:241-259

Bulleri F (2005a) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Mar Ecol Prog Ser 287:53-65

Bulleri F (2005b) Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. Mar Environ Res 60:355-374

Cao XY, Song CL, Li QM, Zhou YY (2007) Dredging effects on P status and phytoplankton density and composition during winter and spring in Lake Taihu, China. Hydrobiologia 581:287-295

Clarke K, Gorley R (2006) PRIMER v6: User Manual. PRIMER-E Ltd, Plymouth, UK

Clynick BG (2006) Assemblages of fish associated with coastal marinas in north-western Italy. J Mar Biol Assoc U K 86:847-852

Clynick BG, Chapman MG, Underwood AJ (2008) Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecol 33:140-150

Crossman D, Choat J, Clements K, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 46:1596-1601

Diamond J (1986) Overview: laboratory experiments, field experiments and natural experiments. In: Diamond J, Case T (eds) Community Ecol. Harper & Row, New York, pp3-22

Elliott J, Elliott J, Mariscal R (1995) Host selection, location, and association behaviours of anemone fishes in field settlement experiments. Mar Biol 122

Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar Biol 144:641-651

Guidetti P, Verginella L, Odorico C, Boero F (2005) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. Journal of the Marine Biological Association of the UK 85:247-255

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75:12-13

Hartney K, Grorud K (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia 131:506-513

Hirata T (1987) Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan. 2. Succession of invertebrates. Mar Ecol Prog Ser 38:25-35

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geoscience 32:1259-1269

Lam K (2003) Coral recruitment onto an experimental pulverised fuel ash-concrete artificial reef. Mar Pollut Bull 46:642-653

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bull Mar Sci 55

Lohrer AM, Wetz JJ (2003) Dredging-induced nutrient release from sediments to the water column in a southeastern saltmarsh tidal creek. Mar Pollut Bull 46:1156-1163

McClanahan T (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reef. J Exp Mar Biol Ecol 218:77-102

McClanahan TR, Cokos BA, Sala E (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. Mar Pollut Bull 44:441-451

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones SH (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar Ecol Prog Ser 261:135-147

McCune B, Mefford M (1999) PC-ORD: Multivariate analysis of ecological data. MjM Software Design, Gleneden Beach, OR

McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52:1053-1071

Nicoletti L, Marzialetti S, Paganelli D, Ardizzone GD (2007) Long-term changes in a benthic assemblage associated with artificial reefs. Hydrobiologia 580:233-240

Nishizaki MT, Ackerman JD (2004) Juvenile-adult associations in sea urchins *Strongylocentrotus franciscanus* and *S. droebachiensis*: Is nutrition involved? Mar Ecol Prog Ser 268:93-103

Osman R, Whitlatch R (2004) The control of the development of a marine benthic community by predation on recruits. J Exp Mar Biol Ecol 311:117-145

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23:195-205

Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Mar Environ Res 59:79-99

Perkol-Finkel S, Benayahu Y (2007) Differential recruitment of benthic communities on neighboring artificial and natural reefs. J Exp Mar Biol Ecol 340:25-39

Perkol-Finkel S, Shashar N, Barneah O, Ben-David-Zaslow R, Oren U, Reichart T, Yacobovich T, Yahel G, Yahel R, Benayahu Y (2005) Fouling reefal communities on artificial reefs: does age matter? Biofouling 21:127-140

Pondella D, Stephens J, Craig M (2002) Fish production of a temperate artificial reef based on the density of embiotocids. ICES J Mar Sci 59:S88-S93

Qian P (1999) Larval settlement of polychaetes. Hydrobiologia 402:239-253

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson C (ed) Status of coral reefs of the World: 2004. Australian Institute of Marine Science, Townsville, pp155-169

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18:63-73

Riegl B (2002) Phoenix from the ashes? Repetitive mass mortality and the biogeology of southern Arabian Gulf (United Arab Emirates) coral systems. The Vienna School of Marine Biology:137-159

Sheppard C, Price A, Roberts C (1992) Marine ecology of the Arabian region: patterns and processes in extreme tropical environments. Academic Press, Toronto

Smit F, Mocke G, Al-Zahed K (2005) Quantifying and managing the coastal response to major offshore developments in Dubai. Proceedings of the 14th Biennial Coastal Zone Conference, New Orleans, Louisiana. NOAA Coastal Services Center

Stephens J, Pondella D (2002) Larval productivity of a mature artificial reef: the ichthyoplankton of King Harbor, California, 1974-1997. ICES J Mar Sci 59:S51-S58

Svane I, Peterson J (2001) On the problems of epibioses, fouling and artificial reefs, a review. Mar Ecol 22:169-188

Tabachnick B, Fidell L (2001) Using multivariate statistics. Allyn and Bacon, Needham Heights MA

Chapter 4: A comparison of natural reefs with large, mature artificial reefs

Introduction

Artificial reefs are often used to mitigate impacts from human activities in coastal ecosystems and to enhance commercial fisheries yield (Svane and Peterson 2001). They are rapidly colonized and usually develop fish and benthic communities with comparable or higher abundance and diversity than surrounding natural reefs (Bohnsack et al. 1994; Lincoln-Smith et al. 1994; Stephens et al. 1994; Pickering and Whitmarsh 1997; Rilov and Benayahu 2000; Pondella et al. 2002; Perkol-Finkel and Benayahu 2004). Artificial reefs may enhance regional biomass and production of commercial fisheries species by providing structure in areas where habitat is not present or is the limiting factor controlling populations (Polovina and Sakai 1989; Bohnsack et al. 1997; Carr and Hixon 1997; Pickering and Whitmarsh 1997), or by creating new foraging opportunities for roving predators (Bohnsack et al. 1994). However, clear evidence in support of using artificial structures for production enhancement is limited, and many artificial reefs may simply attract fish from the surrounding natural area (Bohnsack 1989; Bohnsack et al. 1994; Grossman et al. 1997; Pickering and Whitmarsh 1997). Attraction and aggregation of fish on artificial reefs can be problematic, as concentrated fishing efforts near artificial reefs could ultimately lead to declines in local populations (Bohnsack et al. 1997; Grossman et al. 1997). In addition, artificial reefs could potentially decrease regional productivity if they attract juvenile settlers that would have had better survivorship on natural reefs (Carr and Hixon 1997). Using artificial reefs to mitigate loss of natural reef habitat is also problematic, as artificial reef communities can differ markedly from the natural reef communities they are built to restore or rehabilitate (Clark and Edwards 1999; Rilov and Benayahu 2000).

Artificial reefs must be compared with natural reefs if we are to assess their performance in meeting management goals and to understand their ecological role in the marine environment (Carr and Hixon 1997). Comparisons of community structure in the form of species composition and abundance can lead to an understanding of whether artificial reefs can act as replacements for natural reefs for mitigation purposes, while comparing functional community attributes such as recruitment patterns and size-class distribution can indicate whether artificial reefs are enhancing production (Carr and Hixon 1997).

Many previous comparisons of artificial and natural reef communities have been confounded by inappropriate experimental design. Comparisons with natural reefs have often used small artificial structures covering only a few square meters of area (Bohnsack et al. 1994; Carr and Hixon 1997; Connell 1997b; Tupper and Hunte 1998; Abelson and Shlesinger 2002), where results are likely biased by size-related differences in diversity and abundance, as well as biased functional responses in predation pressure, recruitment patterns, and migration (Bohnsack et al. 1994; Connell 1997b; Tupper and Hunte 1998). It is also likely that small artificial reefs will have negligible impact on local fisheries production given their limited volume relative to natural reef habitats (Bohnsack et al. 1997). In addition to size, the age of the artificial reefs is also of importance but has frequently not been considered. Many comparisons to natural reefs have focused on artificial structures deployed for less than three years (Bohnsack et al. 1994; Connell 1997b; Tupper and Hunte 1998; Clark and Edwards 1999; Badalamenti et al. 2002; Chapman and Clynick 2006). Such structures will be dominated by fouling organisms during the initial stages of development (Perkol-Finkel et al. 2006), and benthic communities will continue changing for several years (Aseltine-Neilson et al. 1999; Perkol-Finkel and Benayahu 2005), perhaps taking decades to mature (Clark and Edwards 1999; Perkol-Finkel et al. 2005). Associated fish communities are also likely to change during this period due to obligate requirements for particular benthic organisms as food, shelter, or settlement habitat, making comparisons to established natural reefs during such early developmental stages premature and inappropriate.

There is increasing recognition that man-made coastal defense structures such as breakwaters and sea-walls can act as large-scale unplanned artificial reef habitat (Svane and Peterson 2001; Bulleri 2005c). Although not designed to mitigate damage to natural reefs or enhance fisheries, they nonetheless provide significant hard-bottom habitat and three-dimensional structure in developed coastal areas, particularly compared with small-scale, purpose-built artificial reefs, and they are likely to become increasingly common as human populations grow. As such, there is an interest in determining the ecological role that these artificial reefs play in coastal ecosystems (Lincoln-Smith et al. 1994; Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Moschella et al. 2005).

Such man-made rocky reefs are now an important part of the coastal environment in Dubai, United Arab Emirates. Here, approximately 200 km of man-made shoreline have been added to the 50 km of natural sandy coast, with over by 65 km of protective rocky breakwaters substantially increasing the amount of hard-bottom habitat in this area. The addition of this large-scale artificial habitat may be particularly important in Dubai as natural reefs are restricted to a series of discontinuous patch reefs isolated to a 10 km near-shore band in western Dubai, and the remaining coastal area is dominated by mobile sands and silt unsuitable for most hard-bottom organisms (Chapter 2; Riegl 1999). While some of these breakwaters have impacted natural coral reef habitat (Chapter 2), most were constructed in sand habitats with limited three dimensional structure.

Coastal defense structures can potentially increase the regional production of reef-associated fauna. By adding a substantial volume of hard-bottom habitat in areas with relatively little natural reef, these breakwaters may capture dispersive larvae of reef fauna that may otherwise have been lost to high planktonic mortality or advection away from suitable settlement habitats (Carr and Hixon 1997). This may be particularly applicable to these breakwaters as there are natural reefs up-current in Dubai and Abu Dhabi (Riegl 2002a; EWS-WWF 2008), and no significant natural reefs down-current from them (Riegl 1999).

The aim of this study is to determine whether the coral and fish communities that develop on large breakwaters that have been in place for decades are comparable to those on natural reefs. This has important implications for marine management, as such structures may inadvertently mitigate impacts from coastal development if communities are comparable or they may enhance local diversity and abundance over the long term. A further goal of this study is to compare seasonal changes in fish abundance, recruitment, and age-class structure on artificial and natural reefs to determine whether functional attributes of the fish community are comparable between reef types. Such information is essential for understanding whether or not artificial reefs function similarly to natural reefs, and whether they may be enhancing fish production.

Methods

This study was conducted in Dubai, United Arab Emirates, in the south-eastern basin of the Persian Gulf. The sea bottom is typically shallow (<10 m) and low relief, with soft-bottom, mobile sands covering most of the area. Hard substrate suitable for corals is found in areas with naturally emergent limestone caprock, as well as on numerous rocky breakwaters along the coastline. Natural patch reefs are found within 1 km of shore along the western 10 km of Dubai where emergent caprock exists, and generally cover areas of 1,500 – 2,500 m^2 each. Six natural reef sites were sampled in this study, along with a pair of sites on each of two breakwaters (Figure 1). The 2.8 km long Jebel Ali port breakwater was built in 1977 and is composed of approximately 420,000 m^3 of 2 m wide concrete tetra-foil jacks, while the dry dock breakwater is made of approximately 400,000 m^3 of 1 m^3 gabbro rock blocks and was constructed in 1982. Overall depth to the natural substrate was comparable between natural and artificial reefs (4 – 9 m), and sampling was standardized at approximately 5 m depth for all sites, with only the windward face of breakwaters sampled.

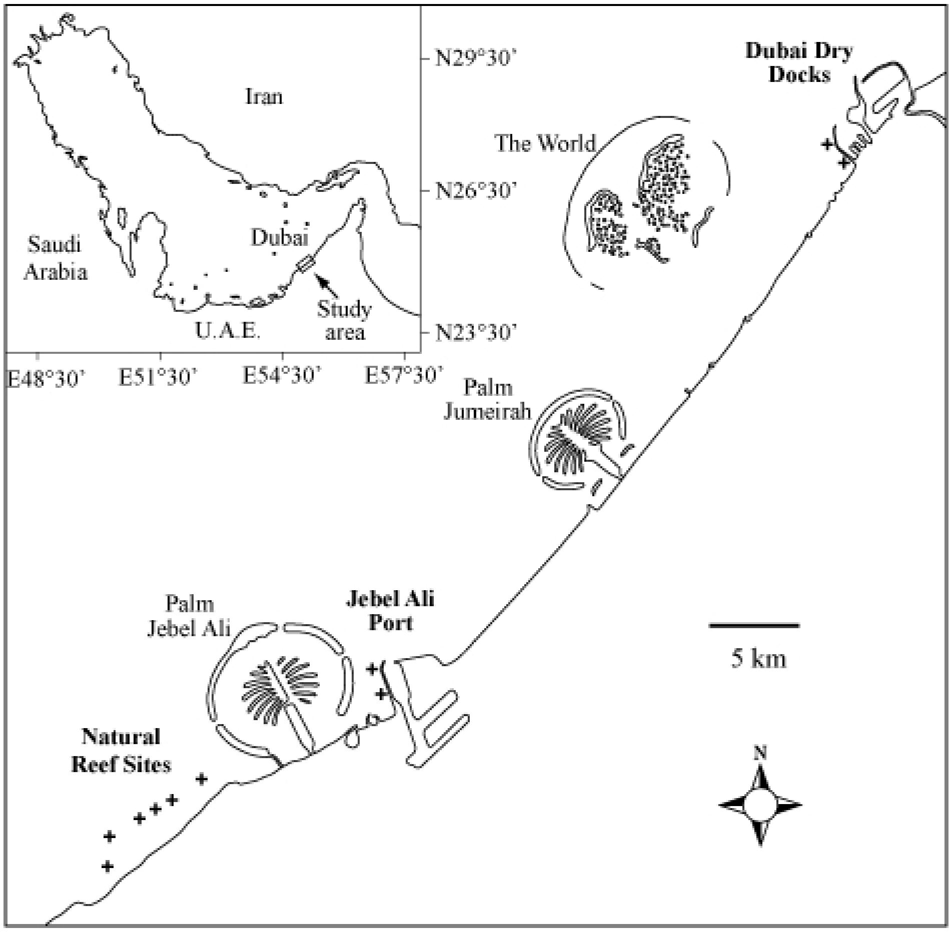

Figure 1: Map illustrating coral and fish sampling sites, with location names in bold. Other structures were not included in this study due to their relatively young (< 5.5 year) age.

Coral sampling was conducted in October 2006. At each site, six replicate 30 m line transects were photographed at 1.5 m intervals using a SeaLife DC500 5.0 mega-pixel camera mounted on a PVC frame, for a total of 126 quadrats per site. Each photo-quadrat enclosed a 0.25 m^2 area. Images were analyzed with 50 randomly placed points using CPCe, version 3.4 (Kohler and Gill 2006). Fish were sampled quarterly from October

2006 to July 2007 to allow examination of seasonal changes in abundance. Abundance was visually estimated from twelve replicate 1 m wide and 30 m long belt transects, with all fish within 1.5 m above the substrate included. Width of transects was estimated with the use of a 1 m hand-held T-bar and speed was maintained at approximately 6 m min^{-1} while maintaining height at approximately 50 cm above the substrate. Fish were categorized as juveniles, sub-adults, or adults where appropriate based on distinguishing characteristics described in Randall (1995).

Coral coverage from quadrats was pooled for each transect. Mean coverage of corals and density of fish (10 m^{-2}) from each site were calculated from transects. Coral data were arc-sine square-root transformed and fish data $\log_{(n+1)}$ transformed to normalize the data prior to analysis. Species occurring in less than 5% of samples were removed prior to multivariate analyses.

Both multivariate and univariate techniques were used to compare coral and fish assemblages on natural and artificial reef sites. Non-metric multidimensional scaling (NMS) on relative Sorenson (i.e. Bray-Curtis) distances was used to provide a graphical depiction of communities on natural and artificial reefs. The NMS autopilot mode of PC-ORD (McCune and Mefford 1999) performed a Monte Carlo significance test on the best of 40 runs of real data with 50 runs of randomized data to optimize the number of axes. To illustrate the strength and direction of correlation of species with ordination axes, joint plots of species were superimposed on overall coral and overall fish community ordinations. Only species with a Pearson's $r > 0.40$ were included in the joint plot. Successional vectors were overlaid on an ordination of fish communities from the entire sampling year to illustrate gross seasonal changes in community structure, and ordination of fish communities was subsequently performed separately for each season. To ease interpretation, all ordinations were rotated to load reef type on the first axis.

The significance of differences between natural and artificial reef groups illustrated in ordinations was calculated using non-metric Multi-response Permutation Procedure (MRPP). This is a non-parametric procedure for testing the hypothesis of no difference between community groups, and is particularly compatible with NMS results. The effect size, A, ranges from $A = 0$, when the heterogeneity within groups is equal to that expected by chance, to $A = 1$ when all samples are identical in a group. In community ecology, $A < 0.1$ is common and $A \geq 0.3$ is considered fairly high (McCune and Grace 2002). Indicator species analysis (Dufrene and Legendre 1997) was used to identify species which had significant affinity for either natural or artificial reefs. This method calculates an indicator value based on a species' relative abundance and fidelity in a group. This value ranges from 0 to 100, where 100 indicates a species is present at all sites in that group, and is not found elsewhere.

One-way ANOVA were used to compare mean coral richness, overall coral cover, and cover of dominant coral species identified from multivariate analysis among reef types. Shannon Wiener diversity was compared using a Shannon *t*-test. For fish, interactions between reef type and season were assessed using two-way ANOVA on mean richness, overall abundance, and abundance of dominant species, juveniles, and piscivores. Post hoc analysis unequal N HSD tests were used to identify different groups where ANOVA found significant differences among groups. Shannon Wiener diversity of fish was compared among reef types seasonally using pair-wise Shannon *t*-tests.

During the course of this study (April 2007), three of the natural reef sites were destroyed by the construction of a causeway. As a result, fish data were available only for fall, winter, and spring at one site, and fall and winter at two sites. This incident would have no impacts on benthic data, as sampling had occurred several months earlier. To assess the impacts of the loss of these sites on fish data, preliminary analyses were performed with the three impacted sites excluded. This analysis gave the same general results as using all six sites (MRPP $A = 0.26$ and 0.27, respectively; $p < 0.001$ for both), so data from all sites were retained to enhance the precision of estimates. Only sites with data for the entire year were included in successional vector diagrams as the purpose was to illustrate seasonal changes in communities at each site over a full year. To account for differences in sample sizes among natural and artificial reefs, post-hoc unequal-N HSD tests were used for comparisons for univariate analyses of fish data.

Results

<u>*Coral communities*</u>

Diversity measures and overall coral cover for the 30 species of coral observed on natural and artificial reefs are listed in Table 1. Overall, natural reefs contained a higher total number of coral species but there was no difference in mean species richness between reef types (ANOVA: $F_{(1)} = 4.1$). However, natural reefs did have significantly higher Shannon-Wiener diversity than artificial reefs (Shannon *t*-test: $p < 0.01$), reflecting higher evenness and richness on natural reefs compared with artificial reefs (Natural reef E: 0.63; Artificial reef E: 0.50). On artificial reefs, three dominant species made up over three-quarters of coral cover, *Cyphastrea microphthalma* (42% of coral cover), *Platygyra daedalea* (20%), and *Porites lutea* (14%), while relative abundance and composition differed on the natural reef, with three quarters of cover made up by five species: *P. lutea* (23% of coral cover), *Porites harrisoni* (22%), *C. microphthalma* (14%), *Acropora downingi* (9%), and *Acropora clathrata* (8%). Artificial reefs contained 50.0 ± 3.3% coral cover, which was significantly higher than the 30.7 ± 5.5% coral cover on the natural reefs (ANOVA: $F_{(1)}=5.4$, $p < 0.05$).

Table 1: Coral richness (S), diversity (H'), and substrate coverage (%) on sites from natural and artificial reefs. The α symbol indicates significant difference at $p < 0.05$.

Reef Type	Total Richness	Mean Richness	Diversity (H')	Coral cover (%)
Natural	29	23.6 ± 1.7	$2.3 \pm 0.1^{\alpha}$	30.7 ± 5.5
Artificial	20	18.8 ± 1.4	1.8 ± 0.1	$50.0 \pm 3.3^{\alpha}$

Multivariate analyses indicated strong differences between coral communities on natural and artificial reefs, as illustrated by separation of reef types in ordination (Figure 2). A two-dimensional representation provided a significant reduction in stress compared with randomized data (Real 2-D stress: 4.4, Stress in randomized data: 26.8; $p < 0.05$), and adding a third dimension did not improve stress significantly. The axis aligned with reef type explained 48% of the variation. Pearson's correlation indicated strong association between several coral species and artificial reefs on Axis 1, *C. microphthalma* (r=0.96), *P. daedalea* (r=0.83), and *Siderastrea savignyana* (r=0.79). These species were also found to be significant indicator species for artificial reefs (Indicator Value (IV)=71.9, $p < 0.01$; IV=74.3, $p < 0.05$; and IV=78.7, $p < 0.05$, respectively), indicating a strong affinity for this reef type. Natural reefs were strongly correlated with *A. downingi* (Pearson's r = -0.61), *P. harrisoni* (r = -0.57), and *Pseudosiderastrea tayamai* (Pearson's r = -0.50), and *P. tayamai* was also a significant indicator species on natural reefs (IV=83.2; p <0.01). MRPP analysis supported the groupings identified by ordination, showing that the coral communities on natural reefs and artificial reefs were significantly different groups (A = 0.27, $p < 0.01$). The second axis, representing 46% of the variation, was related to compositional differences among natural reefs. Sites spread on this axis were strongly correlated with *A. downingi* (Pearson's r = 0.83), *P. harrisoni* (r=0.80), and *A. clathrata* (r=0.78), or moderately with *P. lutea* (r = -0.48). The spread of natural reef sites on this axis contrasts with the tight clumping of artificial reef sites, indicating that natural reef sites were more dissimilar to one another than artificial reef sites on this axis. This reflects results of earlier studies which have found that there are several distinct coral assemblages associated with these natural reef sites (Chapter 3; Riegl 1999)

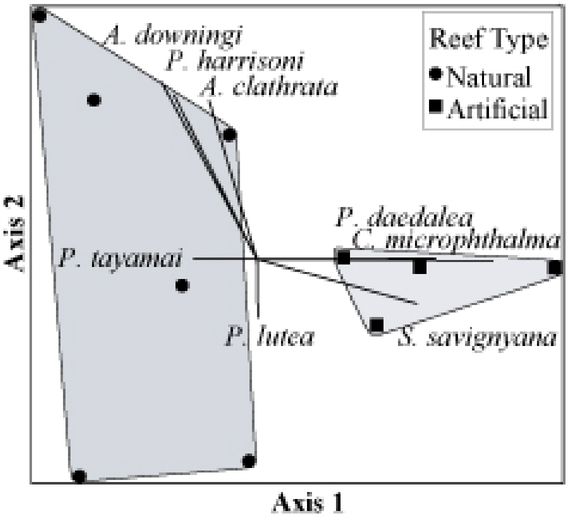

Figure 2. Ordination of natural and artificial reef sites in coral species space, with joint plot of coral species. The relative strength and direction of a species' correlation with the ordination is indicated by the radiating lines.

The composition of each reef type was compared using species found to have strong affinity with either reef type during multivariate analysis (above). ANOVA showed that cover of *A. downingi* and *P. harrisoni,* species associated with natural reefs in multivariate analysis, did not differ significantly from their cover on artificial reefs ($F_{(1)}$=1.9 and 0.4, respectively). However, natural reefs did contain significantly more *Pseudosiderastrea tayamai* ($F_{(1)}$=9.6, $p < 0.05$). Artificial reefs contained significantly more *C. microphthalma*, *P. daedalea*, and *S. savignyana* than were observed on natural reefs ($F_{(1)}$=31.9, 21.9, and 24.1, respectively, $p < 0.01$).

Fish communities

Diversity measures for the 56 species of fish observed on natural and artificial reefs over the entire year are listed in Table 2. Overall, although artificial reefs contained a higher total number of fish species during the year of sampling, mean species richness and Shannon-Wiener diversity did not differ between reef types when averaged for the four seasons (Richness: ANOVA $F_{(1)} = 2.7$; Diversity: Shannon *t*-test: $p = 0.9$). Seasonal changes in fish richness and diversity are illustrated in Figure 3. Two-way ANOVA of mean richness indicated that there was a significant interaction between reef type and season ($F_{(3)}=6.1$, $p < 0.01$). Seasonally, richness was stable on natural reefs (ANOVA $F_{(3)}=0.3$), but varied significantly on artificial reefs (Figure 3a; ANOVA $F_{(3)}=25.4$, $p < 0.001$). Unequal-N HSD tests showed significantly lower richness in the winter and spring than both fall and summer on artificial reefs, with summer having significantly higher mean richness than all other seasons ($p < 0.05$ for all). However, pair-wise comparisons of Shannon-Wiener diversity (*H'*) within and among reef types and season (Figure 3b) showed no significant differences (Shannon *t*-tests, $p > 0.05$ for all), indicating that although richness was higher on artificial reefs in summer, evenness was low.

Table 2: Fish richness (*S*) and diversity (*H'*) on natural and artificial reefs. Means based on the average from four seasons (mean ± SE).

Reef Type	Total Richness	Mean Richness (*S*)	Mean Diversity (*H'*)
Natural	40	17.6 ± 0.6	2.5 ± 0.3
Artificial	51	19.8 ± 1.3	2.6 ± 0.4

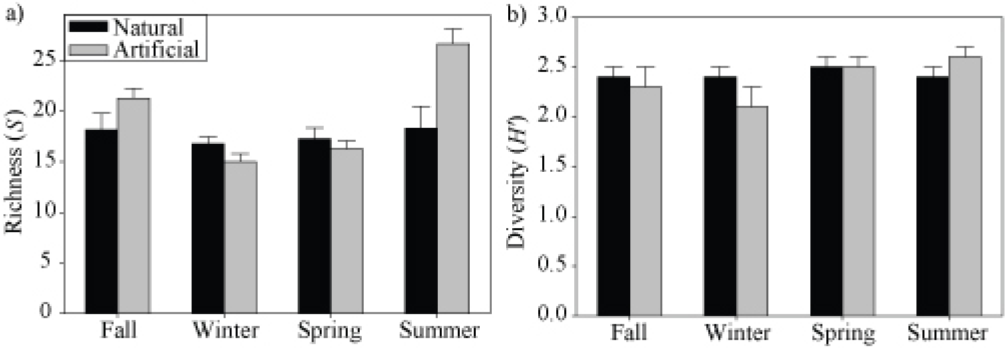

Figure 3. Fish richness (a) and diversity (b) on natural and artificial reefs by season (mean ± SE).

Indicator species analysis indicated that there were seasonal changes in the species that were associated with each reef type. During the fall and summer seasons there were a number of species with significant affinities for each reef type, while there were no species with significant indicator values during the winter and spring seasons (Table 3). Because significant indicator values demonstrate a species relative abundance and fidelity for a group, this indicates that while a number of species were strongly associated with a particular reef type during the fall and/or summer, these species were not strongly associated with either reef during the winter and spring. Only one of the 16 indicator species, *Pomacentrus leptus*, was found to switch habitats during the year, being significant on natural reefs in the fall and then artificial reefs the following summer. All other indicator species showed fidelity for one particular reef type across seasons.

Table 3: Seasonal indicator values for species with affinity for natural or artificial reefs. Only species with significant ($p < 0.05$) indicator values are listed.

Reef Type	Fish Species	Fall	Winter	Spring	Summer
Natural	*Cryptocentrus lutheri*	93%	None	None	
	Halichoeres stigmaticus				100%
	Lutjanus fulviflamma	84%			
	P. leptus	83%			
Artificial	*Cheilodipterus novemstriatus*	70%	None	None	96%
	Ecsenius pulcher	82%			
	Carangoides bajad	100%			
	Chaetodon nigropunctatus	75%			75%
	Lutjanus ehrenbergii	90%			82%
	Pomacenthus maculosus	76%			74%
	Abudefduf vaigiensis				100%
	P. leptus				96%
	Pomacentrus trichourus				98%
	Scarus ghobban				100%
	Siganus canaliculatus	75%			
	Acanthopagrus latus	75%			100%

Ordination of fish communities associated with natural and artificial reef sites throughout the sampling period indicated differences between reef types (Figure 4a; Stress: 12.7, $p < 0.05$). The first axis was aligned with reef type and explained 49% of the variation in fish communities. Pearson's correlation indicated that the Arabian monocle bream, *Scolopsis taeniatus* ($r = -0.53$), was strongly associated with natural reefs, and the sordid sweetlip, *Plectorhinchus sordidus* ($r = -0.45$), and Luther's shrimpgoby, *C. lutheri* ($r = -0.48$), moderately so. Species strongly associated with artificial reef sites included the

Ehrenberg snapper, *L. ehrenbergii* ($r = 0.80$), the pale-tail damsel, *P. trichourus* ($r = 0.75$), the dark butterflyfish, *C. nigropunctatus* ($r = 0.70$), the twospot cardinalfish, *C. novemstriatus* ($r = 0.68$), and the Arabian angelfish *P. maculosus* ($r = 0.54$). These species were also been significant indicator species for artificial reefs, above (Table 3). MRPP analysis of natural and artificial reefs supported ordination results, showing significant difference between these groups ($A = 0.20$, $p < 0.001$). The second axis explained 41% of the variation and was mainly associated with the abundance of the dark damsel, *Pomacentrus aquilus* (Pearson's $r = 0.71$).

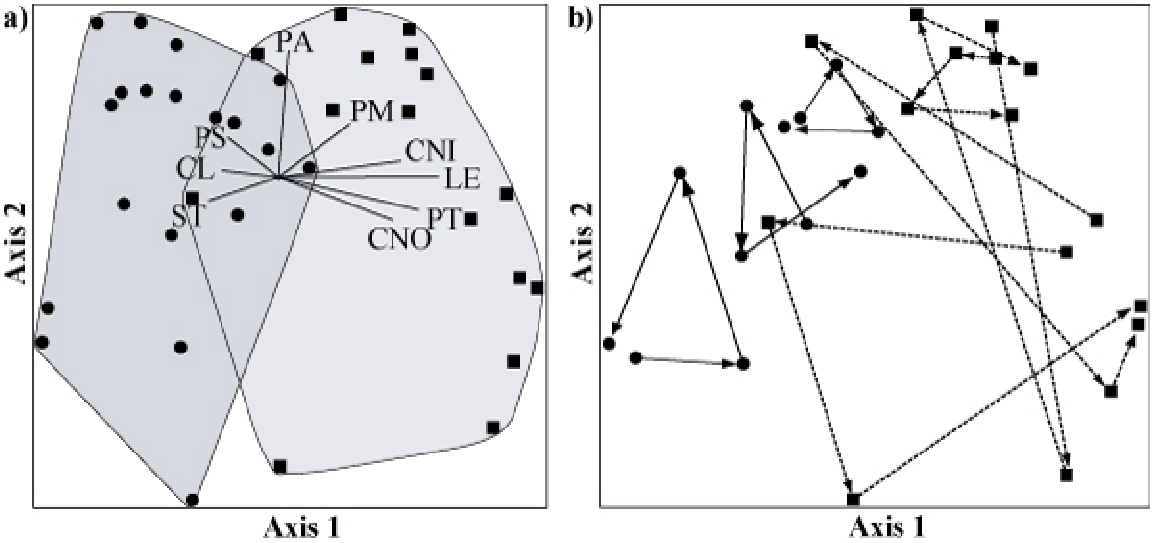

Figure 4. Ordination of fish communities on natural (●) and artificial (■) reef sites. (a) Fish communities at each site over the entire sampling period, with a joint plot of fish species (Stress: 12.7). Radiating lines indicate the relative strength and direction of correlation of each species with the ordination. (b) Fish communities at natural and artificial reef sites with successional vectors connecting consecutive sampling seasons (in series as Fall, Winter, Spring, Summer) (Stress: 11.4). Solid line and circles: natural reefs; dashed line and squares: artificial reefs. Species codes: PA: *P. aquilus*, PM: *P. maculosus*, CNI: *C. nigropunctatus*, LE: *L. ehrenbergii*, PT: *P. trichourus*, CNO: *C. novemstriatus*, ST: *S. taeniatus*, CL: *C. lutheri*, PS: *P. sordidus*.

Successional vectors were combined with ordination to examine the temporal changes in fish communities throughout the sampling year (Figure 4b; Stress: 11.4, $p < 0.05$). This analysis was limited to sites which had been sampled over the entire year. The ordination provided a significant reduction in stress over randomized data (Stress: 11.4 vs. 21.2 for randomized data, $p < 0.05$), with the axis aligned with reef type (Axis 1) representing 55% of the variation. All sites, both on natural and on artificial reefs, showed community change during the year, with fish communities at each site showing most dissimilarity during the winter and spring, while summer samples returned to communities similar to those seen the previous fall. However, there appeared to have been substantial differences in the amount of community change over the year on natural and artificial reefs. The relatively tight clustering of each natural reef site indicates limited changes in fish communities with seasons, while the wide spacing between seasons on most artificial reef sites indicates substantial changes in community structure throughout the year. In addition, successional vectors indicated that artificial reef communities were dissimilar from natural reefs in the fall and the summer, but shifted towards natural reef communities through the winter and/or spring. Overall, these successional vectors indicate larger excursions in community structure on artificial reefs over the course of the year compared with natural reefs, but that each reef community tended to return to similar structure in the summer to what was observed the previous fall.

Seasonal changes in fish communities were further examined by comparing natural and artificial reefs during each sampling period. Plots of fish communities by season indicated that the strength of differences between natural and artificial reefs changed through the year (Figure 5). During the fall, fish assemblages on natural and artificial reefs clearly separated from each other, and were significantly different (Figure 5a; MRPP: $A = 0.38$, $p < 0.01$). Communities on natural and artificial reefs converged during the winter and spring (Figure 5b,c), resulting in no significant difference as a result of increased similarity (MRPP, Winter: $A = 0.03$, $p > 0.05$, Spring: $A = 0.08$, $p > 0.05$). However, with the onset of summer fish communities on natural and artificial reefs again diverged from one another, becoming significantly different (Figure 5d; MRPP: $A = 0.27$, $p < 0.05$).

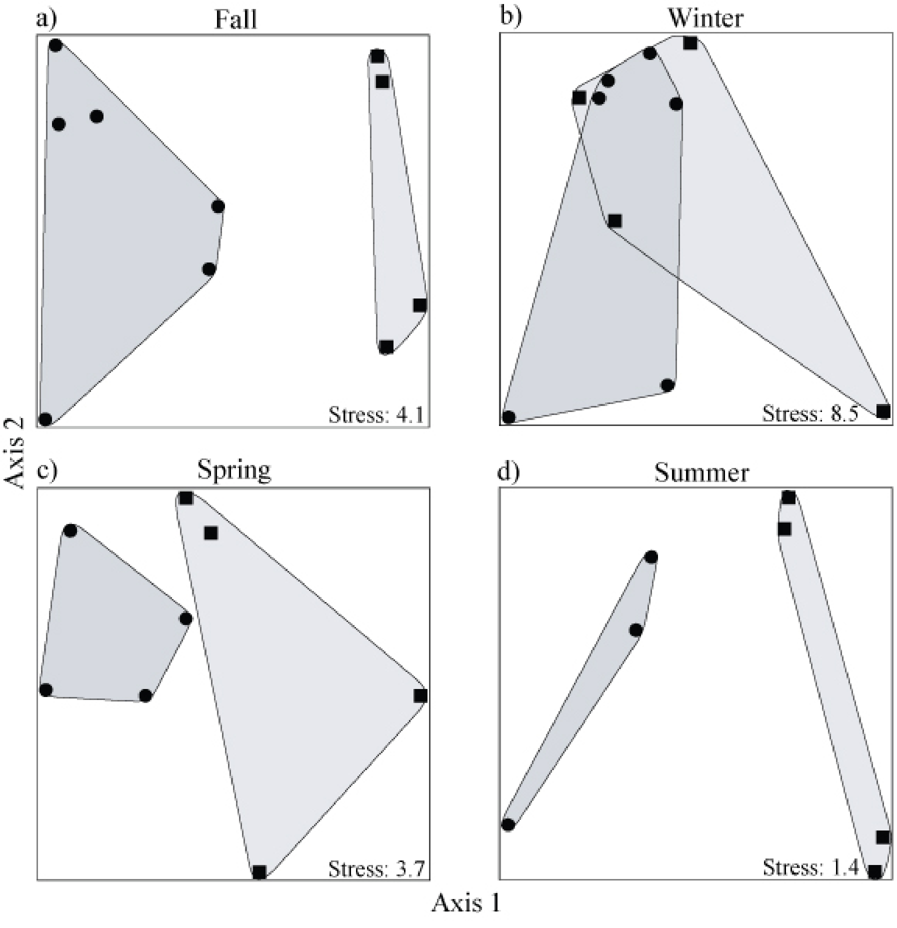

Figure 5. Ordinations illustrating seasonal changes in similarity of in fish communities on natural (●) and artificial (■) reefs.

Because multivariate analysis had indicated important seasonal changes in communities, univariate techniques were used to examine the relative contribution of different life stages to seasonal changes (Figure 6). Juvenile abundance was observed to increase in summer samples after a mass recruitment pulse in late spring (Figure 6a). A two-way ANOVA between season and reef type indicated that this seasonal change in juvenile abundance was significant ($F_{(1)}=20.1$, $p < 0.001$), but that there was no difference between reef types ($F_{(1)}=3.1$) nor an interaction among seasons and reef types ($F_{(1)}=0.1$). The increase in abundance in summer was significant compared with all other seasons on both natural and artificial reefs (ANOVA $F_{(3)}=14.5$ and 8.1, respectively; Unequal N HSD: $p < 0.05$). The increase in the abundance of juveniles on both reef types was associated mainly with one species, *P. aquilus*, which made up 64% and 68% of juveniles on natural and artificial reefs, respectively. This species had not been associated with either reef type during multivariate analysis, above (Table 3; Figure 4). A two-way ANOVA of sub-adult abundance between the main effects of season and reef type indicated that there were significant differences among seasons ($F_{(3)}=4.1$, $p < 0.05$), but not between reef types ($F_{(1)}=2.7$), and there was no interaction between main effects ($F_{(3)}=1.7$). There were significantly fewer sub-adult fish during the spring season than any other season (Figure 6b; Unequal N HSD: $p < 0.05$ for each). The abundance of adult fish differed between seasons and reef types (two-way ANOVA: $F_{(3)}=9.9$ and $F_{(1)}=18.1$, respectively, $p < 0.001$ each), and there was a significant interaction between these main effects ($F_{(3)}=3.1$, $p < 0.05$). There were no significant differences in adult abundance among seasons on natural reefs (Figure 6c; ANOVA $F_{(3)}=1.6$). However, the abundance of adults increased significantly on artificial reefs in the summer compared with winter and spring (Figure 6c; ANOVA $F_{(1)}$=8.7, $p < 0.01$; Unequal N HSD: $p < 0.01$ each), and this represented the largest numerical change in abundance observed between seasons for any age-classes on either reef type. The tripling in adult abundance on artificial reefs between spring and summer likely indicates a seasonal attraction of adults to these structures during this time period.

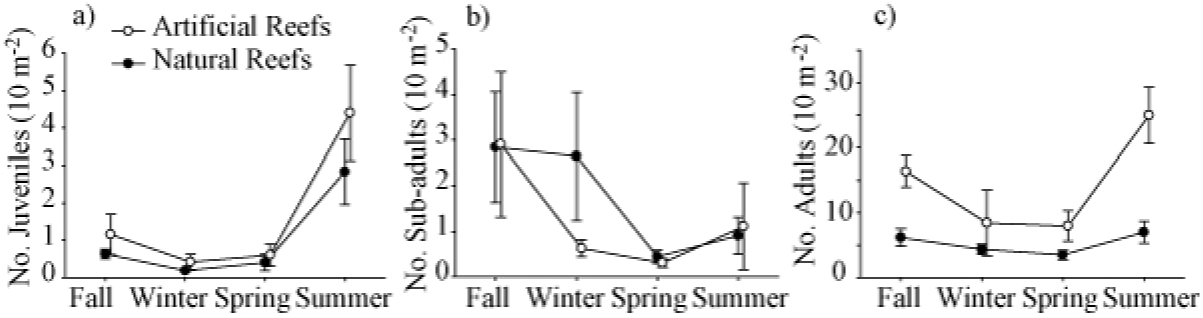

Figure 6. Seasonal abundance of (a) juvenile (b) sub-adult, and (c) adult fish on natural and artificial reefs (mean ± SE).

The increase in adult abundance on the artificial reefs in the summer (Figure 6c) was mainly associated with three species, together making up 55% of adults observed during the summer: the Ehrenberg snapper, *L. ehrenbergii* (24% of all adults), the two-spot cardinalfish, *C. novemstriatus* (18%), and the Arabian angelfish, *P. maculosus* (13%). These species were each strongly associated with artificial reefs in ordination (Figure 4a) as well as in indicator species analysis (Table 3), indicating that they were strong drivers of differences between natural and artificial reefs. ANOVA showed significant differences in seasonal abundance of *L. ehrenbergii* ($F_{(3,12)}$=12.9, $p < 0.001$) and *P. maculosus* ($F_{(3,12)}$=4.9, $p < 0.05$), with post-hoc Tukey's tests showing significantly higher abundance in the fall and summer over the winter and/or spring ($p < 0.05$). During the winter and spring the abundance of each of these species on artificial reefs had declined to the point that they were statistically indistinguishable from natural reefs, partially explaining both the convergence of natural and artificial reefs in ordination as well their lack of significance as indicator species during these seasons (*L. ehrenbergii*: $F_{(1)}=2.7$,$F_{(1)}=3.8$; *P. maculosus*: $F_{(1)}=0.0$,$F_{(1)}=2.5$; *C. novemstriatus*: $F_{(1)}=1.6$,$F_{(1)}=1.0$, winter/spring, respectively). The seasonal patterns of abundance of adults of these species, therefore, likely explain much of the seasonal change in community structure identified from multivariate analyses.

Pooling all life stages illustrates seasonal differences in overall fish abundance on natural and artificial reefs (Figure 7a). Two-way analysis of variance found a significant interaction between reef type and season ($F_{(3)}=3.1$, $p < 0.05$). Post-hoc unequal N HSD tests showed that on artificial reefs, there were significantly more fish in the summer than in the winter and spring ($p < 0.001$ each), while abundance did not change seasonally on natural reefs. In summer, there were significantly more fish on artificial reefs than were observed on natural reefs during any season ($p < 0.05$ for all).

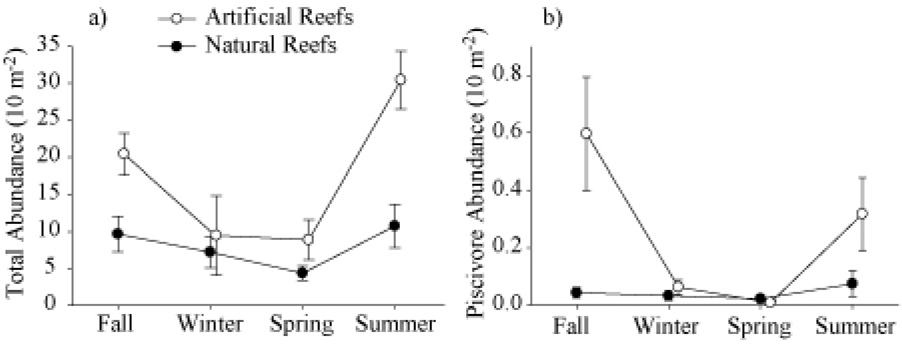

Figure 7. Seasonal changes in abundance of all fish (a) and predatory fish (b) on natural and artificial reefs (mean ± SE).

To investigate the role that predation may have played in altering abundance of fish, the abundance of piscivorous fish was compared on natural and artificial reefs through seasons (Figure 7b). Species were classified as piscivores on the basis of Randall (1995), and include the groupers *Epinephelus coioides*, *Epinephelus stoliczkae*, *Cephalopholis hemistiktos*, the jack *C. bajad*, and the barracuda *Sphyraena flavicauda*. A two-way ANOVA indicated significant interactions between reef type and seasons ($F_{(3)}=6.2$, $p < 0.01$). Subsequent one-way ANOVA's showed that piscivore abundance was significantly higher on artificial reefs than natural reefs ($F_{(1)}=8.0$, $p < 0.01$). In particular, abundance was significantly higher in the fall than in the winter or spring on artificial reefs, with predatory fish near an order of magnitude more abundant in the fall (ANOVA $F_{(3)}=5.8$, $p < 0.05$; unequal N HSD tests: $p < 0.05$ for both). Abundance of predators subsequently increased during the summer on artificial reefs, but this did not differ significantly from the other seasons. On natural reefs, piscivores were stable throughout the year (ANOVA $F_{(3)}=0.7$). These results suggest that seasonal changes in fish abundance on artificial reefs may, in part, be the result of predation.

Discussion

Large-scale artificial reefs in the form of breakwaters, jetties, seawalls, and related coastal defense structures currently contribute more than half of the length of coastlines in many areas (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005), and they are likely to become increasingly common with accelerated population growth in coastal areas. In Dubai, recent coastal development activities have lengthened the formerly rather straight, sandy shoreline from 50 km to >1600 km (Hansen 2005), of which >65 km are breakwaters. The results of this study indicated that abundant and diverse coral and fish communities can develop on the artificial reefs that result from such breakwaters, but that these communities differ from those on natural reefs.

Coral communities

Coral cover on artificial structures in this study was significantly higher than on nearby natural reefs. Habitat differences between the natural and artificial reefs examined here likely explain the difference in coral cover between these reef types. The lower coral cover on the natural reef compared with the artificial reefs likely results from higher sedimentation rates. Corals in the natural reef grow on low relief caprock sheets that are overlain by fine to course mobile sands (Chapter 2; Riegl 1999), which frequently partially or fully cover coral colonies on these reefs (pers. obs.; Riegl 1999). Such sedimentation impairs juvenile recruitment and survivorship (Babcock and Mundy 1996;

Clark and Edwards 1999; Dikou and van Woesik 2006), as well as adult respiratory activity (Riegl and Branch 1995), and has been suggested as a leading cause of coral mortality on these natural reefs in Dubai (Riegl 1999). In contrast, the artificial reefs examined here are elevated above the sandy substratum and are exposed to the flushing action of waves. It is likely that these differences in environmental conditions are at least partially responsible for the higher coral cover on these artificial reefs compared with the natural reefs.

These observation of higher coral cover on artificial reefs than natural reefs here contrast many earlier studies which have compared natural and artificial reefs in tropical systems, where artificial reefs have generally contained significantly less hard-coral cover than natural reefs (Abelson and Shlesinger 2002; Edwards and Smith 2005; Perkol-Finkel and Benayahu 2005). However, in each of these cases, the artificial reefs being compared with natural reefs were less than 10 years old. Given that mature coral communities may take decades to develop (Perkol-Finkel et al. 2005; Perkol-Finkel et al. 2006), these studies are likely underestimating the amount of corals that may develop on artificial structures. Similar to results here, mature artificial breakwater reefs in north- and south-western Taiwan have been found to contain 25 to 40% cover, exceeding that of the surrounding area (Wen et al. 2007), and 119 year old reefs in the Red Sea contain 47% hard-coral cover (Perkol-Finkel et al. 2006), indicating that mature artificial reefs can develop coral cover that is comparable or higher than adjacent natural reefs if enough time passes. If the purpose of examining coral cover on artificial reefs is to compare it with natural reefs, these results indicate that more than three decades of immersion may be necessary to allow the coral community on artificial structures to develop sufficiently.

In addition to coral cover, coral community composition and diversity were found to differ between artificial reefs and natural reefs. Diversity of the artificial reef coral community was lower than on the natural reefs. This echoes results from studies in the Red Sea, where artificial reefs that had been immersed for at least 30 years still contained lower hard-coral diversity than adjacent natural reefs (Perkol-Finkel and Benayahu 2004; Perkol-Finkel et al. 2005; Perkol-Finkel et al. 2006). In addition, similar to the findings here, community composition often differs between artificial and natural reefs both for corals (Perkol-Finkel and Benayahu 2004), and the wider assemblage (Bulleri 2005c; Edwards and Smith 2005). Differences in community composition and diversity on artificial reefs and natural reefs is often suggested to be the result of differences in habitat characteristics such as structural material, orientation, and complexity (Clark and Edwards 1999; Abelson and Shlesinger 2002; Edwards and Smith 2005; Perkol-Finkel et al. 2005; 2006; Creed and DePaula 2007). The natural reefs and the artificial breakwater reefs do offer distinct habitats that differ in each of these respects, and coral planulae are known to differentially settle as a result of preferences for different habitat characteristics (Chapter 5; Babcock and Mundy 1996; Petersen et al. 2005; Creed and DePaula 2007; Field et al. 2007), perhaps explaining the community differences. However, differences in composition and diversity may also be a result of differential larval supply. The natural reefs in Jebel Ali lie closer to larger natural reefs in Abu Dhabi (Riegl 1999; EWS-WWF

2008), and may be receiving a higher influx of larvae than the artificial reefs which are more isolated. Further research is needed to determine the cause of community differences among reef types.

Fish communities

The community structure of fish on artificial reefs has often been found to differ from that of natural reefs in the same area. Artificial reefs generally contain higher fish densities than adjacent natural reefs (Bohnsack 1989; Bohnsack et al. 1994; Rilov and Benayahu 2000; Abelson and Shlesinger 2002), and this is also true for rocky breakwater reefs (Stephens et al. 1984; Lincoln-Smith et al. 1994; Stephens et al. 1994; Pondella et al. 2002; Perez-Ruzafa et al. 2006). They also tend to support distinct assemblages that differ in species composition (Clark and Edwards 1999; Rilov and Benayahu 2000; Edwards and Smith 2005; Clynick et al. 2008), and artificial reefs generally contain more species of fish than is observed on natural reefs (Lincoln-Smith et al. 1994; Carr and Hixon 1997; Rilov and Benayahu 2000; Abelson and Shlesinger 2002; Perez-Ruzafa et al. 2006). The results of this study also found higher fish abundance and species richness on artificial reefs, and different community composition from natural reefs, but only during certain seasons.

Differences in fish communities between natural and artificial reefs changed seasonally. In terms of multivariate community structure as well as richness and overall abundance, fish communities on natural reefs were relatively stable through the year while those on artificial reefs were dynamic. During the warmer summer and fall seasons there were significant increases in fish abundance and richness on artificial reefs, but not on natural reefs. These seasonal changes in abundance were driven mainly by adults. Although there was a substantial increase in juvenile abundance from spring to summer (Figure 6a), these represent only a small proportion of the increase in total abundance on the artificial reefs (Figure 7a), while adult abundance more than tripled during the same period to make up over four-fifths of the total abundance during the summer (Figure 6c). The relatively small increase in sub-adult abundance during the fall likely results from the maturation of juveniles that had recruited during the preceding summer. Piscivore abundance increased in the summer in concert with juvenile recruitment on artificial reefs and remained in high densities during the fall (Figure 7b), and predation is likely to have contributed to the decline in abundance of sub-adults and smaller adult fish (Figure 6b and c). The abundance of piscivores on artificial reefs declines to its lowest level during the winter and spring in concert with the decline in other adult fish (Figure 7b; Figure 6c). Overall, these results suggest that differences between natural and artificial reef fish communities are associated mainly with the movement of fish on and off of artificial reefs, and that predation may also play a role in decreasing the abundance of smaller age-class fish on artificial reefs. Similar seasonal changes in abundance have been observed elsewhere in the Arabian Gulf, where migration of fish has been suggested to cause peak fish abundance on off-shore reefs during the summer and fall, and subsequent declines in abundance during the winter and spring over a two year period (Coles and Tarr 1990).

This is not the only study to note dynamic seasonal changes in fish communities on artificial reefs. In a two year study of fish communities on breakwaters in Australia, Lincoln-Smith et al. (1994) also found breakwaters to have higher fish abundance and richness than natural reefs, but that breakwater fish communities often varied considerably over time compared with natural reefs. Recruitment and migration are often tied to the dynamics of community structure on artificial reefs. Tupper and Hunte (1998) reported that fish assemblages on artificial reefs tended to differ most from natural reefs during the summer following recruitment, while Fujita et al. (1996) similarly noted that natural reefs and artificial reef fish communities differed most during the summer, but suggested that it was mainly the result of fish returning to artificial reefs after emigrating during the spawning season. Bohnsack et al. (1994) also found abundance to change seasonally on artificial reefs over two years in Florida, with total abundance increasing during the summer as fish recruited to the reefs and predators immigrated. Similar to what was observed here, abundance declined in subsequent seasons as a result of predation and emigration of fish from the artificial reefs (Bohnsack et al. 1994). These findings, in concert with what was observed in this study, suggest that dynamic changes in composition and abundance are common on artificial reefs and can result in seasonally convergent or divergent community structure compared with natural reefs.

Overall, the results of this show that artificial reefs can develop diverse and abundant fish communities, but seasonal changes in community structure make for temporally inconsistent similarity with natural reef communities. In addition, abundance of fish on these artificial structures appears primarily to change as a result of migration of adults that are attracted to these structures, rather than through larval recruitment. However, this result must be interpreted with caution, as it represents only one year of sampling. Further investigation is warranted to determine whether these patterns are consistent over longer time periods.

In closing, increasing coastal development in Dubai, and in other areas, is resulting in the substantial loss of natural reef habitat (Chapter 2; Wilkinson 2004), and over-exploitation of marine resources is decimating commercial fisheries here as abroad (Grandcourt et al. 2005; 2006; 2007). Proponents suggest that artificial reefs may be a means to mitigate these impacts by providing alternative habitat on which hard-bottom communities can develop as replacements for natural reefs. The results of this study indicate that the artificial structures examined in this study support substantive, diverse, and dynamic reef communities, with higher coral cover and seasonally higher fish abundance than observed on natural reefs. However, these communities are not mirrors of those on natural reefs. Both coral and fish community composition differed between natural and artificial reefs, and temporal changes in fish communities indicated functional differences between assemblages on different types of reef. This suggests that the promotion of artificial reefs as replacements for natural reef habitats needs to be approached with caution. These results also suggest caution when comparing natural and artificial reefs. Coral cover on artificial structures may take decades to develop, and examination of benthic or associated fish assemblages on young structures is clearly inappropriate despite being fairly common. In addition, the dynamic seasonal changes in fish abundance indicate that censusing should be repeated seasonally, rather than annually, to understand changes in community structure on artificial reefs.

References

Abelson A, Shlesinger Y (2002) Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. Journal of Marine Science 59: 122-126

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Aseltine-Neilson D, Bernstein B, Palmer-Zwahlen M, Riege L, Smith R (1999) Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. Bulletin of Marine Science 65: 37-57

Babcock R, Mundy C (1996) Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. Journal of Experimental Marine Biology and Ecology 206: 179-201

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Badalamenti F, Chemello R, D'Anna G, Heriquez R, P, S.Riggio (2002) Are artificial reefs comparable to neighbouring natural rocky area? A mollusc case study in the Gulf of Castellammare. Journal of Marine Science 59: 127-131

Bohnsack J (1989) Are high densities of fishes at artificial reefs the result of habitat limitation of behavioral preference? Bulletin of Marine Science 44: 631-645

Bohnsack J, Harper D, McClellan D, Hulsbeck M (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bulletin of Marine Science 55: 796-823

Bohnsack JA, Ecklund AM, Szmant AM (1997) Artificial reef research: is there more than the attraction-production issue? Fisheries 22: 14-16

Bulleri F (2005) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Marine Ecology-Progress Series 287: 53-65

Carr M, Hixon M (1997) Artificial reefs: The importance of comparisons with natural reefs. Fisheries 22: 28-33

Chapman MG, Clynick BG (2006) Experiments testing the use of waste material in estuaries as habitat for subtidal organisms. Journal of Experimental Marine Biology and Ecology 338: 164-178

Clark S, Edwards AJ (1999) An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. Aquatic Conservation-Marine and Freshwater Ecosystems 9: 5-21

Clynick BG, Chapman MG, Underwood AJ (2008) Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33: 140-150

Coles S, Tarr A (1990) Reef fish assemblages in the western Arabian Gulf: A geographically isolated population in an extreme environment. Bulletin of Marine Science 47: 696-720

Connell SD (1997) The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. Journal of Experimental Marine Biology and Ecology 209: 261-278

Creed J, DePaula A (2007) Substratum preference during recruitment of two invasive alien corals onto shallow-subtidal tropical rocky shores. Marine Ecology-Progress Series 330: 101-111

Dikou A, van Woesik R (2006) Survival under chronic stress from sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. Marine Pollution Bulletin 52: 1340-1354

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366

Edwards RA, Smith SDA (2005) Subtidal assemblages associated with a geotextile reef in south-east Queensland, Australia. Marine and Freshwater Research 56: 133-142

EWS-WWF (2008) Coral reef investigations in Abu Dhabi and eastern Qatar: final report. Emirates Wildlife Society - World Wide Fund for Nature, Abu Dhabi, UAE

Field S, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs 26: 279-289

Fujita T, Kitagawa D, Okuyama Y, Jin Y, Ishito Y, Inada T (1996) Comparison of fish assemblages among an artificial reef, a natural reef and a sandy-mud bottom site on the shelf off Iwate, northern Japan46: 351-364

Grandcourt E, Al Abdessalaam T, Francis F, Al Shamsi A (2007) Population biology and assessment of the white-spotted spinefoot, *Siganus canaliculatus* (Park, 1797), in the southern Arabian Gulf. Journal of Applied Ichthyology 23: 53-59

Grandcourt EM, Al Abdessalaam TZ, Al Shamsi AT, Francis F (2006) Biology and assessment of the painted sweetlips (*Diagramma pictum* (Thunberg, 1792)) and the spangled emperor (*Lethrinus nebulosus* (Forsskal, 1775)) in the southern Arabian Gulf. Fishery Bulletin 104: 75-88

Grandcourt EM, Al Abdessalaam TZ, Francis F, Al Shamsi AT (2005) Population biology and assessment of the orange-spotted grouper, *Epinephelus coioides* (Hamilton, 1822), in the southern Arabian Gulf. Fisheries Research 74: 55-68

Grossman GD, Jones GP, Seaman WJ (1997) Do artificial reefs increase regional fish production? A review of existing data. Fisheries 22: 17-23

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75: 12-13

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geoscience 32: 1259-1269

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bulletin of Marine Science 55

McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR

McCune B, Mefford M (1999) PC-ORD: Multivariate analysis of ecological data. MjM Software Design, Gleneden Beach, OR

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52: 1053-1071

Perez-Ruzafa A, Garcia-Charton JA, Barcala E, Marcos C (2006) Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: The Mar Menor (Spain, Western Mediterranean): Recent developments in estuarine ecology and management. Marine Pollution Bulletin 53: 107-120

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23: 195-205

Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Marine Environmental Research 59: 79-99

Perkol-Finkel S, Shashar N, Barneah O, Ben-David-Zaslow R, Oren U, Reichart T, Yacobovich T, Yahel G, Yahel R, Benayahu Y (2005) Fouling reefal communities on artificial reefs: does age matter? Biofouling 21: 127-140

Perkol-Finkel S, Shashar N, Benayahu Y (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. Marine Environmental Research 61: 121-135

Petersen D, Laterveer M, Schuhmacher H (2005) Innovative substrate tiles to spatially control larval settlement in coral culture. Marine Biology 146: 937-942

Pickering H, Whitmarsh D (1997) Artificial reefs and fisheries exploitation: A review of the 'attraction versus production' debate, the influence of design and its significance for policy. Fisheries Research 31: 39-59

Polovina J, Sakai I (1989) Impacts of artificial reefs on fishery production in Shimamaki, Japan. Bulletin of Marine Science 44: 997-1003

Pondella D, Stephens J, Craig M (2002) Fish production of a temperate artificial reef based on the density of embiotocids. Journal of Marine Science 59: S88-S93

Randall J (1995) Coastal Fishes of Oman. University of Hawaii Press, Honolulu

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18: 63-73

Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Marine Biology 140: 29-40

Riegl B, Branch G (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. Journal of Experimental Marine Biology and Ecology 186: 259-275

Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Marine Biology 136: 931-942

Stephens J, Morris P, Pondella D, Koonce T, Jordan G (1994) Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California, USA, 1974-1991: A recruitment driven system. Bulletin of Marine Science 55: 1224-1239

Stephens J, Morris P, Zerba K, Love M (1984) Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974–1981. Environmental Biology of Fishes 11: 259-275

Svane I, Peterson J (2001) On the problems of epibioses, fouling and artificial reefs, a review. Marine Ecology 22: 169-188

Tupper M, Hunte W (1998) Predictability of fish assemblages on artificial and natural reefs in Barbados. Bulletin of Marine Science 62: 919-935

Wen K, Hsu C, Chen K, Liao M, Chen C, Chen C (2007) Unexpected coral diversity on the breakwaters: potential refuges for depleting coral reefs. Coral Reefs 26: 127

Wilkinson C (2004) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville

Chapter 5: Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs

Introduction

The majority of the world population currently lives within 100 km of a coastline, and coastal populations are projected to continue growing (UNEP 2002). This increases pressure on marine ecosystems adjacent to urban areas through over-exploitation of marine resources and destruction of coastal habitats by development and pollution.

Artificial reefs are increasingly being promoted as a means to mitigate impacts from human activities in coastal areas (Svane and Peterson 2001). Such structures are known to develop diverse and abundant benthic and fish communities (Lincoln-Smith et al. 1994; Rilov and Benayahu 2000; Pondella et al. 2002; Perkol-Finkel and Benayahu 2004), and may increase production of commercial species in areas where reef habitat is limiting populations (Bohnsack et al. 1997). In coastal urban areas, perhaps the most important artificial reefs come in the form of man-made coastal defense structures such as breakwaters, sea-walls, and jetties. These structures contribute substantially more hard-bottom habitat than is provided by traditional artificial reefs, in some cases making up more than half of the coastal length in an area (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005), and they are likely to become increasingly common with coastal urbanization. Although coastal defenses can also support diverse and abundant communities (Lincoln-Smith et al. 1994; Stephens et al. 1994; Pondella et al. 2002;

Moschella et al. 2005; Wen et al. 2007), the development of communities on such structures is not well understood (Baine 2001; Airoldi et al. 2005; Moschella et al. 2005). Basic design-related research is needed to address the possible ecological and management implications that such large-scale artificial reefs may play.

Most attention in artificial reef research has been given to enhancement of fisheries. As a result, design of artificial structures has tended to focus on issues relating to habitat complexity and configuration, factors known to strongly affect fish diversity and abundance (Baine 2001; Abelson and Shlesinger 2002; Charbonnel et al. 2002; Sherman et al. 2002). In regions where these structures are likely to be colonized by major habitat-forming sessile fauna such as corals and sponges, attention needs to be paid to the suitability of materials used in the construction of artificial structures. Yet the importance of substrate remains relatively understudied (Baine 2001). Many benthic organisms are selective of the geochemical signatures provided by substrates, and differences in larval preference can result in development of divergent communities where different substrate materials are used to construct man-made reefs. Given that the benthos provides food, shelter, and settlement habitat for a variety of reef-associated organisms, including fish (Elliott et al. 1995; Qian 1999; Crossman et al. 2001; Hartney and Grorud 2002; Nishizaki and Ackerman 2004), construction material may have an impact on the reef communities that develop on these structures and therefore have management implications.

The purpose of this study was to examine the influence of materials commonly used in the construction of artificial reefs and coastal defense structures on benthic community development. We deployed standard-size tiles made from concrete, gabbro, granite, sandstone, and terra-cotta. The first four materials are commonly used in construction of breakwaters both here and abroad, while terra cotta is commonly used in research studies that assess benthic recruitment (Mundy 2000; Baird et al. 2003; Adjeroud et al. 2007), and was included for comparison with other studies. Both the abundance of juvenile corals and the composition of the overall benthic community were compared among materials.

Methods

This study was conducted in Dubai, United Arab Emirates, in the south-eastern basin of the Persian Gulf. Two natural reef sites and two breakwater reef sites were selected for comparison (Figure 1). The natural reefs (NR1 and NR2) are associated with areas of exposed cap-rock formed from consolidated sand that emerge from the sandy bottom. Coral on natural reefs in this area averages 35% cover (Chapter 2), and exist as low-relief patches typically <1000 m^2 in area on an otherwise sandy floor. Both the Dubai Dry Dock (DDD) and the Jebel Ali Port (PRT) breakwaters were constructed over 25 years ago, and each reef contained > 40% coral coverage when sampled in 2007 (Chapter 3; Chapter 4). The DDD breakwater is composed of 4 – 6 ton limestone blocks, while the Port breakwater is made of interlocked concrete tetra-foil jacks of similar size. Both breakwaters exceed 400,000 m^3 volume. All study sites are surrounded by a substratum mainly dominated by mobile sands and silts and are of comparable depth, with maximum depths of approximately 8 m

.

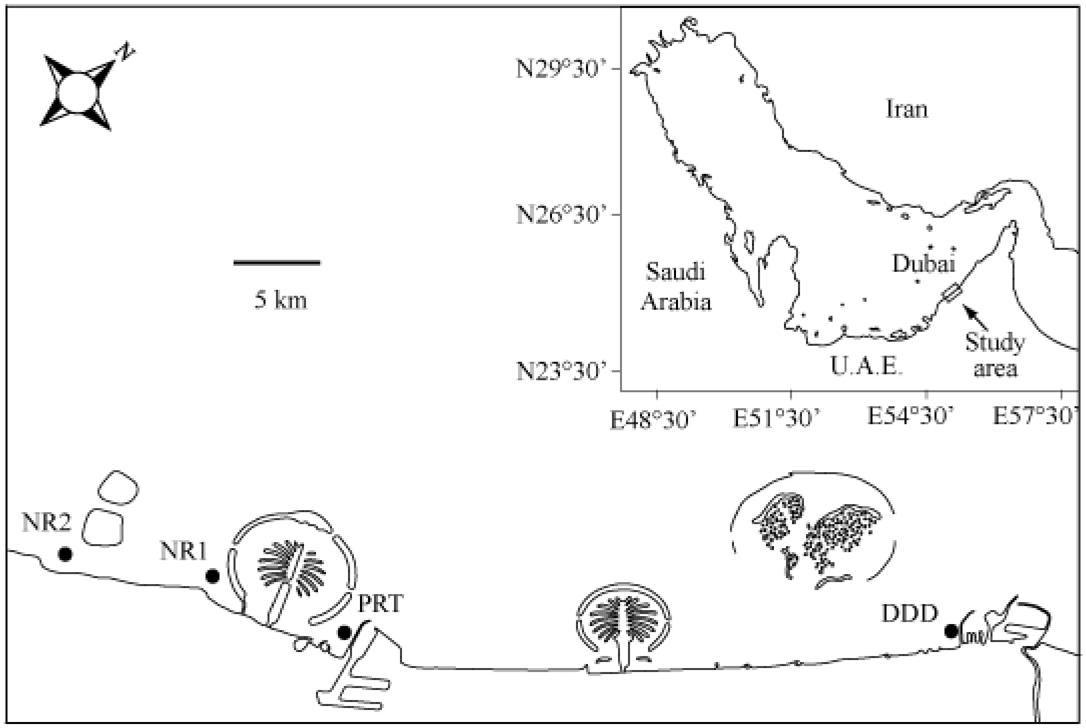

Figure 1: Location of sites where substrate tiles were deployed. NR: Natural reef; PRT: Jebel Ali port breakwater; DDD: Dubai dry dock breakwater.

Five materials were compared in this study, including concrete, gabbro, granite, sandstone, and terra cotta. To allow assessment of recruitment on standard surface areas, blocks of each material were machined to a tile size of 100 x 100 x 15 mm using a diamond-tipped rock saw. Each was provided with a central hole 10 mm in diameter to facilitate attachment to the substratum. Although there were geological differences in texture, the surfaces were generally comparable among materials.

At each site, 25 tiles of each material were individually bolted to the substratum with the aid of a pneumatic drill, for a total of 125 tiles per site. This technique has both statistical and practical advantages over the use of tile racks, and provides similar results (Mundy 2000). Tiles were deployed in random order at approximately 4 m depth, and were spaced 1 – 3 m apart. A plastic washer was used to maintain each tile 10 – 15 mm above the substrate, providing a 'gap habitat' for settling fauna. Tiles were installed parallel to the reef surface so that the natural range of substrate orientations was represented. Tiles were deployed in April 2007 before coral spawning events occurring from May through October in this region (Shlesinger and Loya 1991; Fadlallah 1996; Shlesinger et al. 1998), and were retrieved a year later. In total, 95% of tiles were recovered with the remainder lost to wave action.

Overall community cover and the density of coral recruits on the bottoms of tiles were examined in the laboratory. Only the bottom surfaces of tiles were included, as benthic organisms typically recruit to tile bottoms in higher densities (Nzali 1998; Adjeroud et al. 2007). Image analysis was used to examine community structure. The bottom of each tile was photographed with a 10 mega-pixel Nikon D-80 digital camera fitted with a macro lens. Community structure was examined using CPCe image analysis software (Kohler and Gill 2006), with benthic coverage tabulated from 50 random point intercepts per tile. Due to the small size of <1 year old coral recruits and their relatively limited coverage, density of coral juveniles was tabulated separately. Following photography for community analysis, tiles were immersed in bleach for 24 hrs to remove organic tissue.

The number of coral recruits was subsequently tabulated on the bottom of each tile using an Olympus DP-70 stereo-microscope.

Mean densities of coral recruits were estimated for each material at each site, and data were $\log_{(n+1)}$ transformed prior to analysis. Despite transformation, data were significantly non-normal (Shapiro-Wilk's $W = 0.61$, $p < 0.001$). Therefore, non-parametric Kruskal-Wallis ANOVAs were used to test for differences in coral recruitment among sites and among materials at each site. Where significant differences were shown, pair-wise Mann-Whitney *U*-tests were performed to identify different groups.

Data on benthic communities were pre-screened prior to multivariate analyses. To eliminate the effects of rare benthos, only taxa observed in more than 5% of samples were considered. In addition, outlier analysis was used to identify tiles which were greater than two standard deviations from the mean and these were excluded (Tabachnick and Fidell 2001). Mean coverage of benthos was obtained by pooling results for each material from individual tiles at each site. To prepare for analysis, samples were standardized as a percent of total cover to account for differences in benthic coverage and were normalized using square root transformations.

The benthic composition of each treatment and site was ordinated using non-metric multidimensional scaling (NMS) on Bray-Curtis distances. The NMS autopilot mode of PC-ORD (McCune and Mefford 1999) performed a Monte Carlo significance test on the best of 40 runs of real data with 50 runs of randomized data to optimize the number of axes. To identify taxa associated with community differences, a joint plot was over-laid on the ordination to illustrate the strength and direction of correlations with ordination axes. Only taxa with a Pearson's $r \geq 0.5$ were included in the joint plot.

A two-way similarity percentage analysis (SIMPER) was performed to determine the percent contribution of each site and material to average Bray-Curtis dissimilarity. In addition, pair-wise analyses of similarity (ANOSIM) were used to test the significance of difference between sites and materials sampled. ANOSIM is a multivariate randomization test analogous to a standard one-way ANOVA being performed on a distance matrix, but with a minimum of assumptions (Clarke and Gorley 2006), and is appropriate for assessing groups that have been assigned a priori. ANOSIM produces a test statistic, R, that assesses the null hypothesis that there are no differences among groups, with $R \approx 0$ when there are no significant differences among groups, with greater differences among groups indicated as R approaches -1 or 1. The significance of the R statistic is generated from randomization tests on the distance matrix. Analyses of variance and post-hoc Tukey's tests were used to identify significant differences among benthos identified as important in multivariate analyses.

Results

Corals

A total of 675 coral juveniles had recruited on the bottoms of all tiles examined in this study. However, Kruskal-Wallis ANOVA indicated significant differences in the overall abundance of coral recruits among sites (Table 1), with significantly higher recruit densities at the Dubai dry dock site than each other site (Mann-Whitney U-tests: PRT: U=2304.5, Z=9.1; UNU1: U=2739, Z=8.8; UNU2: U=2144, Z=9.2; $p < 0.001$ each), and no differences among the remaining sites.

Table 1: Results of Kruskal-Wallis ANOVA comparing mean coral recruit abundance per tile at each site.

	Coral Density (mean ± SE)				Kruskal-Wallis ANOVA		
Site	DDD	PRT	NR1	NR2	*df*	*H*-value	*p*-value
Density	4.9 ± 0.5	0.1 ± 0.04	0.3 ± 0.1	0.1 ± 0.03	3, 474	197.1	$p < 0.001$

Figure 2 illustrates the abundance of coral recruits on each material for each sampling site. There were significant differences in the abundance of coral recruits among tile materials at the Dubai dry docks (DDD) site where the recruit densities were highest (Kruskal-Wallis ANOVA $H_{(4,125)} = 11.1$, $p < 0.05$; Table 1). At the dry docks, recruit density was highest on gabbro rock (Figure 2), which contained significantly more juvenile corals than concrete and sandstone (Mann-Whitney $U = 190.5$ and 170.5, $Z = 2.4$ and -2.8, respectively, $p < 0.01$ each). Sandstone also contained significantly less corals than terra-cotta ($U = 202.5$, $Z = 2.1$, $p < 0.05$). However, there were no differences in recruit densities among substrata at any of the remaining sites (Kruskal-Wallis ANOVA:

PRT $H_{(4,115)} = 4.9$; UNU1 $H_{(4,123)} = 5.9$; UNU2 $H_{(4,112)} = 2.7$), likely due to high variability associated with the relatively low recruit densities at these sites.

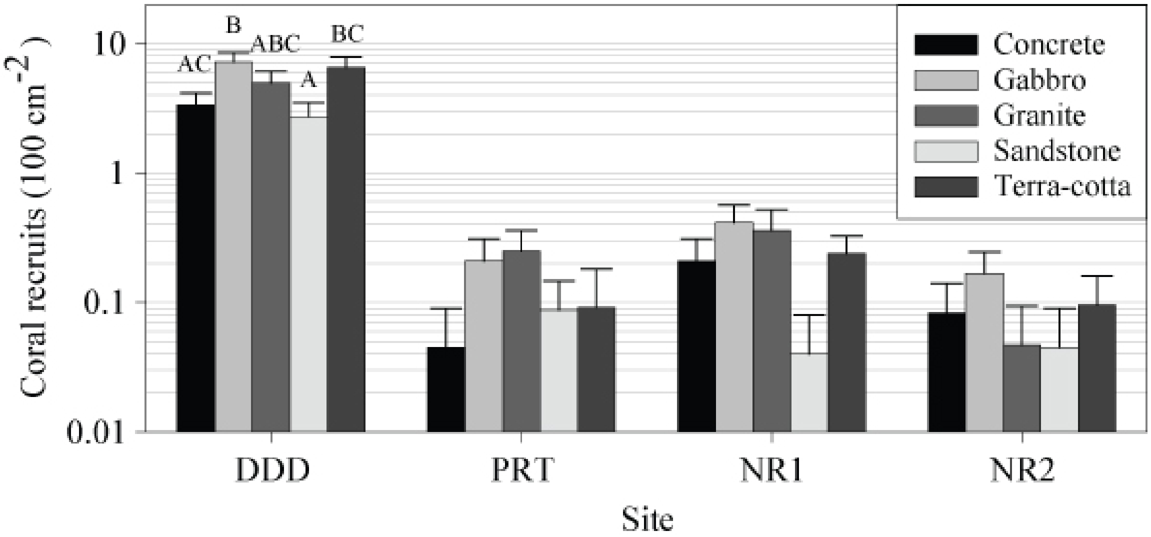

Figure 2: Comparison of coral recruit densities on tiles of different substrata at each sampling site. Bars with the same letter are not significantly different (Mann-Whitney *U*-test, $p < 0.05$).

Overall benthic community

The total of live cover varied among materials, but differences were not significant as a result of high variability (mean ± SE: concrete: 79.2 ± 2.8; gabbro: 80.2 ± 5.7; granite: 85.3 ± 6.5; sandstone: 65.4 ± 8.5; terracotta: 74.5 ± 6.3). To account for these differences, community data were standardized prior to analyses. Separation of samples in ordination indicated differences in benthic communities on tiles (Figure 3), with grouping patterns indicating that similarity was more related to site than to differences in substrate material. Two dimensions in NMS provided a significant reduction in stress compared with randomized data (Real stress: 12.5, Randomized stress: 17.5; $p < 0.05$). The first axis represented 42% of the variation and was mainly associated with differences in the relative abundance of colonial and solitary ascidians (Pearson's $r = -0.81$ and -0.76, respectively) or sponges ($r = 0.59$), while the second axis was associated with coverage of coralline and turf algae ($r = 0.61$ and 0.65, respectively), or bryozoans ($r = -0.55$), and explained 20% of variation.

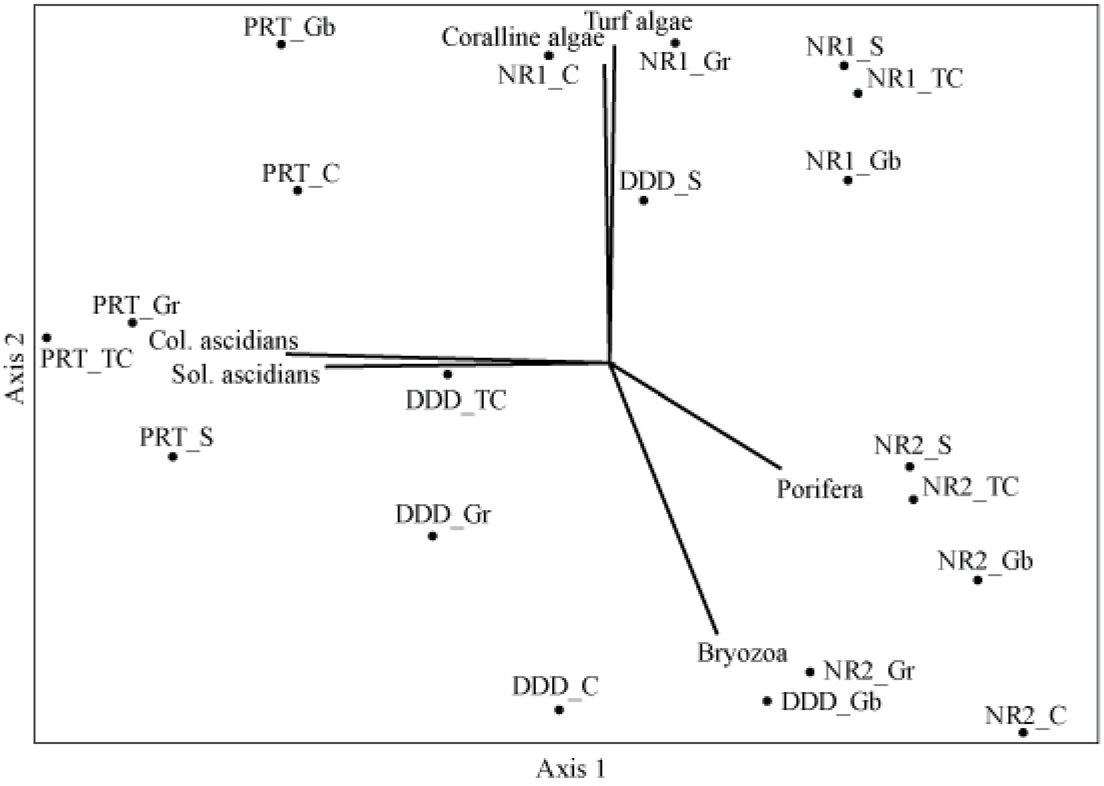

Figure 3: Ordination of benthic communities on each tile material at each sampling site, with a joint plot of benthic taxa that were strongly associated with either axis. Labels refer to Site_Material, where materials include concrete (C), gabbro (Gb), granite (Gr), and terra-cotta (TC).

Both SIMPER and ANOSIM procedures supported the findings from the NMS. Overall, tile communities were more dissimilar among sites than among different materials (Table 2). Percent dissimilarity among sites ranged from 23.8% between the two natural reef sites to 39.3% between the Jebel Ali port and the Dubai dry dock breakwaters. This site-site dissimilarity was consistently higher than any pair-wise comparisons of communities between substrate materials (ranging from 11% to 17.8%, Table 2), indicating that sites were more important in explaining dissimilarity among benthic communities than were differences among substrata. This reflects the spread of points in the ordination plot (Figure 3), where points appear to separate more as a result of site than substrate material. The *R*-values from ANOSIM support the suggestion that differences in communities are more related to site than to material (Table 2), with significant differences in tile communities observed among all sites compared, but not among any materials.

Table 2: Pair-wise comparisons of benthic communities on tiles from different sites or materials for percent dissimilarity (δ) from SIMPER analyses and *R*-statistics and *p*-values from ANOSIM.

Factor	Groups	δ (%)	*R*	Significance
Site	DDD & PRT	39.3	0.99	$p < 0.01$
	DDD & NR1	32.0	0.94	$p < 0.01$
	DDD & NR2	30.1	0.99	$p < 0.01$
	PRT & NR1	30.0	0.84	$p < 0.01$
	PRT & NR2	35.7	0.99	$p < 0.01$
	NR1 & NR2	23.8	0.94	$p < 0.01$
Material	Concrete & Gabbro	17.0	-0.18	$p > 0.05$
	Concrete & Granite	17.8	-0.32	$p > 0.05$
	Concrete & Sandstone	17.4	-0.20	$p > 0.05$
	Concrete & TerraCotta	14.5	-0.27	$p > 0.05$
	Gabbro & Granite	17.5	-0.29	$p > 0.05$
	Gabbro & Sandstone	16.4	-0.16	$p > 0.05$
	Gabbro & TerraCotta	17.8	-0.24	$p > 0.05$
	Granite & Sandstone	14.3	-0.16	$p > 0.05$
	Granite & TerraCotta	15.1	-0.26	$p > 0.05$
	Sandstone & TerraCotta	11.0	-0.25	$p > 0.05$

All benthos that were related to community differences between sites in ordination showed significant difference among sites in univariate analysis (Figure 4; ANOVA $F_{(3,16)}$: coralline algae = 13.2, turf algae = 5.9, Porifera = 20.7, Bryozoa = 12.9,colonial ascidians = 35.6, solitary ascidians = 8.5; $p < 0.01$ for each). However, there were no differences among tile materials for any benthos (ANOVA $F_{(4,15)}$: coralline algae = 0.5, turf algae = 0.2, Porifera = 0.2, Bryozoa = 0.4,colonial ascidians = 0.2, solitary ascidians = 0.9). Post-hoc comparison of benthos among sites supported the site associations identified in multivariate analyses (see Figure 3). Both coralline algae and turf algae were significantly more abundant at the natural reef site NR1 than at any other of the other sites examined (Tukey's HSD test: $p < 0.05$, respectively, for all comparisons). The other natural reef site, NR2, contained significantly more porifera than all other sites, with sponges making up more than three times as much of the benthos as elsewhere. Bryozoans were more common at the dry dock breakwater and the natural reef site NR2 than at the Jebel Ali port ($p < 0.001$ each), while the other natural reef site, NR1, differed only from the dry docks ($p < 0.05$). Colonial ascidians were not observed on the natural reef site NR2; They were significantly more common on the Jebel Ali port site than at the remaining locations ($p < 0.001$). Likewise, solitary ascidians were significantly more common on the Jebel Ali port site than on either natural reef site ($p < 0.01$).

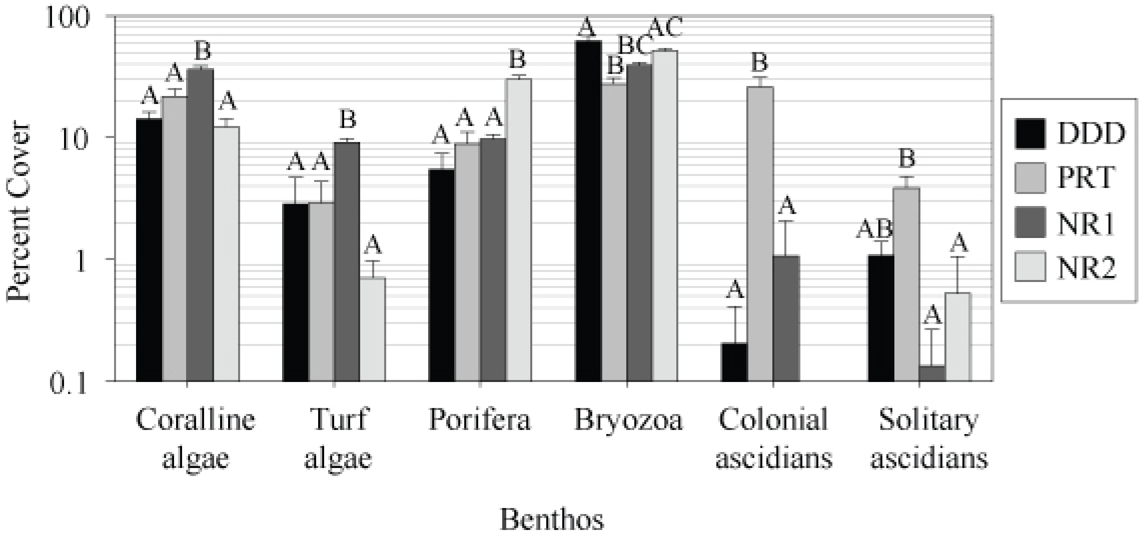

Figure 4: Percent cover of benthos associated with tiles at each sampling site. Bars with the same letter are not significantly different.

Discussion

Artificial structures deployed in the marine environment often develop diverse and abundant benthic communities, but there is little understanding of the mechanisms driving community differences among artificial structures or natural reefs. The results of this study indicated that while differences in substratum used in the construction of traditional artificial reefs and coastal defense structures can impact the recruitment of corals where recruitment is high, differences among sites is far more important in determining coral recruitment rates. In addition, substrate material did not play an important role in driving wider benthic community differences, at least during the early stages of development.

Coral recruitment

Coral recruit densities differed among sites. Juvenile coral density was more than an order of magnitude higher at the dry docks site (4.94 ± 0.5 per 100 cm^2) than at the other three sites examined (0.09 ± 0.03 to 0.25 ± 0.05 recruits per 100 cm^2). The three sites with low recruitment are located in an area that was impacted by a bleaching event while the experiment was on-going (Tupper et al. 2007). No bleaching was observed at the dry docks, perhaps because of deeper surrounding waters (J. Burt, pers. obs.). Coral bleaching is an indication of physiological stress, and the lower recruitment at these three sites may be the result of a combination of decreased adult fecundity or increased pre- or post-settlement mortality resulting from high water temperatures in that area. Coral recruitment is often spatially and temporally variable (Glassom et al. 2004; Adjeroud et al. 2007; Mangubhai et al. 2007), and further monitoring of recruitment in these areas is on-going to determine whether this pattern remains consistent.

In terms of substrate material, gabbro stone was found to have the highest densities of recruits at the DDD site, although the low recruit densities precluded finding statistically significant differences at any other sites. Gabbro rocks have a course-grained geological texture (Sen 2001), and such geochemical signatures are known to influence the development of biofilm and larval settlement in a variety of marine organisms (Rodriguez et al. 1993; Apilanez et al. 1998; Qian 1999). Given that coral planula are known to preferentially settle on surfaces with rougher texture (Carleton and Sammarco 1987;

Harriott and Fisk 1987; Petersen et al. 2005), the granular surface of the gabbro tiles may explain the high densities of coral recruits observed on this material at the dry docks.

The lowest density of coral recruits at the dry docks occurred on caprock sandstone tiles. This was unexpected given that this material had the greatest roughness of all substrates examined, and is the same substratum that forms the foundation of natural reefs in this area (Chapter 2; Riegl 1999). Tiles cut from cap-rock blocks, however, were extremely friable compared with the other materials, and many showed signs of having sloughed particles from their surface during their year of immersion. It is possible that the low recruit abundance on sandstone tiles reflects post-settlement loss of recruits as the surface layer of tiles disintegrated, taking recent recruits with it. It is also likely that this explains the low cover of other benthos on tiles of this material. This process would not be as problematic on the sandstone substrate in the natural reefs, where the substratum is exposed to near constant abrasive action of wave-induced mobile sands, resulting in a relatively consolidated surface upon which corals can recruit and grow.

Coral recruitment to concrete on the dry docks was lower than on gabbro, but not different from that on the other materials, while recruitment on granite was similar to that on all materials examined. This echoes results from a study which compared substrate preference in two invasive azooxanthelate corals in Brazil. This study found that *Tubastraea coccinea* recruited in similar densities among concrete, granite, and terra-cotta tiles, and *T. tagusensis* recruitment was similar among concrete and granite tiles

(Creed and DePaula 2007). These results are somewhat counter-intuitive based on the mineralogy of concrete and granite. Corals prefer to settle to alkaline substrates, and the leaching of calcium hydroxides from the cement in concretes should provide a more chemically attractive substrate for coral settlement (Anderson 1996). Alternately, the silicon-based radicals associated with the high quartz content in granite are known to negatively affect benthos (Cerrano et al. 1999), and should impair the recruitment of corals to granite tiles. It is likely that these geochemical cues were tempered shortly after immersion, resulting in similar recruitment patterns among geologically distinct substrates. Biofilm rapidly colonizes novel substrates placed in the marine environment (Wieczorek and Todd 1998), and their on-going metabolic processes can modify the geochemical signatures of the surface material (Petersen et al. 2005). In addition, chemically reactive cues are generally strongest only shortly after exposure of new substrate, with limited biological impacts over time if new surfaces are not exposed through abrasion (Cerrano et al. 1999). Such processes can mollify the chemical cues being released from the substratum and reduce the preferences of larvae to settle or avoid certain substrates, providing a probable explanation for the recruitment patterns observed here.

Terra-cotta tiles are commonly used as an artificial substrate with which to quantify spatial and temporal patterns of coral recruitment (Mundy 2000; Baird et al. 2003; Adjeroud et al. 2007). In this study, the density of coral recruits on terra-cotta tiles did not differ from gabbro, granite, or concrete. These materials commonly form the foundation of natural rocky reefs and/or coastal defenses and other artificial reefs (Baine 2001; Guidetti et al. 2004; Creed and DePaula 2007), indicating that terra-cotta is a representative substratum upon which to assess patterns of coral recruitment in many reef settings. These results support the continued use of this inexpensive material in studies of coral recruitment.

Benthic community development

The mature benthic assemblages associated with the natural reefs, the Jebel Ali port breakwater, and the Dubai dry dock breakwater were found to differ from one another in an earlier study (Chapter 3). The natural reef has a sandstone caprock substrate, while the breakwaters were constructed from concrete (Jebel Ali port) and gabbro (Dubai dry dock), and these differences in substrate composition provide a possible explanation for the differences in the adult benthic assemblage. The results of this study, however, indicate that the substratum material had no influence on the development of benthic communities during their first year. Differences in community structure were observed among each of the sites examined in this study that were unrelated to substratum, indicating that other site-specific processes such as the supply of larvae or environmental conditions are of more importance in early benthic community development.

The similarity of benthic communities among the different substrate materials reflects the results of a study by Creed and DePaula (2007), who found no difference in the benthic communities among cement, granite, and concrete tiles over a 17 month period. Although others have suggested that benthic communities can differ between substrates of different material (Connell and Glasby 1999; Glasby 1999), these results are likely confounded by use of materials of different arrangement, complexity, and immersion time. Those that have monitored benthic development over periods longer than the first few months on different materials cut as standardized tiles have reported that physical aspects of the tile orientation or placement method have far more influence on benthic composition than substrate material (Glasby 2000; Qiu et al. 2003; Field et al. 2007), and this is echoed by field studies which have compared these variables (Anderson and Underwood 1994; Connell 1999; Chapman and Clynick 2006). Overall, this suggests that inherent characteristics of the substrates examined here are unlikely to impact development of the overall benthic community.

Recommendation for design of artificial reef structures

These results have important implications for the design of artificial reefs as well as coastal defense structures. Currently, the majority of artificial reefs around the world are constructed from concrete (Baine 2001), and sea-walls, jetties, and breakwaters are also made from quarried granite and sandstone (Bulleri 2005c; Moschella et al. 2005; Creed and DePaula 2007). Gabbro, however, has received less use, despite having one of the most widespread geologies on earth (Sen 2001). If artificial reefs or coastal defense structures are to be designed to encourage recruitment of corals, the results here indicate that gabbro should be used preferentially over concrete and sandstone where it is feasible, but that granite may serve as a suitable alternative in areas where it is the dominant stone. The results of community analyses indicate that using materials more amenable to coral recruitment is unlikely to have any negative consequences for the recruitment of other fauna, and early benthic communities are likely to develop similarly regardless of what material is used. However, the findings from this study are based on the first year of benthic community development and must, therefore, be interpreted with caution. It is possible that long-term successional processes could lead to convergence of coral communities or to divergence of the overall benthic community on substrates of different materials over time. Further research would be required to address the long-term dynamics of benthic communities on different substrate materials.

This study also highlights the importance of site selection. Both the density of coral recruits and the composition of the benthic community were more affected by differences among sites than by differences among materials, reflecting findings elsewhere (Harriott and Fisk 1987; Glasby 2000). This suggests that pilot assessments of potential deployment sites should be an integral part of the planning process in designing artificial structures to be added to marine systems. It also indicates the importance of spatial replication in marine research. A number of published studies examining the impacts of substrate material on benthic development have been limited to a single site (Qiu et al. 2003; Brown 2005; Creed and DePaula 2007; Field et al. 2007). The results here suggest that benthic community development and coral recruitment differ from sites to site and that the use of multiple sites is warranted for a wider understanding of community development.

References

Abelson A, Shlesinger Y (2002) Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. Journal of Marine Science 59: 122-126

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. Journal of Experimental Marine Biology and Ecology 341: 204-218

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Anderson MJ (1996) A chemical cue induces settlement of sydney rock oysters, *Saccostrea commercialis*, in the laboratory and in the field. Biology Bulletin 190: 350-358

Anderson MJ, Underwood AJ (1994) Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. Journal of Experimental Marine Biology and Ecology 184: 217-236

Apilanez I, Gutierrez A, Diaz M (1998) Effect of surface materials on initial biofilm development. Bioresource Technology 66: 225-230

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Baine M (2001) Artificial reefs: A review of their design, application, management and performance. Ocean & Coastal Management 44: 241-259

Baird AH, Babcock RC, Mundy CP (2003) Habitat selection by larvae influences the depth distribution of six common coral species. Marine Ecology-Progress Series 252: 289-293

Bohnsack JA, Ecklund AM, Szmant AM (1997) Artificial reef research: is there more than the attraction-production issue? Fisheries 22: 14-16

Brown CJ (2005) Epifaunal colonization of the loch linnhe artificial reef: influence of substratum on epifaunal assemblage structure. Biofouling 21: 73-85

Bulleri F (2005) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Marine Ecology-Progress Series 287: 53-65

Carleton JH, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. Bulletin of Marine Science 40: 85-98

Cerrano C, Arillo A, Bavestrello G, Benatti U, Calcinai B, Cattaneo-Vietti R, Cortesogno L, Gaggero L, Giovine M, Puce S, Sara M (1999) Organism-quartz interactions in structuring benthic communities: towards a marine bio-mineralogy? Ecology Letters 2: 1-3

Chapman MG, Clynick BG (2006) Experiments testing the use of waste material in estuaries as habitat for subtidal organisms. Journal of Experimental Marine Biology and Ecology 338: 164-178

Charbonnel E, Serre C, Ruitton S, Harmelin J, A.Jensen (2002) Effects of increased habitat complexity on fish assemblages associated with large reef units (French Mediterranean coast). Journal of Marine Science 59: 208-213

Clarke K, Gorley R (2006) PRIMER v6: User Manual. PRIMER-E Ltd, Plymouth, UK

Connell SD (1999) Effects of surface orientation on the cover of epibiota. Biofouling 14: 219-226

Connell SD, Glasby TM (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. Marine Environmental Research 47: 373-387

Creed J, DePaula A (2007) Substratum preference during recruitment of two invasive alien corals onto shallow-subtidal tropical rocky shores. Marine Ecology-Progress Series 330: 101-111

Crossman D, Choat J, Clements K, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnology and Oceanography 46: 1596-1601

Elliott J, Elliott J, Mariscal R (1995) Host selection, location, and association behaviours of anemone fishes in field settlement experiments. Marine Biology 122

Fadlallah YH (1996) Synchronous spawning of *Acropora clathrata* coral colonies from the western Arabian Gulf (Saudi Arabia). Bulletin of Marine Science 59: 209-216

Field S, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs 26: 279-289

Glasby TM (1999) Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. Estuarine Coastal and Shelf Science 48: 281-290

Glasby TM (2000) Surface composition and orientation interact to affect subtidal epibiota. Journal of Experimental Marine Biology and Ecology 248: 177-190

Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Marine Biology 144: 641-651

Guidetti P, Bianchi C, Chiantore M, Schiaparelli S, Morri C, Cattaneo-Vietti R (2004) Living on the Rocks: Substrate Mineralogy and the Structure of Subtidal Rocky Substrate Communities in the Mediterranean Sea. Marine Ecology-Progress Series 274: 57-68

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75: 12-13

Harriott V, Fisk D (1987) A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. Marine Ecology-Progress Series 37: 201 - 208

Hartney K, Grorud K (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia 131: 506-513

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geoscience 32: 1259-1269

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bulletin of Marine Science 55

Mangubhai S, Harrison PL, Obura DO (2007) Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. Marine Ecology-Progress Series 348: 149-159

McCune B, Mefford M (1999) PC-ORD: Multivariate analysis of ecological data. MjM Software Design, Gleneden Beach, OR

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52: 1053-1071

Mundy C (2000) An appraisal of methods used in coral recruitment studies. Coral Reefs 19: 124-131

Nishizaki MT, Ackerman JD (2004) Juvenile-adult associations in sea urchins *Strongylocentrotus franciscanus* and *S. droebachiensis*: Is nutrition involved? Marine Ecology-Progress Series 268: 93-103

Nzali L, Johnstone, R., Mgaya, Y. (1998) Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. Ambio 27: 717-722

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23: 195-205

Petersen D, Laterveer M, Schuhmacher H (2005) Innovative substrate tiles to spatially control larval settlement in coral culture. Marine Biology 146: 937-942

Pondella D, Stephens J, Craig M (2002) Fish production of a temperate artificial reef based on the density of embiotocids. Journal of Marine Science 59: S88-S93

Qian P (1999) Larval settlement of polychaetes. Hydrobiologia 402: 239-253

Qiu JW, Thiyagarajan V, Leung AWY, Qian PY (2003) Development of a marine subtidal epibiotic community in Hong Kong: Implications for deployment of artificial reefs. Biofouling 19: 37-46

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18: 63-73

Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Marine Biology 136: 931-942

Rodriguez S, Ojeda F, Inestrosa N (1993) Settlement of benthic marine invertebrates. Marine Ecology-Progress Series 97: 193-207

Sen G (2001) Earth's materials: minerals and rocks. Prentice-Hall, Upper Saddle River, NJ

Sherman R, Gilliam D, Spieler R (2002) Artificial reef design: Void space, compexity, and attractants. Journal of Marine Science 59: 196-200

Shlesinger Y, Goulet TL, Loya Y (1998) Reproductive patterns of scleractinian corals in the northern Red Sea. Marine Biology 132: 691-701

Shlesinger Y, Loya Y (1991) Larval Development and Survivorship in the Corals *Favia favus* and *Platygyra lamellina*. Hydrobiologia 216: 101-108

Stephens J, Morris P, Pondella D, Koonce T, Jordan G (1994) Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California, USA, 1974-1991: A recruitment driven system. Bulletin of Marine Science 55: 1224-1239

Svane I, Peterson J (2001) On the problems of epibioses, fouling and artificial reefs, a review. Marine Ecology 22: 169-188

Tabachnick B, Fidell L (2001) Using multivariate statistics. Allyn and Bacon, Needham Heights MA

Tupper M, Tewfik A, Tan M, Tan S, Teh L, Radius M, Abdullah S (2007) ReefBase: A Global Information System on Coral Reefs. Retrieved 30 Sept. 2008, from http://www.reefbase.org/global_database/default.aspx?section=t4

UNEP (2002) Percent of the population living within 100 kilometers from the coast. Retrieved 21 Feb 2005, from http://geocompendium.grid.unep.ch/data_sets/coastal/document/pop_100km_coast_MD.htm

Wen K, Hsu C, Chen K, Liao M, Chen C, Chen C (2007) Unexpected coral diversity on the breakwaters: potential refuges for depleting coral reefs. Coral Reefs 26: 127

Wieczorek S, Todd C (1998) Inhibition and facilitation of settlement of epifaunal marine invertebrate larvae by microbial biofilm cues. Biofouling 12: 81-118

Chapter 6: Coral community dynamics on a breakwater and natural reef

Introduction

Coastal defense structures such as breakwaters, groynes, and sea-walls are becoming increasingly common features in coastal urban areas. Such structures now make up more than half of the coastline in many regions (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005; Wen et al. 2007), providing a substantial amount of hard-bottom habitat upon which diverse and abundant fish and benthic communities develop (Lincoln-Smith et al. 1994; Pondella et al. 2002; Bulleri 2005c; Guidetti et al. 2005b; Moschella et al. 2005). In tropical areas, such structures develop extensive coral communities which can provide food, settlement habitat, and shelter for a variety of reef organisms (Chapter 3; Chapter 4; Wen et al. 2007), and increase the aesthetic appeal and recreational value of coastal defenses for human use (Airoldi et al. 2005). Such artificial structures can also be of value in replacing or enhancing natural coral reefs that have been degraded by natural or anthropogenic stress (Clark and Edwards 1999; Miller 2002), and may increase productivity in areas where natural reef habitat is limiting (Carr and Hixon 1997).

In recognition of the important ecological role that coastal defense structures play in the marine system, there is increasing interest in understanding how design features can influence the development of communities associated with these artificial structures (Baine 2001; Airoldi et al. 2005). One of the most basic aspects of design which is likely to influence community development is exposure to wave action. Wave exposure can substantially influence the composition and abundance of epifaunal communities that develop on coastal defense structures in temperate environments (Southward and Orton 1954; Moschella et al. 2005), and has been associated with differences in coral community structure on natural coral reefs in the tropics (Riegl and Piller 1997; Reinicke et al. 2003; Steiner 2003). However, the influence of exposure on the development of coral communities on coastal defense structures is unknown.

The purpose of this study is to investigate the influence of wave exposure on the development of coral communities associated with breakwaters in Dubai, UAE. breakwaters are a dominant feature of the marine environment in Dubai, where over 65 km of rocky breakwater have been added to the coastline in the past decade. The addition of this artificial hard-bottom habitat may be particularly important here, where corals are generally restricted to a 10 km near-shore band of small, discontinuous patch reefs in western Dubai, and the remaining coastal area is dominated by mobile sands and silt unsuitable for coral reef development (Chapter 2; Riegl 1999). Coral community composition, cover, size structure, demographics, and growth rates were compared between leeward and windward breakwaters to explore the influence of wave exposure on coral community development, and these were compared with those on a natural coral reef to gain an understanding of how community structure and dynamics compare between these artificial and natural habitats.

Methods

This study was conducted in Dubai, United Arab Emirates. The sea-bed in this area is dominated by mobile sand and silt substrates (Riegl 1999), with natural reefs restricted to isolated areas of exposed cap-rock which occur mainly to the south-west of the city (Figure 1). Large-scale (> 2 km long) breakwaters also provide a substantial amount of hard-bottom habitat upon which coral communities develop (Chapter 3, Chapter 4). One such breakwater, on the Palm Jumeirah, is composed of approximately 225,000 m^2 of quarried rock, with an estimated volume exceeding 1.2 million m^3 (Figure 1). Sampling was conducted at two leeward (PJ1 and PJ4) and two windward (PJ2 and PJ3) sites on the Palm Jumeirah breakwater, as well as at a natural reef site (JR; Figure 1). The leeward breakwater sites have a substrate that is mainly dominated by turf algae and bivalves, with higher water turbidity than at the windward sites (pers. obs.). At the windward sites the sea urchin, *Echinometra mathai*, is found in higher densities and bare pavement is more common than at the leeward sites (pers. obs.). The substrate on the natural reef is composed mainly of a veneer of fine to course mobile sands overlaying caprock, and fleshy algae is rare.

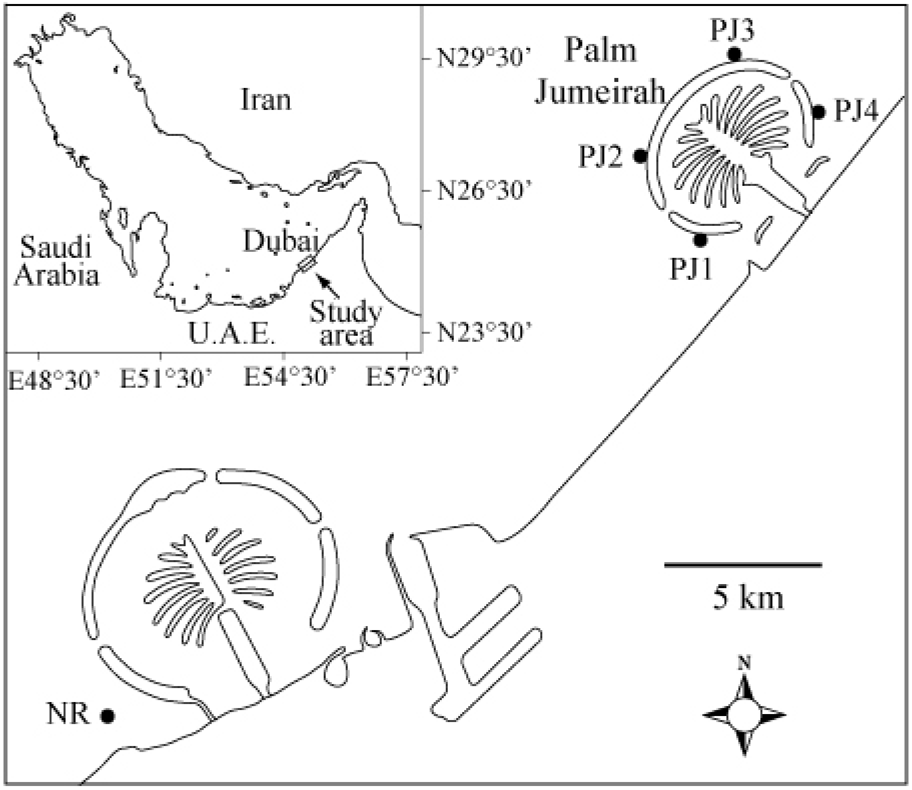

Figure 1. Map of study sites on leeward (PJ1 and PJ4) and windward (PJ2 and PJ3) breakwaters and on the natural reef (NR).

Ten permanent 0.25 m^2 quadrats were installed at approximately 5 – 6 m depth at each site. Stainless steel bolts were installed to mark the corners of each permanent quadrat using a Chicago Pneumatic CP-9 hammer-drill, and quadrats were spaced 3 – 5 m apart. Because the natural reef has little vertical relief (Chapter 2; Riegl 1999), quadrats on the breakwater were installed only on approximately horizontal substrates for consistency.

Quadrats were photographed quarterly from July 2007 through July 2008 to obtain seasonal estimates of coral cover, demographics, and growth rates. Photographs were captured with a Nikon D-80 10 mega-pixel digital camera mounted on a PVC frame outlining the quadrat area. The perimeter of individual coral colonies was traced seasonally to calculate total colony area (cm^2) using CPCe image analysis software (Kohler and Gill 2006). All statistical comparisons were performed using coral area. However, in some cases the diameter of colonies was also calculated for comparison to other studies, where the diameter of coral colonies was estimated from colony area using the formula $D = 2\cdot\sqrt{(A/\pi)}$, assuming circular colonies.

Seasons were defined as Summer (July to October 2007), Fall (October 2007 to January 2008), Winter (January to April 2008), and Spring (April to July 2008). Coral cover was estimated at the end of each season. Size-frequency distributions were created using the mean number of colonies in each size-class across seasons, with juveniles defined as those with an area < 12.5 cm^2, equating with a circular colony < 4 cm in diameter. Demographic changes and growth rates were measured as the change from the preceding season. Recruitment was defined as the appearance of a new colony within quadrats, while mortality was defined as the permanent loss of a colony from a quadrat. Mobile coral rubble was excluded from analysis, and colonies which were partially or fully obscured by the quadrat frame during any season were not included in demographics or growth rate analysis to avoid confounding these estimates.

All data were transformed prior to analyses. Percent coral cover were converted to proportion and arc-sine square root transformed, while a $\log_{(n+1)}$ transformation was applied to estimates of recruitment and mortality. A cube-root transformation was applied to growth data to account for the occurrence of negative coral growth rates.

Reef types were classified as leeward breakwater, windward breakwater, or natural reef for analysis. Repeated measures ANOVAs were used to test differences in coral cover and coral growth rates between reef types and seasons, with post-hoc unequal-N HSD tests used to identify significantly different groups. A frequency distribution of coral colony sizes was created for each reef type using mean colony surface areas across seasons. Demographics were analyzed using non-parametric tests as $\log_{(n+1)}$ transformations failed to normalize data. Seasonal differences in coral recruitment and mortality were tested with pair-wise Friedman's ANOVAs, while differences among reef types were tested seasonally using Kruskal-Wallis ANOVA by Ranks. Linear regression was used to test the relationship between colony size and growth rates, averaged across seasons.

Results

There was comparable coral species richness between the breakwaters and natural reef with 10 and 12 species observed on each, respectively. However, species dominance differed between reef types, with coral cover on the breakwater dominated by *Favia pallida* (52.1% of coral cover), *Porites lobata* (19.5%), and *Porites lutea* (13.1%), while the natural reef was dominated by *P. lutea* (35.8% of cover), *Porites harrisoni* (31.3%)

and *Cyphastrea microphthalma* (23.4%). The relative proportion of *P. lobata* and *P. lutea* did not differ with exposure on the breakwater reef (repeated measures ANOVA: $F_{(1,37)}$ = 0.7 and 3.8, respectively). However, *F. pallida* was significantly more common on the windward breakwater sites than at leeward locations (repeated measures ANOVA: $F_{(1,37)}$ = 19.3, $p < 0.001$).

Repeated measure ANOVA of coral cover indicated a significant interaction between reef type and season (Pillai's $F_{(6,90)}$ = 7.9, $p < 0.001$). Post hoc Tukey's unequal-N HSD tests indicated that the leeward breakwater had significantly lower coral cover than the natural reef during each season ($p < 0.05$ each), but that coral cover on the windward breakwater did not differ from either the leeward breakwater or the natural reef during any season (Figure 2). In addition, coral cover did not change through the year on the leeward breakwater, while seasonal changes in cover were observed on the windward breakwater and the natural reef (Figure 2). There was a significant increase in the amount of coral cover on the windward breakwater at the end of the year compared with the previous summer (Figure 2; Unequal N-HSD: $p < 0.001$). However, on the natural reef, coral cover increased significantly from summer to winter ($p < 0.001$), and then declined in the spring such that it did not differ from any previous season (Figure 2). Several large breakwaters were constructed within a kilometer of this natural reef site during the spring season, and the decline in live coral cover during this period likely reflects impacts from sedimentation on corals in the natural reef.

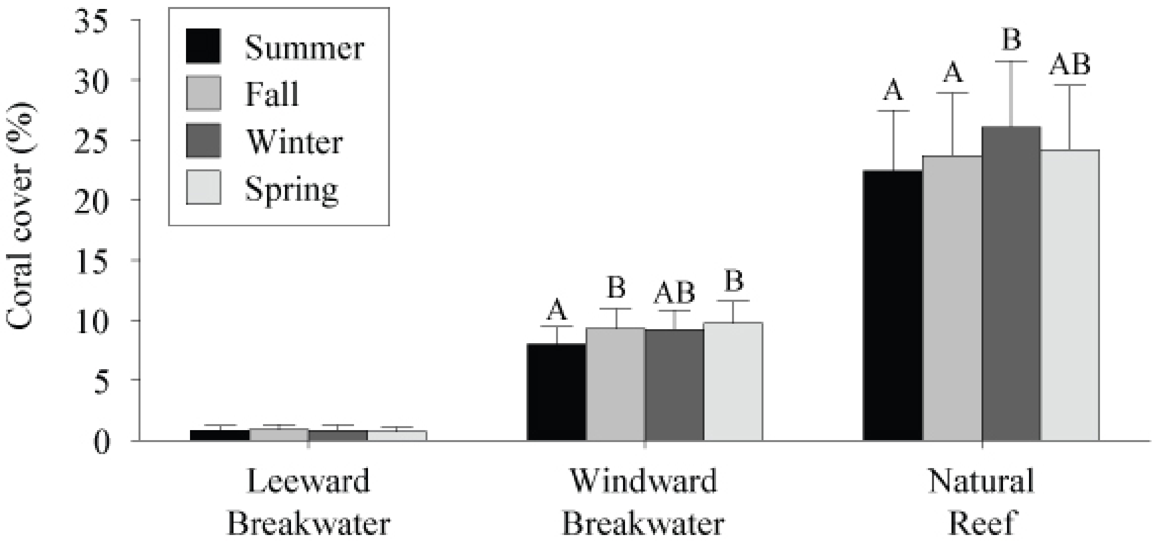

Figure 2. Seasonal coral cover (mean ± SE %) on the leeward and windward breakwaters and the natural reef. Bars with the same letter are not significantly different (Unequal-N HSD test, $p < 0.05$).

The relative frequency of coral colony size classes on each reef type is illustrated in Figure 3. Juvenile colonies (< 12.5 cm^2 area; < 4 cm diameter) were the most common size class observed at each location. However, the relative abundance of juveniles differed between locations. Juveniles made up over three-quarters of all colonies observed on the leeward breakwater, and few colonies were observed in larger size classes (Figure 3), indicating that few colonies survive to reach adulthood here. On the windward breakwater face there was a better representation of colonies through medium (< 75 cm^2) size classes, with the result that there was a decline in the relative frequency of juveniles in the overall community here (Figure 3). The relatively infrequent occurrence of large (>75 cm^2) colonies on either the leeward or windward breakwaters is not surprising, given the relatively young (5.5 yr) age of this breakwater. There was a more equitable distribution of corals in medium to large colony size-classes on the natural reef, with an eighth of all colonies falling into the largest size class (> 125 cm^2).

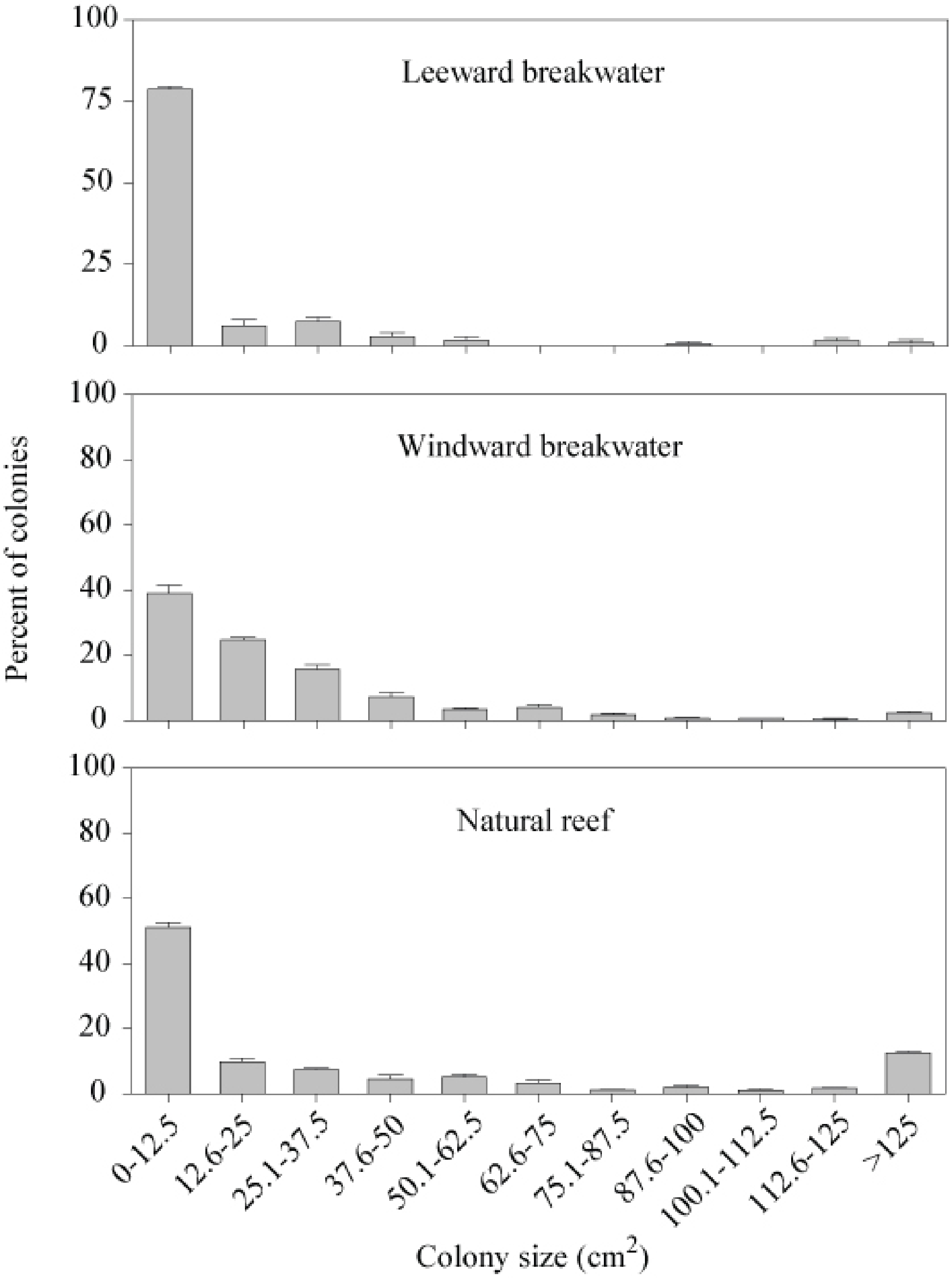

Figure 3: Frequency distribution of mean (±SE) coral colony sizes among leeward and windward breakwaters and the natural reef.

Overall, seasonal densities of new recruits averaged 0.5 ± 0.2 m^{-2} across sites, with new recruits accounting for 9.5% of all corals observed during the course of the study. Mortality resulted in a loss of an average of 0.8 ± 0.3 colonies m^{-2} each season across sites, representing 16.2% of all colonies over the year.

Coral recruits were observed exclusively in the fall season on breakwaters, and also had highest densities on the natural reef during this period (Table 1). Pair-wise Friedman's ANOVA indicated that recruitment was higher during the fall period than any other season (Fall-Summer $\chi = 13.0$, Fall-Winter $\chi = 9.3$, Fall-Spring $\chi = 10.3$; $p < 0.01$ each), and these other seasons did not differ from one another. However, Kruskal-Wallis ANOVA by Ranks indicated that there were no differences in recruitment among reef types during any season ($H_{(2,42)}$: Summer= 0.0, Fall=5.1; Winter=3.3;Spring=3.3). There were also significant seasonal differences in coral mortality (Table 1; Friedman's ANOVA $\chi = 15.6$, $p < 0.01$). The highest mortality occurred during the spring, when mortality was significantly higher than in the summer and fall (Friedman's ANOVA: $\chi = 14.0$ and $\chi = 6.3$, respectively, $p < 0.05$ each). Mortality was also higher in the winter than summer ($\chi = 4.5$, $p < 0.05$). The high incidence of mortality in the spring was mainly due to the five-fold increase in mortality on the natural reef compared with previous seasons (Table 1), likely as a result of increased sedimentation associated with nearby coastal development. There were no differences in mortality in the earlier seasons on the natural reef when mortality on the natural reef during the spring was excluded to account for potential anthropogenic effects (Friedman's ANOVA $\chi = 0$). Coral mortality did not differ among the leeward and windward breakwaters and the natural reef during any season (Table 1; $H_{(n=43)}$: Summer = 6.7, Fall = 7.5, Winter = 0.6, Spring = 4.2).

Table 1. Seasonal coral recruitment and mortality (mean ± SE colonies m^{-2}) at each location.

	Recruitment				Mortality			
Location	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring
Leeward breakwater		1.6 ± 0.5				0.5 ± 0.4	0.8 ± 0.4	1.6 ± 0.5
Windward breakwater		0.9 ± 0.7				0.2 ± 0.2	0.9 ± 0.5	0.9 ± 0.4
Natural reef		3.2 ± 1.6	0.8 ± 0.8	0.4 ± 0.4	0.8 ± 0.5	0.8 ± 0.5	0.8 ± 0.5	4.0 ± 1.7

Although there were no differences in the overall density of corals lost to mortality among locations, mortality affected different proportions of the population as a result of differences in overall population sizes. Mortality resulted in the loss of nearly a third of all corals on the leeward breakwater during the year, compared with less than a tenth on the windward breakwater, when represented as a percent of the total number of coral colonies at each location (Figure 4). The natural reef lost approximately a fifth of its corals to mortality over the year, but two-thirds of this mortality was during the spring (light shading, Figure 4) in association with nearby marine construction activity, indicating probable anthropogenic influences.

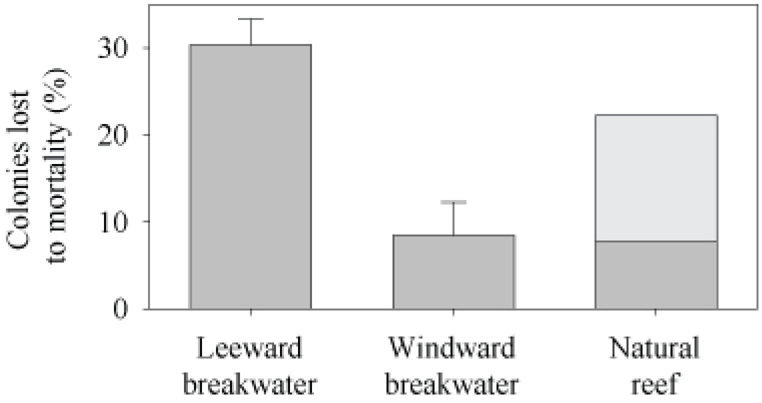

Figure 4. Mean (± SE) percentage of colonies lost to mortality out of the whole coral community at each location over one year. Light shading on natural reef indicates percent lost in spring alone.

Mortality was entirely restricted to juvenile corals on both the leeward and windward breakwaters, and to all but one colony on the natural reef. A frequency distribution of mortality versus colony size indicates that coral mortality is highest in new recruits less than 1.5 cm^2 in area, or 0.7 cm in diameter (Figure 5). On the leeward breakwater, coral mortality was almost entirely restricted to colonies $<3\ cm^2$, or <2 cm diameter, while mortality affected relatively more larger colonies on the windward breakwater and the natural reef.

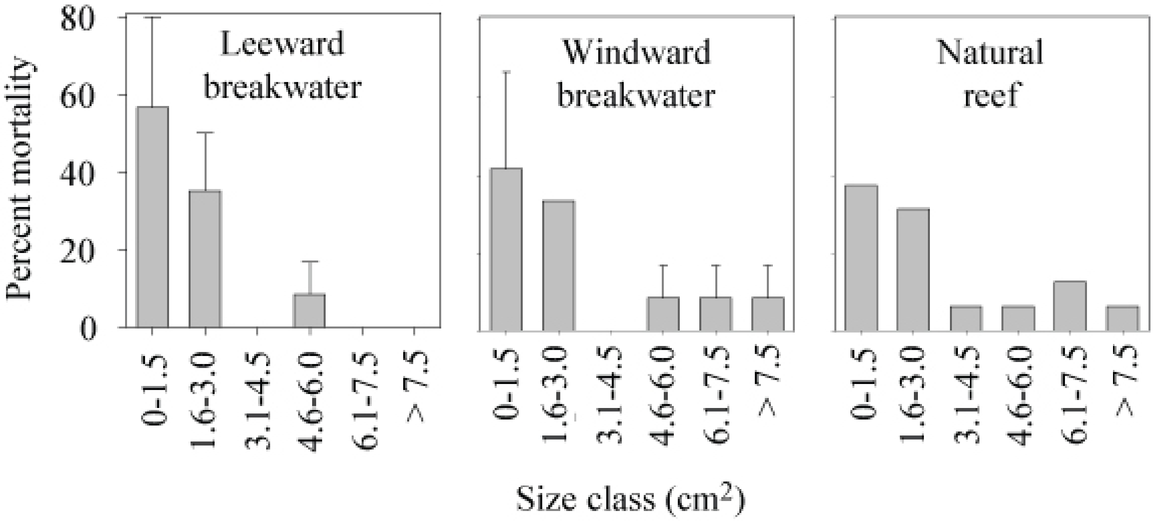

Figure 5: Relationship between colony size and percent mortality (mean ± SE) on leeward and windward breakwaters and the natural reef.

Two species were responsible for all demographic change on breakwaters. *Siderastrea savignyana* made up 90% of all recruits on breakwaters, and were the only recruits observed on the windward sites. This dominance in recruitment was balanced by high mortality, with 70% of all breakwater mortality occurring in this species. *F. pallida* made up the remainder of breakwater recruitment and mortality, with 10% of recruitment and 30% of mortality occurring in this species. On the natural reef, demographic change was more evenly divided among three species. Recruitment was evenly divided between *P. harrisoni*, *P. lutea*, and *Coscinaraea monile*, at 27. 3% of recruitment each. This recruitment was nearly balanced by mortality in *P. lutea* and *C. monile* (31.3% of mortality each), although mortality was lower in *P. harrisoni* at 18.8% of mortality.

The annual coral growth rate, averaged across all sites and seasons, was a 4.5 ± 3.0 cm^2 yr^{-1} increase in area, or a 2.4 ± 2.0 cm yr^{-1} increase in diameter. However, there were fluctuations in coral growth rates among seasons and reef types, with coral growth rates sometimes negative as a result of partial colony mortality resulting in colony shrinkage (Figure 6). Repeated measure ANOVA showed significant a significant interaction between seasonal growth rates and location (Pillai's $F_{(6,332)} = 3.4$, $p < 0.01$).

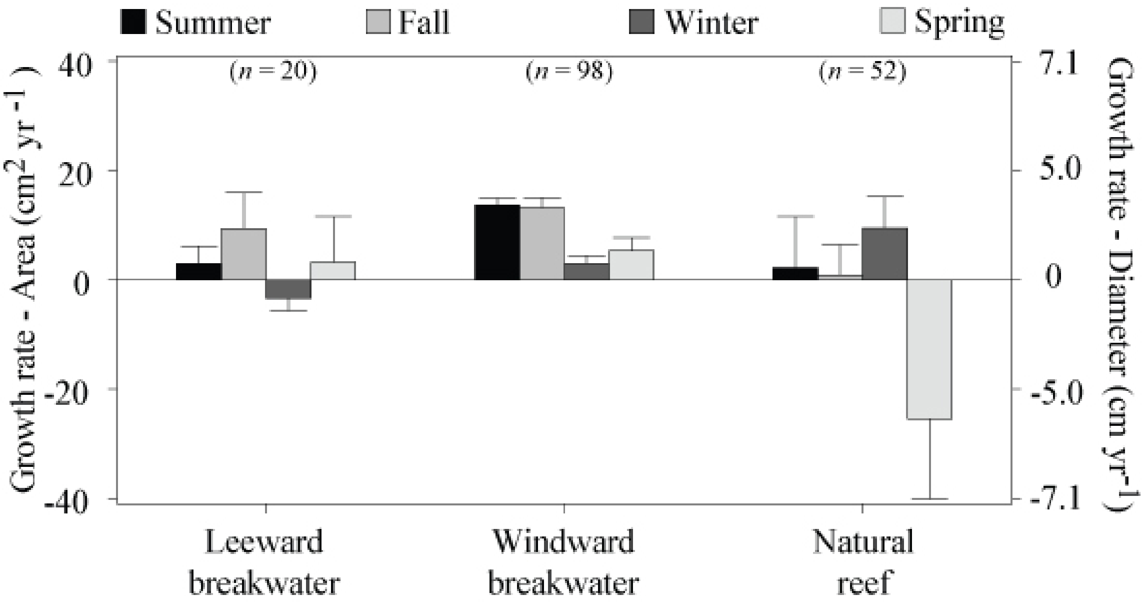

Figure 6. Mean (± SE) seasonal coral growth rates for each reef type. Growth rates provided as change in area (left axis) and diameter (right axis). Note differences in axes scale. Sample size indicated in parentheses.

Post-hoc Tukey's unequal-N HSD tests were used to explore differences in growth rates among reef types and seasons. In terms of differences among reef types, growth rates on the windward breakwater were significantly higher than those on the natural reef during the summer and the spring (Figure 6; $p < 0.05$ and $p < 0.01$, respectively). However, coral growth rates did not differ between leeward and windward breakwaters, nor between leeward breakwaters and natural reefs, during any season. In terms of seasonal differences, coral growth rates on the leeward breakwater were negative during the winter as a result of partial colony mortality during the cool winter months when water temperatures are regularly in the teens (Figure 6; G. Cavalcante, pers. comm.), but growth rates did not differ significantly among seasons. Coral growth rates also declined in the winter on the windward breakwater (Figure 6), with coral growth rates in the winter and spring significantly lower than during the summer ($p < 0.001$). On the natural reef there were no significant changes in coral growth rates until the spring, when coral growth rates declined significantly ($p < 0.01$). The rapid negative growth rate (colony shrinkage) on natural reefs during the spring corresponds to nearby coastal development (see above), and was associated with partial colony mortality in 61.5% of colonies compared with 36.5 ± 2.2 % of colonies in earlier seasons.

Linear regression showed that there was a significant positive relationship between colony size and mean annual growth rate on the windward breakwater ($F_{(1,91)} = 65.6$, $p < 0.001$; $r = 0.65$), but not on the leeward breakwater ($F_{(1,17)} = 0.8$; $r = 0.20$) nor the natural reef ($F_{(1,45)} = 0.3$; $r = 0.08$). However, there was a significant relationship between colony size and mean annual growth rates on natural reefs when the spring season was excluded to avoid probable confounding effects from coastal development impact during this season ($F_{(1,45)} = 4.6$, $p < 0.05$; $r = 0.3$).

Discussion

Coastal defense structures such as breakwaters, jetties, and sea walls are increasingly common features in coastal urban areas as human populations grow. These structures can develop diverse and abundant benthic and fish assemblages (Lincoln-Smith et al. 1994; Pondella et al. 2002; Bulleri 2005c; Guidetti et al. 2005b; Moschella et al. 2005), with potential benefits to ecosystem productivity and related economic activity. The results of this study indicate that breakwaters can develop coral communities that are comparable in many respects to those on natural reefs, but that design features of the breakwaters themselves can particularly influence the processes structuring their coral community development.

The leeward breakwater appears to offer a suboptimal habitat for coral community development compared with the windward breakwaters and natural reef. Coral cover on the leeward breakwater was low compared with the natural reef. This low cover appears to be primarily the result of high early post-settlement mortality. Examination of colony sizes indicated high mortality during early life on the leeward breakwater where only a quarter of corals survived to adulthood (Figure 3), compared with over half of colonies on the windward breakwater and the natural reef. This is reflected in the relationship between colony size and mortality (Figure 5), where coral mortality on the leeward breakwater was almost entirely restricted to recent recruits less than 3 cm^2 (2 cm diameter). In addition, mortality had a disproportional effect on the leeward breakwater community due to the low coral abundance, resulting in the annual loss of nearly a third of all colonies here compared with less than a tenth on the windward breakwater (Figure 4). Coral recruitment rates and growth rates were comparable among all reef types, and growth rates were unrelated to colony size on the leeward breakwater, indicating that these processes likely had little influence on the low coral cover on the leeward breakwater. Overall, these results suggests that the low coral cover on the leeward breakwater results from high early post-settlement mortality, resulting in a low abundance community made up primarily of small colonies.

These results suggest that the leeward areas on this breakwater represent a suboptimal habitat compared with the windward breakwater and the natural reef. Leeward and windward natural reef faces often have coral communities that differ in cover and composition (Riegl and Piller 1997; Reinicke et al. 2003; Steiner 2003), and breakwater exposure is also known to affect benthic communities in temperate areas (Moschella et al. 2005). The leeward sites examined in this study have a significant wave height that is half of that on the exposed windward face (Smit et al. 2005), and have the high levels of turbidity and sedimentation that are characteristic of sites protected from wind driven waves (Purcell 2000; Walker 2007). More than three-quarters of the substratum on the leeward breakwaters is dominated by turf algae and bivalves, and little bare space is available for colonization (unpubl. data). In contrast, bare pavement makes up almost half of the substrata on the windward breakwater (Chapter 3). The high turf abundance on leeward sites likely results from the low densities of sea urchins here (pers.obs.), with urchin recruitment and survivorship likely impaired by the high sedimentation rates characteristic of these sheltered breakwaters (Purcell 2000; Walker 2007). As both sedimentation and algae can inhibit coral recruitment, growth, and survival (Hodgson 1990; McCook et al. 2001; Birrell et al. 2005; Crabbe and Smith 2005; Box and Mumby 2007; Birrell et al. 2008), it is likely that the physical and biological conditions resulting from low wave action explain the low coral cover, skewed size distribution, and proportionately high mortality of corals on the leeward breakwater. Further investigation of these factors is warranted.

Despite the evident differences in coral demography between windward and leeward breakwaters, this study confirms that the processes structuring coral community development on the windward breakwater sites are comparable to that of the natural reef during this year. After only 5.5 years since construction, the windward breakwater has developed 9.8% coral cover compared with 24.1% on the natural reef site, and coral recruitment, mortality, and growth rates were comparable between these reef types. However, this one year may not be representative of longer term changes in these communities. On the windward breakwater there is likely to be an increase in recruitment in the coming years as these colonies reach puberty, with fecundity increasing as colonies grow larger (Soong and Lang 1992; Sakai 1998; Kai and Sakai 2008), perhaps contributing to increased coral cover on windward reefs in the coming years. It is also likely that community structure and dynamics will change on the natural reef. These natural reefs are exposed to recurrent mass mortality every 10 – 15 years (Riegl 1999; Riegl 2002b; Riegl and Purkis 2009), and are currently in the process of recovery

(Chapter 2). Such events particularly affect the taxa associated with natural reefs in this area and have minimal impacts on the faviids and poritids which dominate breakwaters (Riegl 1999; Riegl 2002a; Sheppard and Loughland 2002), suggesting bleaching events predicted to occur with increasing frequency and magnitude in this region (Coles and Brown 2003; Sheppard 2003) are likely to differentially impact coral community structure and dynamics on natural reefs. In addition, coastal development is likely to exacerbate these effects. There is evidence from this study that the development of breakwaters adjacent to this natural reef was associated with a more than fourfold increase in whole colony mortality, a near doubling of partial colony mortality, and a decline in coral growth rates such that colonies were shrinking by 25 cm^2 $year^{-1}$ during the season following construction. It is likely that on-going and planned coastal developments adjacent to these natural reefs will continue to have negative impacts on these coral communities in the coming years. Overall, this suggests that while coral community dynamics on the windward breakwater and the natural reef are currently comparable, natural and anthropogenic changes are likely to result in divergence in the long term.

In addition to spatial differences in coral community dynamics among reef types, this study also highlights the importance of season for these high-latitude assemblages. The Arabian Gulf is characterized by temperature extremes, with water temperatures here regularly exceeding 35 °C in the summer and declining below 16 °C in the winter (Coles 2003). Although corals in this region have adapted to withstand these temperature extremes (Coles 2003; Coles and Brown 2003), mass coral bleaching and mortality have been associated with both high and low sea-surface temperatures here (Coles and Fadlallah 1991; Riegl 2002a; Sheppard and Loughland 2002), indicating that these corals are living at the margins of their thermal tolerance limits. In this study, coral mortality was highest, and colony growth rates typically lowest, during the winter or spring seasons, suggesting that these seasons represent a more stressful environment for corals. However, this is likely the result of seasonal competition with algae rather than temperature differences. Benthic algae are highly seasonal in this region, with most growth occurring during the winter before dying off with the onset of warm summer water temperatures (McCain et al. 1984; Coles and Fadlallah 1991; Ateweberhan et al. 2006). Competition with algae is known to decrease coral growth rates and partial- and whole-colony survivorship (Birrell et al. 2005; Box and Mumby 2007; Titlyanov et al. 2007; Birrell et al. 2008), and the extensive winter/spring growth of algae in this region has been suggested to be a leading cause of coral mortality on reefs here (McCain et al. 1984; Coles 2003). Most significant differences in coral growth rates and all significant differences in coral recruitment and mortality observed in this study were related to differences among seasons rather than differences among locations, suggesting that season may be more important in influencing these community dynamics than reef types.

Overall recruitment densities of 1.9 ± 0.7 recruits m^{-2} yr^{-1} were observed across sites in this study, which is comparable to recruit densities observed on natural substrates in the Caribbean (Chiappone and Sullivan 1996), the Red Sea (Abelson et al. 2005), and the

Great Barrier Reef (Connell et al. 1997). The higher annual recruitment observed on the natural reef (4.4 recruits m^{-2} yr^{-1}) than on the breakwater (1.3 ± 0.5 recruits m^{-2} yr^{-1}) is likely a reflection of the higher proportion of larger, and presumably reproductive, colonies on the natural reef compared with the breakwater. In addition, the overall growth rates of corals associated with the breakwater and natural reefs currently average 4.5 ± 3.0 cm^2 yr^{-1} (2.4 ± 2.0 cm yr-^{1} diameter). This is comparable to average overall growth rates of corals in the Caribbean (3.4 ± 0.2 mm yr^{-1}, Edmunds 2007) and the Red Sea (4.9 mm yr^{-1}, Glassom and Chadwick 2006), and slightly faster than corals from subtropical Australian reefs (0.6 to 2.0 mm yr^{-1}, Wilson and Harrison 2005). Overall, this suggests that despite the severity of environmental conditions in the Arabian Gulf, coral recruitment and growth rates are comparable to those in other areas. Interestingly, coral growth rates were positively correlated with colony size in this study, while studies elsewhere generally show reduced growth rates in larger colonies (Chadwick-Furman et al. 2000; Edmunds et al. 2004; Goffredo et al. 2004; Bramanti et al. 2005). This likely reflects the relatively small size of colonies in this study versus in other areas. There were very few colonies > 125 cm^2 (12.6 cm diameter) on either the breakwater or natural reef sites examined in this study as a result of the young breakwater age or the ongoing recovery from bleaching, respectively. As a result, many of the colonies examined here have not yet reached puberty. Given that coral growth rates generally decline as colonies become reproductive (Richmond 1987; Ward 1995; Guzman and Tudhope 1998; Mendes 2004), it is likely that the current positive relationship between size and growth will change in the coming years as these colonies become reproductive.

Overall the results of this study highlight the importance of breakwaters as an artificial reef habitat on which coral communities can develop. With appropriate design, such structures can develop coral communities with comparable coral cover, demographics, and growth rates to natural reefs. This study also highlights the potential impacts of coastal development on coral community dynamics, where partial- and whole-colony mortality increased and average colonies shrank on the natural reef in association with nearby breakwater construction. Although it could be suggested that breakwater construction may mitigate these impacts by creating novel hard-bottom habitats upon which coral communities will develop, the results of this and other studies (Chapter 4) indicate that the composition of these breakwater coral communities is distinct throughout their development, and that breakwater coral communities are not surrogates for natural reefs.

References

Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: Temporal and spatial variation, and possible effects of anthropogenic disturbances. Marine Pollution Bulletin 50: 576-582

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Ateweberhan M, Bruggemann J, Breeman A (2006) Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). Coral Reefs 25: 391-406

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Baine M (2001) Artificial reefs: A review of their design, application, management and performance. Ocean & Coastal Management 44: 241-259

Birrell C, McCook L, Willis B (2005) Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin 51: 408-414

Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanography and Marine Biology: An Annual Review 46: 25-63

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Marine Ecology-Progress Series 342: 139-149

Bramanti L, Magagnini G, De Maio L, Santangelo G (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. Journal of Experimental Marine Biology and Ecology 314: 69-78

Bulleri F (2005) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Marine Ecology-Progress Series 287: 53-65

Carr M, Hixon M (1997) Artificial reefs: The importance of comparisons with natural reefs. Fisheries 22: 28-33

Chadwick-Furman NE, Goffredo S, Loya Y (2000) Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. Journal of Experimental Marine Biology and Ecology 249: 199-218

Chiappone M, Sullivan KM (1996) Distribution, abundance and species composition of juvenile scleractinian corals in the Florida Reef Tract. Bulletin of Marine Science 58: 555-569

Clark S, Edwards AJ (1999) An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. Aquatic Conservation-Marine and Freshwater Ecosystems 9: 5-21

Coles S (2003) Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific region. Atoll Research Bulletin 507: 1-19

Coles S, Brown B (2003) Coral bleaching - capacity for acclimatization and adaptation. Advances in Marine Biology 46: 183-223

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low-temperatures in the Arabian Gulf - new species-specific lower temperature limits. Coral Reefs 9: 231-237

Connell J, Hughes T, Wallace C (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67: 461-488

Crabbe MJC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24: 437-441

Edmunds PJ (2007) Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. Marine Ecology-Progress Series 341: 1-13

Edmunds PJ, Bruno JF, Carlon DB (2004) Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. Marine Ecology-Progress Series 278: 115-124

Glassom D, Chadwick NE (2006) Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. Marine Ecology-Progress Series 318: 111-122

Goffredo S, Mattioli G, Zaccanti F (2004) Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Coral Reefs 23: 433-443

Guidetti P, Verginella L, Odorico C, Boero F (2005) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. Journal of the Marine Biological Association of the UK 85: 247-255

Guzman HM, Tudhope AW (1998) Seasonal variation in skeletal extension rate and stable isotopic (C-13/C-12 and O-18/O-16) composition in response to several environmental variables in the Caribbean reef coral *Siderastrea siderea*. Marine Ecology-Progress Series 166: 109-118

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75: 12-13

Hodgson G (1990) Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. Coral Reefs 9: 41-43

Kai S, Sakai K (2008) Effect of colony size and age on resource allocation between growth and reproduction in the corals *Goniastrea aspera* and *Favites chinensis*. Marine Ecology-Progress Series 354: 133-139

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geoscience 32: 1259-1269

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bulletin of Marine Science 55

McCain J, Tarr A, Carpenter K, Coles S (1984) Marine Ecology of Saudi Arabia: A survey of coral reefs and reef fishes in the Northern area, Arabian Gulf, Saudi Arabia. Fauna of Saudi Arabia 6: 102-126

McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19: 400 - 417

Mendes J (2004) Timing of skeletal band formation in *Montastraea annularis*: Relationship to environmental and endogenous factors. Bulletin of Marine Science 75: 423-437

Miller M (2002) Using ecological processes to advance artificial reef goals. ICES Journal of Marine Science 59: S27-S31

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52: 1053-1071

Pondella D, Stephens J, Craig M (2002) Fish production of a temperate artificial reef based on the density of embiotocids. Journal of Marine Science 59: S88-S93

Purcell SW (2000) Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. Bulletin of Marine Science 66: 199-214

Reinicke GB, Kroll DK, Schuhmacher H (2003) Patterns and changes of reef-coral communities at the Sanganeb-Atoll (Sudan, central Red Sea): 1980 to 1991. Facies 49: 271-298

Richmond RH (1987) Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. Bulletin of Marine Science 41: 594-604

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): Fauna and community structure in response to recurring mass mortality. Coral Reefs 18: 63-73

Riegl B (2002a) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Marine Biology 140: 29-40

Riegl B (2002b) Phoenix from the ashes? Repetitive mass mortality and the biogeology of southern Arabian Gulf (United Arab Emirates) coral systems. The Vienna School of Marine Biology: 137-159

Riegl B, Piller WE (1997) Distribution and environmental control of coral assemblages in northern Safaga Bay (Red Sea, Egypt). Facies 36: 141-162

Riegl B, Purkis S (2009) Model of coral population response to accelerated bleaching and mass mortality in a changing climate. Ecological Modelling 220: 192-208

Sakai K (1998) Effect of colony size, polyp size, and budding mode on egg production in a colonial coral. Biological Bulletin 195: 319-325

Sheppard C (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425: 294-297

Sheppard C, Loughland R (2002) Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. Aquatic Ecosystem Health & Management 5: 395-402

Smit F, Mocke G, Al-Zahed K (2005) Quantifying and managing the coastal response to major offshore developments in Dubai Proceedings of the 14th Biennial Coastal Zone Conference. NOAA Coastal Services Center, New Orleans, Louisiana

Soong KY, Lang JC (1992) Reproductive integration in reef corals. Biological Bulletin 183: 418-431

Southward AJ, Orton JH (1954) The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth Breakwater. Journal of the Marine Biological Association of the United Kingdom 33: 1-19

Steiner SCC (2003) Stony corals and reefs of Dominica, Lesser Antilles. Atoll Research Bulletin: A1-A15

Titlyanov EA, Yakovleva IM, Titlyanova TV (2007) Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. Journal of Experimental Marine Biology and Ecology 342: 282-291

Walker JW (2007) Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. Marine Ecology-Progress Series 331: 109-118

Ward S (1995) 2 patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral *Pocillopora damicornis*. Coral Reefs 14: 87-90

Wen K, Hsu C, Chen K, Liao M, Chen C, Chen C (2007) Unexpected coral diversity on the breakwaters: potential refuges for depleting coral reefs. Coral Reefs 26: 127

Wilson J, Harrison P (2005) Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. Coral Reefs 24: 418-421

Chapter 7: The influence of fish and sea-urchin grazing on early benthic community development

Introduction

Colonization of new substrates in marine environments occurs rapidly due to the two-phase life cycle of most marine organisms, where adults are generally sedentary but their propogules can travel varying distances in the water column (Mora and Sale 2002; Shanks et al. 2003; Kinlan et al. 2005). The chance supply of larvae capable of colonizing novel substrates determines, in part, the resultant community which develops. However, as the community matures the patterns of colonization are often tempered by post-settlement processes as residents facilitate or inhibit the recruitment of new species into the assemblage (Connell and Slatyer 1977). Such interactions can drastically modify the composition of the developing assemblage, setting communities onto divergent successional trajectories.

Consumers are one of the primary determinants of post-settlement community change in marine systems (Bertness et al. 2004; Osman and Whitlatch 2004; Almany and Webster 2006; Nydam and Stachowicz 2007). In hard-bottom benthic communities the grazing action of fish and sea urchins removes sessile benthic organisms, directly and indirectly affecting recruitment of subsequent colonists (Hata et al. 2002; Osman and Whitlatch 2004; Cebrian and Uriz 2006). Numerous studies have demonstrated the impact of fish and sea urchin grazing in structuring algal assemblages (Hixon and Brostoff 1996; Leinaas and Hartvig 1996; McClanahan 1997; McClanahan et al. 2002; Wright et al. 2005; Gobler et al. 2006), but their impact on the wider benthic epifaunal community is not well understood.

The ‘bulldozing’ action of sea urchins is suggested to be among the most important cause of early post-settlement mortality in sessile invertebrates (Gosselin and Qian 1997; Maldonado and Uriz 1998), and several studies have shown that even nominally herbivorous sea urchins can have diets dominated by animal tissues (Cobb and Lawrence 2005; Endo et al. 2007), in some cases specialized on particular invertebrate prey (Briscoe and Sebens 1988). Likewise, large fish often consume invertebrates directly as part of a specialist diet or as secondary foods by grazing herbivorous fish (Choat et al. 2002; Crossman et al. 2005). As such, both sea urchin and fish grazing can substantially impact the structure of epifaunal assemblages (Himmelman et al. 1983; Relini et al. 1994; Miller and Hay 1996; Hill 1998; Connell and Anderson 1999), particularly on recently colonized substrates (Hurlbut 1991; Osman and Whitlatch 1996; Osman and Whitlatch 2004). Thus, both fish and sea urchins are likely to play a role in structuring epifaunal community development, but the relative importance of each is poorly understood.

The purpose of this study was to examine the importance of the grazing action of fish and sea urchins on early benthic community succession using a series of exclusion cages. Novel substrates in the form of breakwaters, jetties, and sea-walls are increasingly being added to coastal ecosystems in urban areas, with some areas having more coastal defense than natural shoreline (Bacchiocchi and Airoldi 2003; Airoldi et al. 2005; Hansen 2005; Wen et al. 2007). Understanding the role that grazing fish and sea urchins play in structuring benthic communities develop on these structures has implications for marine management, particularly in areas where fishing pressure may be altering the populations of these consumers.

Methods

This study was conducted from February to September 2008 on the windward face of the Palm Jumeirah breakwater in Dubai, United Arab Emirates. This area is protected from commercial fishing. The numerically dominant large grazing fish in this area include the angelfish *Pomacanthus maculosus*, the rabbitfish *Siganus canaliculatus*, and the parrotfish *Scarus ghoban*, in order of abundance; *Echinometra mathai* is the numerically dominant urchin, while *Diadema setosum* is present in lower densities (unpubl. data).

A caging experiment was used to determine the influence of grazing on benthic community development. Terra-cotta was used as the experimental substrate as it is inexpensive, has a standard size and shape (10 x 10 x 1 cm), and develops comparable benthic communities to other materials (Chapter 5). Each tile was held mid-water on a stainless steel bolt inside a standardized cage measuring 23 cm x 23 cm x 19 cm (D x W x H) constructed from PVC pipe. Cages were modified to represent one of four treatments (Figure 1): (a) 'full cages' (FC) were completely wrapped in PVC garden fencing (2 x 2 cm mesh size) to reduce grazing of all organisms with a body width larger than 2 cm width, (b) 'fish exclusion' cages (FE) were enclosed in PVC fencing fitted with small (< 5 cm) holes on the sides and bottom to prevent grazing by larger fish but allowing access of smaller bodied grazers such as *E. mathai* urchins, (c) 'urchin exclusion' cages (UE) which were open on to fish grazing from above and below, but had inverted funnels fixed to the side of the cage to prevent urchin access, and (d) 'control' cages (C) which were unmodified.

To allow monitoring and maintenance access, a hinged opening held together with industrial-grade plastic Velcro TM was fitted to the full- and fish-exclusion cages. Four cages representing each grazing treatment were mounted on a PVC rack and each rack was bolted to the substratum using a pneumatic drill operated on SCUBA. Although independent cages would have been preferable from a statistical perspective (Mundy 2000), the logistic difficulty of drilling individual cages into the dense rock at this site necessitated the use of racks. Six replicate racks were spaced approximately 3 – 5 m apart, for a total deployment of 24 cages, with the order of treatments randomized on each rack. Racks and cages were cleaned of fouling organisms approximately biweekly through the course of the experiment.

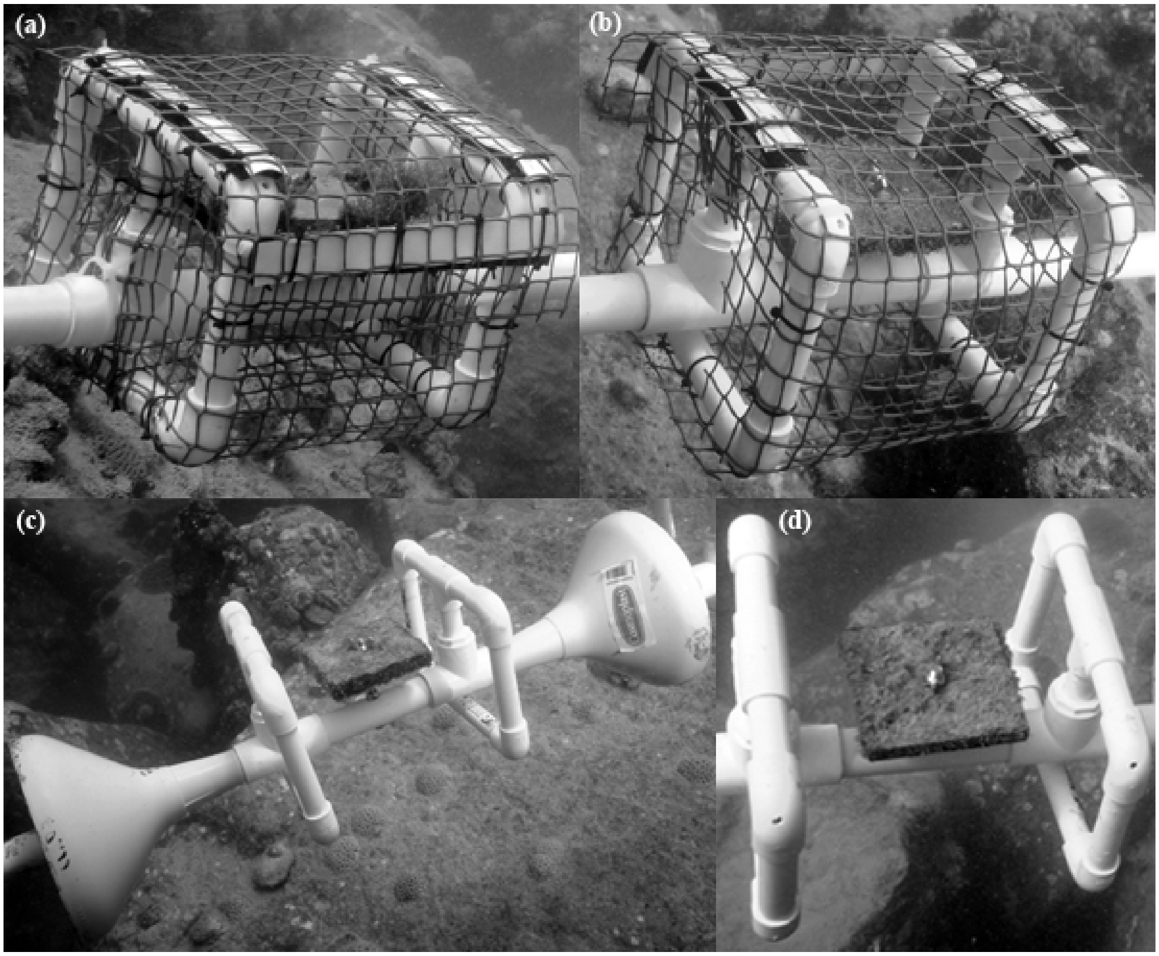

Figure 1. Photographs of experimental cages used for grazer exclusion. (a) Full cage, (b) fish exclusion, (c) urchin exclusion, and (d) control.

To monitor benthic development through time, the upper and lower surface of each tile was photographed at 2, 4, 8, 12, and 24 weeks. Each tile was removed from the cage by its sides and placed on frame-mounted bolt designed to hold tiles at a standardized distance and angle from the camera. Photographs of each tile surface (and its label) were captured with a Nikon D80 digital camera fitted with a macro lens at 10 mega-pixel resolution. Images were analyzed using CPCe version 3.4 (Kohler and Gill 2006), with all benthos under 50 randomly placed points identified to the lowest possible taxonomic level to generate percent cover estimates.

Communities associated with the upper and lower surfaces of the tiles were examined separately to avoid possible confounding effects of orientation. Data were pre-treated prior to analyses. Only benthos present in more than 5% of samples were included in analysis to avoid the influence of rare taxa (Tabachnick and Fidell 2001). Outlier analysis was performed to identify any samples that were more than two standard deviations from the mean. Three of the 238 samples were identified as outliers and these were removed from subsequent analysis. All data were normalized using square root transformations.

A repeated measures analysis of variance (ANOVA) was used to compare the cover of individual benthic components among grazing treatments and sampling dates. To avoid violations of assumptions of sphericity and compound symmetry associated with univariate analyses, Pillai's Trace multivariate test for repeated measures was used to assess interactions.

In addition to changes in individual benthos, changes in overall community structure were explored using multivariate analyses. To separate the effects of treatment and immersion time any differences among treatments were tested at each sampling period, while a separate test of differences among time periods was performed within each treatment using one-way analyses of similarity (ANOSIM) and illustrated using non-metric multidimensional scaling (NMS) ordinations. A two-way ANOSIM test crossing time and treatment would be inappropriate as the repeated measures of tile benthos are not independent and would represent pseudo-replicates for such an analysis. ANOSIM is a multivariate randomization technique which uses a distance matrix to test for differences between groups assigned a priori; it is analogous to ANOVA but with minimum assumptions (Clarke and Gorley 2006). ANOSIM assesses the null hypothesis of no difference between groups based on an *R*-statistic, with $R \approx 0$ when there are no significant differences among groups and greater differences among communities indicated as *R* approaches ±1. Randomization tests are used to assess the significance of the *R*-value. An *R*-value of <0.25 indicates that groups are barely separable, even if they are found to be significantly different due to large sample sizes (i.e. Type I error) (Clarke and Warwick 2001).

Results

Observation of the exclusion cages over the course of the study indicated that the cages were effective in excluding target organisms while allowing other grazers. The two species of sea urchin here, *Echinometra mathai* and *Diadema setosum*, were never observed within the urchin exclusion treatment nor inside the full exclusion cage, with the exception of a single *E. mathai* recruit that was removed from a full cage. Likewise, the fish exclusion treatment was designed to prevent access to fish >5 cm body width, and none were observed grazing within these cages or the full exclusion treatment. However, fish were observed grazing on the control and urchin exclusion treatment tiles, and sea urchins were observed grazing within the fish exclusion and control tiles.

Benthic communities, pooled across grazing treatment and time since immersion, differed in composition and coverage between the upper and lower tile surface (Table 1). The upper tile surface was mainly dominated by turf algae and bare tile which covered over 90% of the substrates. A higher number of benthic taxa were observed on the underside of tiles, and cover was more equally distributed among benthic categories compared with the upper surface.

Table 1. Percent cover of benthic categories (mean ± SE) associated with upper and lower surface of tiles pooled across all grazing treatments and times since immersion. Only taxa present in more than 5% of samples are included.

Benthos	Upper tile	Lower tile
Coralline algae	3.7 ± 0.7	13 ± 1.3
Turf algae	71.9 ± 2.6	12.4 ± 1.8
Serpulid tubeworms	0.9 ± 0.2	12.7 ± 1.4
Spirorbid tubeworms	-	0.7 ± 0.1
Cirripedia	-	6 ± 0.9
Bivalves	2.2 ± 0.8	16.4 ± 2.7
Gastropods	-	1.2 ± 0.3
Bryozoans	-	3 ± 0.6
Solitary ascidians	-	2.3 ± 0.8
Colonial ascidians	-	4.7 ± 1.6
Bare tile	20.1 ± 2.3	25.6 ± 2.9

Upper tile community

Changes in the cover of individual benthos on the upper surface of tiles over time in each grazing treatment are illustrated in Figure 2. Repeated measures ANOVA showed significant interactions among grazing treatments, time since immersion, and individual benthos (Pillai's trace $F_{(48,21)} = 5.4$, $p < 0.001$).

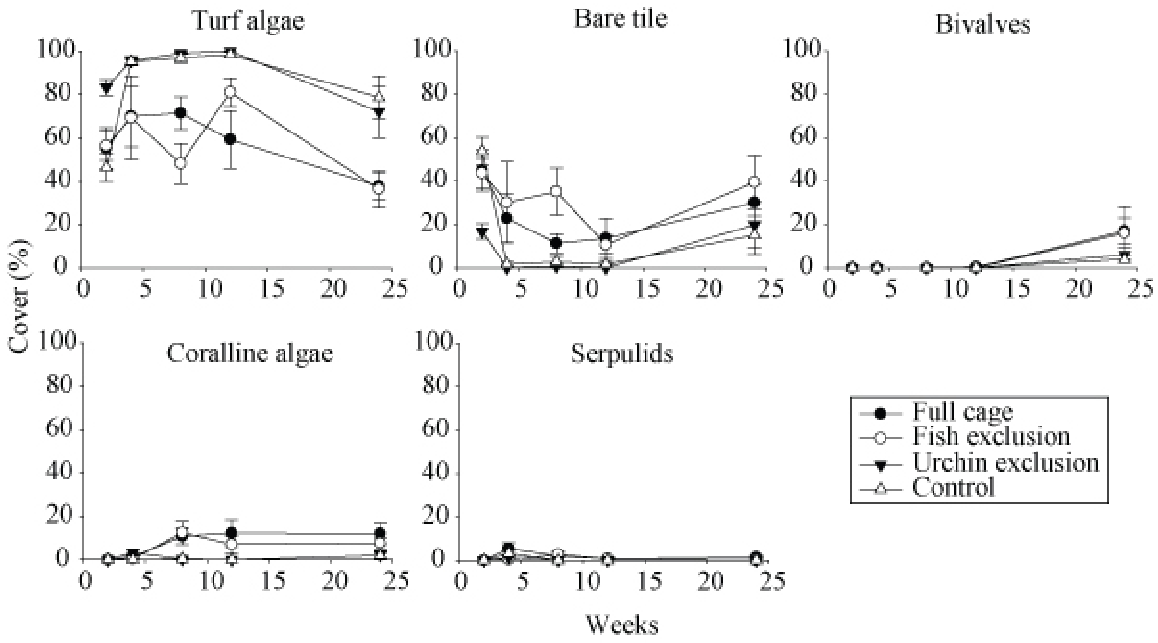

Figure 2. Changes in percent cover of benthic components on the upper surface of tiles over time for each grazing treatment.

Differences among grazing treatment, immersion time, and benthos were further explored using post-hoc Tukey's HSD tests. Turf algae dominated the benthos across sampling periods, but its cover varied among weeks and grazing treatments (Figure 2). The highest turf cover was found in urchin exclusion treatments, which contained significantly more turf than fish exclusion and full cages over every sampling period ($p < 0.05$ each). Although turf algae was lower in control treatments than in urchin exclusion treatments during week 2 ($p < 0.05$), it had increased to comparable levels by week 4 and did not differ for the remainder of the study. By week 8 turf algae in the control treatment had become significantly higher than in the full cage and fish exclusion treatments and remained so during each subsequent sampling period ($p < 0.05$ each). Although there appears to be a decline in turf algae cover from week 12 to 24 in all treatments, this was significant only in fish exclusion cages ($p < 0.05$).

The amount of bare tile cover generally inversely reflected changes in the growth of turf cover over time (Figure 2). With the exception of a decline in bare tile from week 2 to week 4 in the control group (Tukey's HSD: $p < 0.05$), there were no significant changes in bare tile over time in any treatments. Due to the dominance of turf in the urchin exclusion and control treatments (Figure 2), these treatments had significantly lower bare tile than the fish exclusion treatment at the close of the experiment.

The remaining taxa observed on the upper tile surface, coralline algae, serpulid tubeworms, and bivalves, did not vary significantly among grazing treatments and/or weeks since immersion ($p > 0.05$ for all).

In addition to changes in individual benthos, ANOSIM showed that overall community structure differed significantly among grazing treatments during several sampling periods on the upper tile surfaces (Table 2). During weeks 2, 8, and 12, benthic communities differed significantly among grazing treatments. Pair-wise comparisons among treatments show significant differences in overall community structure in many of the same treatment-time combinations where significant differences in turf cover were observed with repeated measures ANOVAs, above. During week 2, significant differences in community structure were observed between urchin exclusion treatment and all other treatments. By week 8, both the urchin exclusion and control treatments differed significantly from the full cage and fish exclusion treatments, and the urchin exclusion treatment remained significantly different from these latter treatments through week 12. The similarity of the results from ANOSIM and repeated measures ANOVA reflects the dominance of turf in the benthic assemblage, and indicates that this group is driving overall community differences.

Table 2. Comparison of benthic communities among all grazing treatments (overall) for each time period on the upper tile surface from ANOSIM. Pair-wise R-values are provided where significant. Asterisks indicate significance ($p<0.05$: *; $p<0.01$:**; $p<0.001$:***).

Time period	Overall comparison		Pair-wise comparisons					
	R-value	p-value	C-FC	C-FE	C-UE	FC-FE	FC-UE	FE-UE
Week 2	0.22	$p < 0.01$			0.74**		0.26*	0.47**
Week 4	0.08	ns						
Week 8	0.40	$p < 0.001$	0.38*	0.78**			0.39*	0.84**
Week 12	0.22	$p < 0.01$					0.34**	0.37*
Week 24	0.12	ns						

It should be noted, however, that the overall R-values during week 2 and week 12 were low (Table 2), indicating substantial overlap in benthic community structure among grazing treatments during these time periods, despite being significantly different. Likewise, there is only a moderate difference among treatments in week 8. The relatively weak strength of differences between communities are reflected in the considerable overlap among treatments in NMS ordinations during any of the time periods examined on the upper tile surface, including those that were shown to be significantly different in ANOSIM (Figure 3). Overall, these results indicate that although there were statistically significant differences in individual community components and in overall community structure among grazing treatments, these differences are unlikely to be biologically significant.

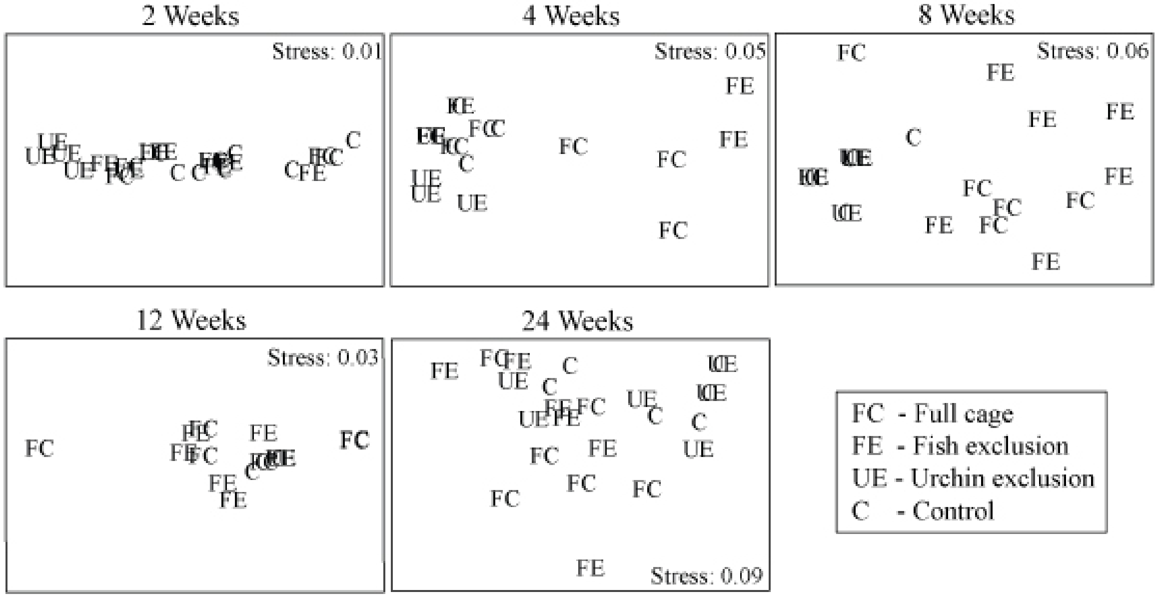

Figure 3. NMS ordinations of upper tile benthic communities among grazing treatments by week since immersion.

The only significant difference related to grazing in univariate and multivariate analyses was due to differences in turf cover, and this was likely the result of caging effects. Univariate results indicated higher turf abundance in the control and urchin exclusion treatments with tiles open to the surrounding water column, while turf cover was low and bare tile high in the fish exclusion and full exclusion treatments which were surrounded by caging (Figure 1; Figure 2), and there were no differences in other benthos. Overall community structure weakly reflected these patterns in multivariate analyses. There was no evidence of difference in benthos among grazing treatments, full exclusion, and control tiles consistent with impacts of either fish or sea urchin grazing on the upper tile surface.

Lower tile community

Changes in the cover of benthos on the undersides of tiles over the course of the study for each treatment are shown in Figure 4. Turf algae did not consistently dominate the lower tile surface as it had the upper surface, and the community was represented by a wider variety of taxa. Repeated measures ANOVA indicated that there were significant differences in cover among benthos and time since immersion (Pillai's $F_{(10,180)} = 313.8$ and $F_{(4,72)} = 8.8$, $p < 0.001$, respectively), but that there were no differences among grazing treatments ($F_{(3,18)} = 1.4$) nor an interaction ($F_{(120,720)} = 1.1$). These results indicate that while there were successional changes in community structure over time as the community developed, these changes were unrelated to grazing by fish or urchins.

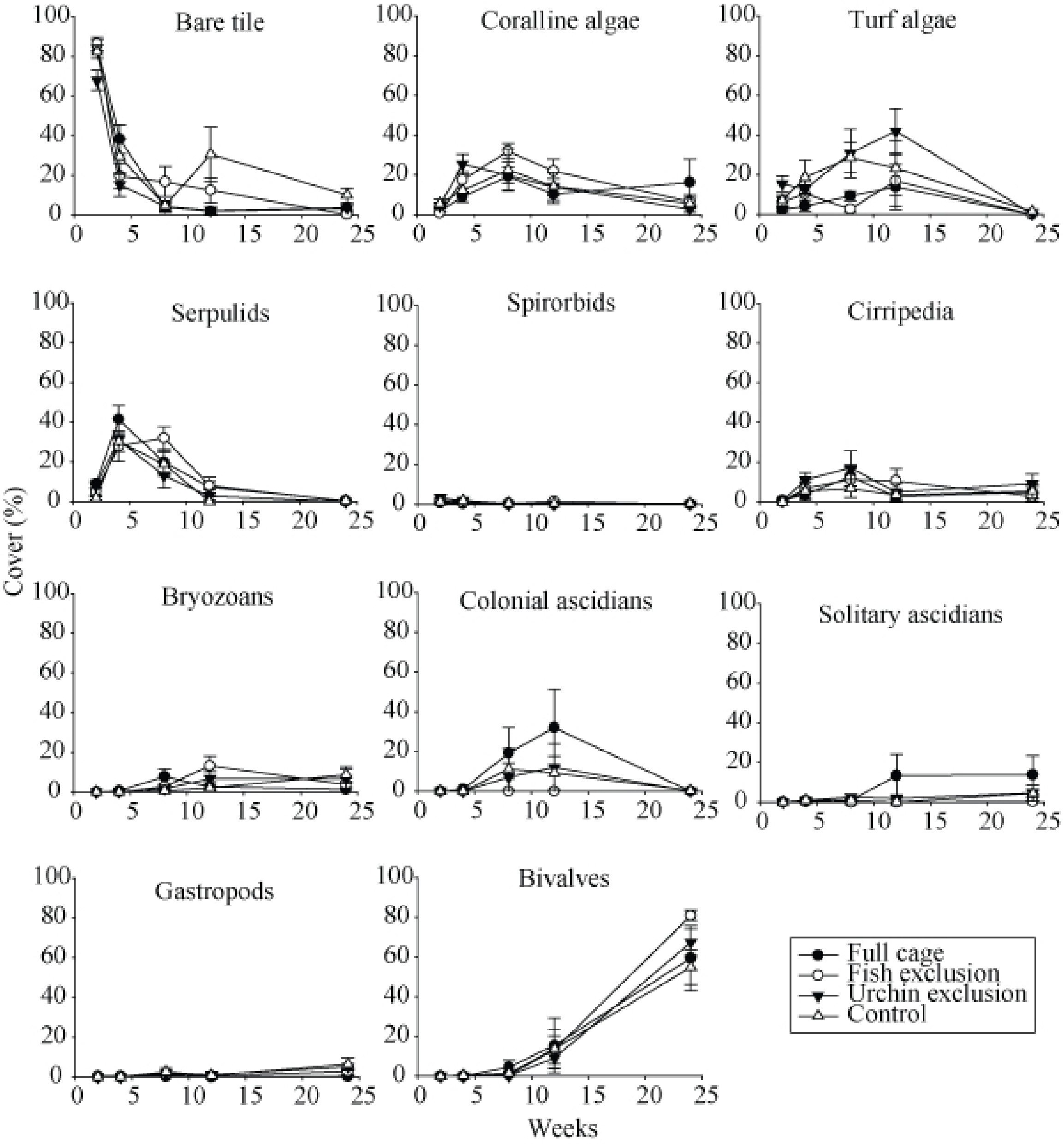

Figure 4. Changes in percent cover of benthic components on the undersides of tiles over time for each grazing treatment.

Post-hoc Tukey's HSD tests were used to examine the changes in relative abundance of benthos over time. During the first sampling period, week 2, most of the tile surface was uncolonized; bare tile represented over four-fifths of the substratum, and was significantly more common than any of the live benthos ($p < 0.001$ each). By week 4 the amount of bare tile had declined significantly ($p < 0.001$) as serpulid tubeworms grew to occupy a third of the tile area, more than all other living organisms ($p < 0.001$ each), except coralline algae. At two months (week 8), benthic cover was dominated by serpulids as well as turf and coralline algae, and each of these groups were significantly more abundant than all other fauna except Cirripedia ($p < 0.05$ for all). Serpulids declined significantly over the next month to Week 12 ($p < 0.001$). During this time, turf algae and bivalves increased in abundance, although not significantly, to cover significantly more space than all fauna except coralline algae, colonial ascidians, and bryozoans ($p < 0.01$). By the close of the experiment three months later (week 24), however, the cover of serpulid tubeworms and turf algae that had previously dominated the benthos had declined significantly from their peak to occupy less than 1% of the cover in combination ($p < 0.001$). This decline was associated with a significant increase in the relative abundance of bivalves from week 12 to week 24 ($p < 0.001$), where bivalves covered over two-thirds of the substrate at the close of the experiment – an order of magnitude higher than any other benthos, and significantly higher than any other benthic category ($p < 0.001$).

Just as cover of individual taxa failed to differ among grazing treatments, multivariate ANOSIM found few changes in overall community structure related to grazing over the course of the study. The only significant differences were observed during the first sampling period, week 2 (Table 3), when the benthic community on the underside of the control group tiles differed from all other treatments, while the urchin exclusion and fish exclusion treatments differed from one another. However, these differences were weak (*R* = 0.29) and are not consistent with any direct influence of grazing. No significant differences among treatments were observed thereafter. The absence of grazing effects were reflected in NMS ordination (Figure 5) which show little separation of communities among grazing treatments during all time periods. Overall, the results of both univariate and multivariate analysis show no evidence that the benthic community on the undersides of the tiles were impacted by grazing activity.

Table 3. Results from ANOSIM analysis of differences in benthic communities among grazing treatments on lower tile surfaces. *R*- and *p*-values are provided for the overall comparison among treatments, as well as separate *R*-values for pair-wise comparisons between treatments. Asterisks indicate significance (p<0.05: *; p<0.01:**; p<0.001:***).

Time period	Overall comparison		Pair-wise comparisons					
	R-value	*p*-value	C-FC	C-FE	C-UE	FC-FE	FC-UE	FE-UE
Week 2	0.29	$p < 0.01$	0.55**	0.33*	0.28*		0.46**	
Week 4	0.06	ns						
Week 8	0.09	ns						
Week 12	0.07	ns						
Week 24	0.12	ns						

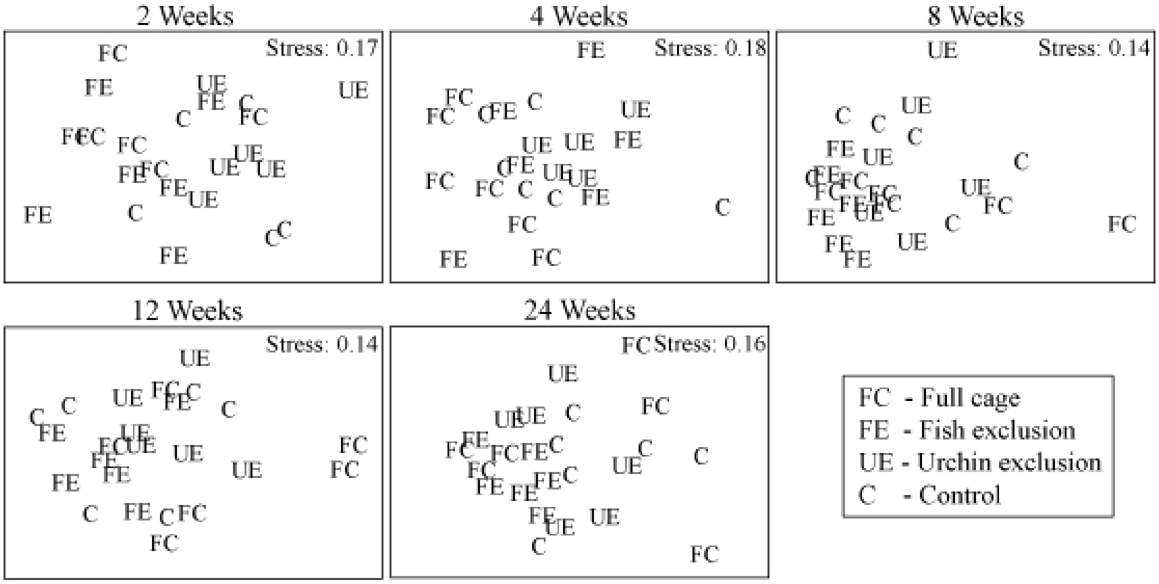

Figure 5. NMS ordinations of the benthic communities on the undersides of tiles among grazing treatments by week since immersion.

Discussion

There were differences in the composition of the benthic community between the upper and lower tile surfaces. On average, over 90% of the upper tile surface was covered with turf algae or was bare, while 11 benthic taxa had relatively equitable cover on the lower tile surface. This is typical of benthic tile communities in tropical systems, where upper tile surfaces are generally low in diversity and dominated by algae while tile bottoms generally contain higher densities and diversity of benthos as a result of differential larval settlement preferences and/or post-settlement survival among tile surfaces (Nzali 1998; Thomason et al. 2002; Adjeroud et al. 2007).

Observations of fish and sea urchin grazing in the field indicated that treatments were effective in excluding or allowing fish and sea urchin grazing on tiles as designed. However, there was no evidence that early benthic community development was influenced by fish or sea urchin grazing. Univariate and multivariate analysis of the upper and lower tile communities indicated that significant differences relating to treatments were few, and were not consistent with impacts due to grazing. These results suggest that the grazing action of fish and sea urchins do not play a substantial role in structuring these tile communities.

The only significant benthic component that showed any significant difference relating to treatment was turf algae on the upper surface of tiles. However, this difference was likely the result of caging artifacts. Univariate analysis indicated that there was higher turf algae cover in the control and urchin exclusion treatments than in the fish exclusion and full cage treatments from the first month. Both the control and urchin exclusion treatment tiles were open to the surrounding water column (see Figure 1), while the fish exclusion and full cages were surrounded by mesh caging material. Mesh caging material can reduce water flow, increase sedimentation rates, and decrease light intensity (Schmidt and Warner 1984; Kennelly 1991; Connell 1997a; Miller and Gaylord 2007). These cage effects could result in lower supply of algal spores, decreased growth or higher mortality of turf algae, providing a probable explanation of the lower abundance of turf in the full cage and fish exclusion treatments. The lack of consistent differences in turf cover between the control tiles, the urchin exclusion, and the full cage, which also would have excluded urchins, indicates that these differences were likely unrelated to grazing activity. These differences in turf cover drove changes in multivariate community structure among treatments as well. However, the few significant differences between treatments were weak, and there was considerable overlap of communities among grazing treatments in ordination. Altogether, these results indicate that differences in turf algae among treatments resulted from caging effects, and that there were no consistent effects of grazing by either fish or urchins on the wider benthic community.

In the absence of impacts by grazers, benthic community succession was consistent among treatments. On the upper tile surface, turf algae dominated the benthic community within a month of immersion and remained dominant through the course of the study. Such long-term dominance by turf algae is common on substrates where grazing pressure is limited (McClanahan 1997), further supporting the suggestion that there was limited grazing activity on the tiles during this study. However, community development on the lower tile surface was much more dynamic. A month after immersion, the amount of bare tile declined as serpulid tubeworms established dominance. Serpulids are frequently among the most abundant early colonists (Chalmer 1982; Lin and Shao 2002; Manoudis et al. 2005) and settle preferentially to bare surfaces (Dean 1981). Serpulids remained relatively abundant during the following month, while cover of turf and coralline algae had increased to comparable levels. By the third month, however, the relative abundance of serpulids had declined, while turf algae and bivalve cover increased such that they were more common than almost all other benthos. Serpulid abundance commonly declines as benthic communities develop through time (Lin and Shao 2002; Manoudis et al. 2005), and it is likely that their decreased abundance here reflects decreased availability of its preferred bare settlement substrates (Dean 1981) as well as the increase in relative abundance of turf and bivalves. Bivalves are considered a later successional species as a result of their low abundance in early community development (Chalmer 1982; Greene and Grizzle 2007), with increased abundance over time likely resulting from their preference for biogenic settlement substrates (Dean 1981; Lindsay et al. 2006). The larvae of the oyster, *Pinctada radiata*, which dominated this bivalve community exhibits preference for carbonate shells (Al-Sayed et al. 1997), and it is likely that the presence of the earlier serpulid colonists facilitated their entry into the tile community. Once bivalves establish in the benthic community they can often come to dominate the substrates by preventing recruitment of earlier successional colonists (Dürr and Wahl 2004; Lindsay et al. 2006) or attracting gregarious conspecific settlers (Chalmer 1982; Al-Sayed et al. 1997; Johnson and Geller 2006). By six month, bivalves covered two-thirds of the tile substrates examined here and were significantly more abundant than any other benthos. As well, cover of the serpulid tubeworms and turf algae which had dominated during earlier periods has virtually disappeared, indicating that their presence likely does inhibit the growth and/or recruitment of these taxa. Overall, these results show that while grazing did not impact community development, there was a consistent successional sequence on these tiles.

References

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. Journal of Experimental Marine Biology and Ecology 341: 204-218

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Al-Sayed H, Al-Rumaidh M, Nayar N (1997) Spat settlement and growth of yearling of the pearl oyster *Pinctada radiata* in Bahrain water. Arab Gulf Journal of Scientific Research 15: 467-480

Almany G, Webster M (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25: 19-22

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Benedetti-Cecchi L (2000) Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. Ecological Monographs 70: 45-72

Bertness M, Trussel G, Ewanchuk P, Sillman B, Crain C (2004) Consumer-controlled community states on Gulf of Maine rocky shores. Ecology 85: 1321-1331

Briscoe CS, Sebens KP (1988) Omnivory in *Strongylocentrotus droebachiensis* (Müller) (Echinodermata: Echinoidea): predation on subtidal mussels. Journal of Experimental Marine Biology and Ecology 115: 1-24

Cebrian E, Uriz MJ (2006) Grazing on fleshy seaweeds by sea urchins facilitates sponge *Cliona viridis* growth. Marine Ecology-Progress Series 323: 83-89

Chalmer PN (1982) Settlement patterns of species in a marine fouling community and some mechanisms of succession. Journal of Experimental Marine Biology and Ecology 58: 73-85

Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs - I: Dietary analyses. Marine Biology 140: 613-623

Clarke K, Gorley R (2006) PRIMER v6: User Manual. PRIMER-E Ltd, Plymouth, UK

Clarke K, Warwick R (2001) Change in marine communities: An approach to statistical analysis and interpretation. PRIMER-E Ltd, Plymouth, UK

Cobb J, Lawrence J (2005) Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. Marine Ecology-Progress Series 295: 171-182

Connell J, Slatyer R (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. The American Naturalist 111: 1199-1144

Connell S, Anderson M (1999) Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. Journal of Experimental Marine Biology and Ecology 241: 15-29

Connell SD (1997) Exclusion of predatory fish on a coral reef: The anticipation, pre-emption and evaluation of some caging artefacts. Journal of Experimental Marine Biology and Ecology 213: 181-198

Crossman D, Choat J, Clements K (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. Marine Ecology-Progress Series 296: 129-142

Dean T (1981) Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. Marine Biology and Ecology 53: 163-180

Dürr S, Wahl M (2004) Isolated and combined impacts of blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) on structure and diversity of a fouling community. Journal of Experimental Marine Biology and Ecology 306: 181-195

Endo H, Nakabayashi N, Agatsuma Y, Taniguchi K (2007) Food of the sea urchins Strongylocentrotus nudus and Hemicentrotus pulcherrimus associated with vertical distributions in fucoid beds and crustose coralline flats in northern Honshu, Japan. Marine Ecology-Progress Series 352: 125-135

Field S, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs 26: 279-289

Gobler CJ, Thibault DB, Davis TW, Curran PB, Peterson BJ, Liddle LB (2006) Algal Assemblages Associated With Stegastes Sp Territories on Indo-Pacific Coral Reefs: Characterization of Diversity and Controls on Growth. Journal of Experimental Marine Biology and Ecology 336: 135-145

Gosselin L, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. Marine Ecology-Progress Series 146: 265-282

Greene JK, Grizzle RE (2007) Successional development of fouling communities on open ocean aquaculture fish cages in the western Gulf of Maine, USA. Aquaculture 262: 289-301

Hansen B (2005) Artificial islands reshape Dubai coast. Civil Engineering 75: 12-13

Harley C (2006) Effects of physical ecosystem engineering and herbivory on intertidal community structure. Marine Ecology-Progress Series 317: 29-39

Hata H, Nishihira M, Kamura S (2002) Effects of habitat-conditioning by the damselfish *Stegates nigricans* (Lacepede) on the community structure of benthic algae. Journal of Experimental Marine Biology and Ecology 280: 95-116

Hill MS (1998) Spongivory on Caribbean reefs releases corals from competition with sponges. Oecologia 117: 143-150

Himmelman JH, Cardinal A, Bourget E (1983) Community development following removal of urchins, *Strongylocentrotus droebachiensis* , from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. Oecologia 59: 27-39

Hixon M, Brostoff W (1996) Succession and herbivory: Effects of differential fish grazing on Hawaiian coral-reef algae. Ecological Mongraphs 66: 67-90

Hurlbut C (1991) Community recruitment: Settlement and juvenile survival of seven co-occurring species of sessile marine invertebrates. Marine Biology 109: 507-515

Johnson SB, Geller JB (2006) Larval settlement can explain the adult distribution of *Mytilus californianus* Conrad but not of *M. galloprovincialis* Lamarck or *M. trossulus* Gould in Moss Landing, central California: Evidence from genetic identification of spat. Journal of Experimental Marine Biology and Ecology 328: 136-145

Kennelly SJ (1991) Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. Journal of Experimental Marine Biology and Ecology 147: 207-230

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Diversity and Distributions 11: 139-148

Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geoscience 32: 1259-1269

Korpinen S, Jormalainen V (2008) Grazing effects in macroalgal communities depend on timing of patch colonization. Journal of Experimental Marine Biology and Ecology 360: 39-46

Leinaas H, Hartvig C (1996) Effects of removing sea urchins (*Strongylocentrotus droebachiensis*): Stability of the barren state and succession of kelp forest recovery in the east Atlantic. Oecologia 105: 524 - 536

Lin HJ, Shao KT (2002) The development of subtidal fouling assemblages on artificial structures in Keelung Harbor, northern Taiwan. Zoological Studies 41: 170-182

Lindsay H, Todd C, Fernandes T, Huxham M (2006) Recruitment in epifaunal communities: an experimental test of the effects of species composition and age. Marine Ecology-Progress Series 307: 49-57

Maldonado M, Uriz M (1998) Microrefuge exploitation by subtidal encrusting sponges: Patterns of settlement and post-settlement survival. Marine Ecology-Progress Series 174: 141-150

Manoudis G, Antoniadou C, Dounas K, Chintiroglou CC (2005) Successional stages of experimental artificial reefs deployed in Vistonikos gulf (N. Aegean Sea, Greece): Preliminary results. Belgian Journal of Zoology 135: 209-215

McClanahan T (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reef. Journal of Experimental Marine Biology and Ecology 218: 77-102

McClanahan TR, Cokos BA, Sala E (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. Marine Pollution Bulletin 44: 441-451

Miller LP, Gaylord B (2007) Barriers to flow: The effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. Journal of Experimental Marine Biology and Ecology 344: 215-228

Miller MW, Hay ME (1996) Coral-Seaweed-Grazer-Nutrient Interactions on Temperate Reefs. Ecological Monographs 66: 323-344

Mora C, Sale P (2002) Are populations of coral reef fish open or closed? Trends in Ecology and Evolution 17: 422-428

Mundy C (2000) An appraisal of methods used in coral recruitment studies. Coral Reefs 19: 124-131

Nydam M, Stachowicz JJ (2007) Predator effects on fouling community development. Marine Ecology-Progress Series 337: 93-101

Nzali L, Johnstone, R., Mgaya, Y. (1998) Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. Ambio 27: 717-722

Osman R, Whitlatch R (2004) The control of the development of a marine benthic community by predation on recruits. Journal of Experimental Marine Biology and Ecology 311: 117-145

Osman RW, Whitlatch RB (1996) Processes affecting newly-settled juveniles and the consequences to subsequent community development. Invertebrate Reproduction & Development 30: 217-225

Relini G, Zamboni N, Tixi F, Torchia G (1994) Patterns of sessile macrobenthos community-development on an artificial reef in the Gulf of Genoa (northwestern Mediterranean). Bulletin of Marine Science 55: 745-771

Schmidt GH, Warner GF (1984) Effects of caging on the development of a sessile epifaunal community. Marine Ecology-Progress Series 15: 251-263

Shanks A, Grantham B, Carr M (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13: S159-S169

Tabachnick B, Fidell L (2001) Using multivariate statistics. Allyn and Bacon, Needham Heights MA

Thomason JC, Letissier MDA, Thomason PO, Field SN (2002) Optimising settlement tiles: the effects of surface texture and energy, orientation and deployment duration upon the fouling community. Biofouling 18: 293-304

Wen K, Hsu C, Chen K, Liao M, Chen C, Chen C (2007) Unexpected coral diversity on the breakwaters: potential refuges for depleting coral reefs. Coral Reefs 26: 127

Wright JT, Dworjanyn SA, Rogers CN, Steinberg PD, Williamson JE, Poore AGB (2005) Density-dependent sea urchin grazing: Differential removal of species, changes in community composition and alternative community states. Marine Ecology-Progress Series 298: 143-156

Chapter 8: Discussion

Over 65 km of rocky breakwater have been added to the coastline of Dubai, UAE. This has substantially increased the amount of hard-bottom habitat in the area, where most of the substrate is dominated by sands and silts, and natural reefs are isolated to a series of discontinuous patch reefs in a 10 km near-shore band to the south-west of the city. The results of the preceding study indicates that these breakwaters act as large-scale artificial reefs, supporting diverse and abundant reef communities.

Breakwaters as artificial reefs

Mature breakwaters in Dubai have higher coral cover and seasonally higher fish species richness and abundance than nearby natural reefs (Chapter 4). These breakwaters represent a suitable habitat for juvenile recruitment, with juvenile fish densities comparable to those of natural reefs (Chapter 4), and coral recruitment on one mature breakwater was more than an order of magnitude higher than on natural reefs (Chapter 5). The colonization of these breakwaters occurs early, and community development appears to follow a sequence in which young structures are mainly dominated by a series of fouling communities that change over the first few years of immersion, with coral dominated structures resulting after 25 years. New substrates are colonized by a variety of benthic taxa within weeks of immersion, and benthic community structure begins to change rapidly as early successional species are replaced by later colonists and slower growing organisms over the following months (Chapter 7). The early benthic community structure is consistent across a number of different materials used in the construction of breakwaters (Chapter 5). Over time spans ranging from 1 to 31 yr benthic communities associated with breakwaters appear to follow a predictable sequence of development, with the benthic community becoming more similar to that on natural reefs as coral cover increases with age and other fouling organisms decline in relative abundance (Chapter 3). Corals recruit preferentially to gabbro (Chapter 5), the dominant material used in the construction of breakwaters in this area, indicating that these breakwaters provide a suitable substratum for the development of coral reefs. Corals are among the earliest colonists on breakwaters, with recruits appearing within a year of construction (Chapter 3). Within 5.5 yr, coral communities on breakwaters have patterns of recruitment, mortality, and growth that are comparable to those of natural reefs (Chapter 6), and coral cover increases linearly with age such that it exceeds that of nearby natural reefs within 25 yr (Chapter 3).

Breakwaters versus natural reefs

While breakwaters do represent a substantial artificial reef ecosystem in Dubai, they are not surrogates for natural reefs. Fish species composition and overall community structure differed between breakwaters and natural reefs seasonally, and there is evidence that fish communities function differently between reef types (Chapter 4). Breakwaters had a fish community that was more dynamic than that on natural reefs, mainly due to seasonal movement of adults onto and off of the breakwaters as well as higher seasonal abundance of predators on breakwaters. In addition to fish communities, overall benthic community structure associated with each breakwater examined in Dubai differed from that of natural reefs, regardless of age (Chapter 3). Even on mature breakwaters, coral community composition differed from that of natural reefs, and there was lower diversity than on natural reefs both in terms of species richness and Shannon-Wiener diversity (Chapter 4). Divergence of coral communities on breakwaters from those on natural reefs can be further exacerbated on breakwaters with low wave exposure. Leeward breakwater coral communities had high post-settlement mortality compared with natural reefs, resulting in a low cover coral community characterized by fewer, smaller colonies than those on natural reefs (Chapter 6). Thus, although some aspects of community structure and function are comparable between reef types, there are also substantial differences between breakwater and natural reef communities.

The results of this study increases our understanding of the role that these artificial structures play in the marine environment. This is of particular importance, given the growing demand for coastal development as well as the degradation of natural reefs both here and around the world.

The importance of breakwaters in coastal ecosystems

Breakwaters currently dominate the near-shore marine environment in many areas, and are likely to become more common. Over 65 km of breakwater are currently in place in

Dubai, and this is projected to increase substantially with the completion of several on-going offshore developments. Such development is common in the Arabian Gulf. Over 40% of the Gulf coastline of Saudi Arabia has been developed (Price 1993), and there has been a dramatic rise in the number and volume of breakwaters constructed for developments in Bahrain, Qatar, and Kuwait (Rezai et al. 2004; Al-Jamali et al. 2005). The prevalence of coastal defense structures is not isolated to this region, with breakwaters and related urban structures making up more than half of the coastline in parts of Europe and the Mediterranean (Cencini 1998; Bacchiocchi and Airoldi 2003; Airoldi et al. 2005) and over a quarter of the coastline in Australia's New South Wales (Beeton et al. 2006). Thus, breakwaters are a common feature of coastal areas around the world and can be expected to play an increasingly important role in marine ecosystems with growing development of coastal urban areas.

Implications for community development on breakwaters

The results of the preceding study inform our understanding of how marine communities are likely to develop on these structures. Breakwaters and other off-shore coastal defense structures are typically built in areas dominated by sand, silts, or mud (Baine 2001), and thus represent island-habitats that must be colonized from elsewhere. Due to the two-phase life cycle of most marine organisms, where adults are relatively sedentary but produce larvae which travel varying distances from their natal habitats (Shanks et al. 2003; Kinlan et al. 2005; Paulay and Meyer 2006; Graham et al. 2008), larval supply is one of the main factors controlling early community development.

Several lines of evidence observed in this study suggest that the supply of invertebrate larvae available to colonize these breakwaters is site-specific. Tiles made of different materials developed benthic communities that showed stronger differences among sites than among materials, with each site developing significantly different communities (Chapter 5). This indicates that site-specific patterns of larval supply were more important that substrate material in determining early benthic community structure. Similar site-specific patterns were also observed with corals. Juvenile coral composition on the natural reef sites closely resembled that of the surrounding adult assemblages (Chapter 2), and the composition of recruits and juveniles on the Palm Jumeirah breakwater resembled that of the community associated with surrounding cap-rock outcrops (Chapter 6), suggesting localized recruitment in both cases. In addition, the abundance of coral recruits on settlement tiles composed of different materials differed by more than an order of magnitude among sites, indicating that the supply of recruits was far more important in driving early development of the coral community than were differences among tile materials, which were apparent at only one site. Such site-specific development has also been observed in other regions, where colonizing assemblages on coastal defense structures differed depending on their location and their distance from natural hard-bottom reefs (Airoldi et al. 2005). These results indicate that at least during the early stages of development, localized patterns of recruitment are likely to be important in determining the structure of the benthic communities associated with newly constructed breakwaters.

The localized recruitment patterns structuring early benthic community development reflect the relatively limited dispersal time and distances of many benthic invertebrates (Kinlan and Gaines 2003; Shanks et al. 2003). However, fish generally have much longer pelagic larval durations and larger dispersal distances than benthic invertebrates (Shanks et al. 2003), with most reef fish populations considered more open than closed (Mora and Sale 2002), resulting in patterns of recruitment that are often decoupled from their local populations. As a result, the localized patterns of recruitment observed for benthic invertebrates may not necessarily apply to fish. Abundance and composition of fish recruits observed here were comparable across two breakwaters and six natural reef sites spanning over 30 km of coastline (Chapter 4), suggesting that recruitment to breakwaters was independent of the distinct adult assemblages observed between breakwaters and natural reefs. This suggests that recruitment patterns of fish on breakwaters are less likely to be associated with site-specific patterns of adult abundance than with stochastic recruitment of pelagic larvae from elsewhere. However, hydrodynamic features of breakwaters may result in eddies which retain larvae close to their natal sites. Given that breakwater do represent large impediments to coastal flow (Smit et al. 2005), such retentive eddies are likely and may result in more localized recruitment than is typically observed on natural reefs. Further exploration of fish recruitment patterns on breakwaters is warranted.

Differences in environmental conditions related to wave exposure are likely to further modify recruitment-driven differences in community structure on newly constructed breakwaters. Although coral recruitment was comparable between windward and leeward sites associated with breakwaters examined here, there was proportionally higher early post-settlement mortality on leeward sites likely due to increased sedimentation rates and/or associated grazing pressure (Chapter 6). As a result, coral communities on the leeward sites were distinct from those on exposed sites, and were characterized by having a low-cover coral community made up of less abundant and smaller colonies compared with windward areas. Unpublished data indicate that these differences extend to the wider community, with leeward sites tending to have higher abundances of turf algae and bivalves than do windward areas on a number of breakwaters in the area. This reflects findings of a study examining the influence of exposure on breakwater benthic communities throughout Europe, where windward and leeward sites were found to consistently differ in benthic community structure (Moschella et al. 2005). Differences in exposure have also been associated with differences in fish community structure on breakwaters (Clynick 2006), although this was not examined in the current study. Overall, these results indicate that the level of exposure is likely an important factor structuring community development on breakwaters. Further research is necessary to determine the mechanisms driving these differences.

The benthic communities associated with breakwaters will continue to change over time as these structures mature. The benthic communities associated with the youngest breakwaters in the area were dominated by turf and sponges, while those several years older had developed substantial bivalve communities (Chapter 3). This reflects colonization sequences observed on artificial reefs and breakwaters in other areas (Aseltine-Neilson et al. 1999; Bacchiocchi and Airoldi 2003), suggesting this to be a typical pattern of community development. In tropical regions, slower growing corals begin to recruit early in benthic community development (Abelson and Shlesinger 2002; Lam 2003), but may take decades to become dominant members of the benthic assemblage (Perkol-Finkel and Benayahu 2005; Perkol-Finkel et al. 2005). Here, corals were observed recruiting to tile substrates within months of immersion (Chapter 5), and on breakwater substrates within a year (Chapter 3). There was a linear increase in coral cover on breakwaters of different age, with no signs of asymptote on the oldest breakwaters, with coral cover exceeding that of natural reefs after 25 yr. This reflects findings on breakwaters and artificial reefs in other areas, where the fouling and coral communities continued to change over periods exceeding a decade (Abelson and Shlesinger 2002; Perkol-Finkel and Benayahu 2005; Pinn et al. 2005). Overall, this suggests that newly constructed breakwaters will develop benthic communities that can be expected to continue changing over periods of years, and that more than three decades may be required for development of a relatively stable benthic community structure.

Fish communities associated with breakwaters are also likely to follow successional patterns over time, although the sequence may be more dynamic. Following initial immersion, fish communities associated with breakwaters and other artificial structures generally show increased species richness and diversity with time (Clark and Edwards 1999; Abelson and Shlesinger 2002; Perez-Ruzafa et al. 2006). With the development of the benthic community, particularly corals, it is likely that fish species associated with particular benthic organisms for food, shelter, or settlement habitat will follow similar successional patterns. However, breakwaters and other artificial structures often have dynamic patterns of recruitment and have an adult assemblage that often changes significantly due to seasonal migration, as was observed here (Chapter 4; Bohnsack et al. 1994; Lincoln-Smith et al. 1994; Stephens et al. 1994). Such stochastic patterns may result in a sequence of community change that is less predictable than that of the benthic assemblage.

Grazers were predicted to impact benthic community development (Chapter 7). Both sea urchins and fish are common on breakwaters here and abroad (Guidetti et al. 2005a), and are known to strongly affect the development of communities on natural reefs and other artificial substrates (Relini et al. 1994; Hata et al. 2002; Osman and Whitlatch 2004; Cebrian and Uriz 2006). These grazers can directly consume and inhibit early successional species, opening space for less competitive but slower recruiting later successional species (Hurlbut 1991; Osman and Whitlatch 1996; 2004). However, the results of the grazing experiment conducted here indicate that the grazing action of fish and sea urchins have limited effects on the development of the benthic community. Further exploration of the factors structuring these communities is warranted.

There has been limited understanding of the role that breakwaters play in marine systems and how their communities develop. Results here indicate that the development of benthic breakwater communities is likely to be site-specific during the early stages as a result of differences in propogule supply and environmental conditions. Over the period of decades, long-term community development is likely to result in assemblages that become more comparable with those of natural reefs. However, such structures will remain distinct from natural reefs. Community structure of both coral assemblages and the wider benthic community was found to differ between breakwaters and natural reefs, even on the most mature 31 yr old breakwater in this area. This long-term difference in community structure between reef types has been observed in the Red Sea, where differences in coral and benthic community composition and abundance continue for over thirty years on artificial structures compared with natural reefs (Perkol-Finkel and Benayahu 2004; Perkol-Finkel et al. 2005; 2006). Similar differences in community structure between breakwaters and natural reefs were observed seasonally for fish. Breakwaters and other coastal defense structures are known to contain fish communities that differ in composition and abundance from those on natural reefs in a wide variety of temperate and tropical locations (Clark and Edwards 1999; Rilov and Benayahu 2000; Edwards and Smith 2005; Clynick et al. 2008), suggesting this to be a widespread phenomenon. Overall, this indicates that breakwater communities are likely to remain distinct from those on nearby natural reefs for periods of decades or longer.

Overall the results of this work suggest that the breakwater communities examined in this study are structured mainly by stochastic processes. The chance supply of larvae was the primary determinant of both coral recruitment and wider benthic community development on tiles (Chapter 5), and coral recruitment to natural reefs was also highly site-specific (Chapter 2). Benthic community development on tiles was also highly variable, with no strong and consistent influence from the grazing action of fish and sea urchins suggested to determine community structure in other areas (Chapter 7). However, the results of this work also indicate that deterministic processes can also play a role in structuring these communities, but to a lesser extent. Coral recruitment to tiles can be structured by the type of material available in the substrates in areas where recruitment is high, but stochastic differences in recruitment among sites appears to be more important in structuring communities (Chapter 5). Wave exposure can also be an important determinant of community structure, with leeward breakwater sites having low-cover coral communities dominated by small colonies with relatively high mortality (Chapter 6). Thus, a combination of stochastic and deterministic processes have been shown to structure communities on these breakwaters, with chance processes playing a more important role in this systems.

Implications for the future

The difference in community structure between breakwaters and natural reefs is of importance given that natural reef systems are becoming increasingly degraded around the world due to overfishing, deteriorating water quality, and climate change (Carpenter et al. 2008; Maliao et al. 2008; De'ath et al. 2009). With the impacts of climate change expected to increase in frequency and magnitude over the coming decades (Sheppard 2003), it is likely that natural reefs will continue to be degraded. The results of the studies conducted here indicate that breakwaters may partially mitigate these impacts by providing alternative habitat for the development of marine communities, perhaps reducing impacts on commercially important organisms such as fish. However, communities associated with breakwaters differ from those on natural reefs, and will not serve as surrogates for communities on natural reefs.

References

Abelson A, Shlesinger Y (2002) Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. Journal of Marine Science 59: 122-126

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52: 1073-1087

Al-Jamali F, Bishop JM, Osment J, Jones DA, LeVay L (2005) A review of the impacts of aquaculture and artificial waterways upon coastal ecosystems in the Gulf (Arabian/Persian) including a case study demonstrating how future management may resolve these impacts. Aquatic Ecosystem Health & Management 8: 81-94

Aseltine-Neilson D, Bernstein B, Palmer-Zwahlen M, Riege L, Smith R (1999) Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. Bulletin of Marine Science 65: 37-57

Bacchiocchi F, Airoldi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine Coastal and Shelf Science 56: 1157-1166

Baine M (2001) Artificial reefs: A review of their design, application, management and performance. Ocean & Coastal Management 44: 241-259

Beeton R, Buckley KI, Jones GJ, Morgan D, Reichelt RE, Trewin D (2006) Australia - State of the environment 2006. Department of the Environment and Heritage, Canberra

Bohnsack J, Harper D, McClellan D, Hulsbeck M (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bulletin of Marine Science 55: 796-823

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321: 560-563

Cebrian E, Uriz MJ (2006) Grazing on fleshy seaweeds by sea urchins facilitates sponge *Cliona viridis* growth. Marine Ecology-Progress Series 323: 83-89

Cencini C (1998) Physical processes and human activities in the evolution of the Po delta, Italy. Journal of Coastal Research 14: 774-793

Clark S, Edwards AJ (1999) An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. Aquatic Conservation-Marine and Freshwater Ecosystems 9: 5-21

Clynick BG (2006) Assemblages of fish associated with coastal marinas in north-western Italy. Journal of the Marine Biological Association of the United Kingdom 86: 847-852

Clynick BG, Chapman MG, Underwood AJ (2008) Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33: 140-150

De'ath G, Lough JM, Fabricius KE (2009) Declining Coral Calcification on the Great Barrier Reef. Science 323: 116-119

Edwards RA, Smith SDA (2005) Subtidal assemblages associated with a geotextile reef in south-east Queensland, Australia. Marine and Freshwater Research 56: 133-142

Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27: 529-539

Guidetti P, Bussotti S, Boero F (2005) Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic Sea. Marine Environmental Research 59: 333-348

Hata H, Nishihira M, Kamura S (2002) Effects of habitat-conditioning by the damselfish *Stegates nigricans* (Lacepede) on the community structure of benthic algae. Journal of Experimental Marine Biology and Ecology 280: 95-116

Hurlbut C (1991) Community recruitment: Settlement and juvenile survival of seven co-occurring species of sessile marine invertebrates. Marine Biology 109: 507-515

Kinlan B, Gaines S (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84: 2007-2020

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Diversity and Distributions 11: 139-148

Lam K (2003) Coral recruitment onto an experimental pulverised fuel ash-concrete artificial reef. Marine Pollution Bulletin 46: 642-653

Lincoln-Smith M, Hair C, Bell J (1994) Man-made rock breakwaters as fish habitats: Comparisons between breakwaters and natural reefs within an embayment in southeastern Australia. Bulletin of Marine Science 55

Maliao RJ, Turingan RG, Lin J (2008) Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. Marine Biology 154: 841-853

Mora C, Sale P (2002) Are populations of coral reef fish open or closed? Trends in Ecology and Evolution 17: 422-428

Moschella PS, Abbiati M, Aberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelof A, Thompson RC, Hawkins SJ (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52: 1053-1071

Osman R, Whitlatch R (2004) The control of the development of a marine benthic community by predation on recruits. Journal of Experimental Marine Biology and Ecology 311: 117-145

Osman RW, Whitlatch RB (1996) Processes affecting newly-settled juveniles and the consequences to subsequent community development. Invertebrate Reproduction & Development 30: 217-225

Paulay G, Meyer C (2006) Dispersal and divergence across the greatest ocean region: Do larvae matter? Integrative and Comparative Biology 46: 269-281

Perez-Ruzafa A, Garcia-Charton JA, Barcala E, Marcos C (2006) Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: The Mar Menor (Spain, Western Mediterranean): Recent developments in estuarine ecology and management. Marine Pollution Bulletin 53: 107-120

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23: 195-205

Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Marine Environmental Research 59: 79-99

Perkol-Finkel S, Shashar N, Barneah O, Ben-David-Zaslow R, Oren U, Reichart T, Yacobovich T, Yahel G, Yahel R, Benayahu Y (2005) Fouling reefal communities on artificial reefs: does age matter? Biofouling 21: 127-140

Perkol-Finkel S, Shashar N, Benayahu Y (2006) Can artificial reefs mimic natural reef communities? The roles of structural features and age. Marine Environmental Research 61: 121-135

Pinn EH, Mitchell K, Corkill J (2005) The assemblages of groynes in relation to substratum age, aspect and microhabitat. Estuarine Coastal and Shelf Science 62: 271-282

Price ARG (1993) The Gulf - human impacts and management initiatives. Marine Pollution Bulletin 27: 17-27

Relini G, Zamboni N, Tixi F, Torchia G (1994) Patterns of sessile macrobenthos community-development on an artificial reef in the Gulf of Genoa (northwestern Mediterranean). Bulletin of Marine Science 55: 745-771

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson C (ed) Status of coral reefs of the World: 2004. Australian Institute of Marine Science, Townsville, pp 155-169

Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Marine Biology 136: 931-942

Shanks A, Grantham B, Carr M (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13: S159-S169

Sheppard C (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425: 294-297

Smit F, Mocke G, Al-Zahed K (2005) Quantifying and managing the coastal response to major offshore developments in Dubai Proceedings of the 14th Biennial Coastal Zone Conference. NOAA Coastal Services Center, New Orleans, Louisiana

Stephens J, Morris P, Pondella D, Koonce T, Jordan G (1994) Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California, USA, 1974-1991: A recruitment driven system. Bulletin of Marine Science 55: 1224-1239

APPENDIX

Appendix 1: Springer Rightslink Copyright License for Chapter 2

This is a License Agreement between John Burt ("You") and Springer ("Springer"). Please note that you are liable to account for Value Added Tax (VAT). The license consists of your order details, the terms and conditions provided by Springer, and the payment terms and conditions.

License Number	2017451166139
License date	Aug 28, 2008
Licensed content publisher	Springer

Licensed content publication Marine Biology

Licensed content title Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates

Licensed content author J. Burt

Licensed content date Apr 1, 2008

Volume number 154

Issue number 1

Pages 27 - 36

Type of Use Thesis / Dissertation

Details of use Print; Restricted Access Intranet; University Intranet

Requestor Type Individual

Portion of the article Full text

Title of your thesis Community development on large-scale artificial reefs with a comparison to natural reefs

Expected completion date May 2009

Total 0.00 USD

Terms and Conditions

Introduction The publisher for this copyrighted material is Springer Science + Business Media. By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the Billing and Payment terms and conditions established by Copyright Clearance Center, Inc. ("CCC"), at the time that you opened your Rightslink account and that are available at any time at http://myaccount.copyright.com).

Limited License With reference to your request to reprint in your thesis material on which Springer Science and Business Media control the copyright, permission is granted, free of charge, for the use indicated in your enquiry. Licenses are for one-time use only with a maximum distribution equal to the number that you identified in the licensing process.

This License includes use in an electronic form, provided it is password protected or on the university's intranet, destined to microfilming by UMI and University repository.

VITA AUCTORIS

John Burt was born in 1974 in Sydney, Nova Scotia. He received a Bachelor of Science from the Cape Breton University in 1996, a Master of Science from the University of Windsor in 1998, and a Post-Graduate Certificate in Education from the University of Sunderland (U.K.) in 2004. He is currently a candidate for a Doctor of Philosophy at the University of Windsor, and will be graduating in 2009.