Fulton, Christopher John (2005) ***Wave energy and the role of swimming in reef fish ecology*****. PhD thesis, James Cook University.**

Wave energy and the role of swimming in reef fish ecology.

Thesis submitted by

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in July 2005

for the degree of Doctor of Philosophy in Marine Biology
within the School of Marine Biology and Aquaculture,
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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisor Prof. David Bellwood, and Prof. Peter Wainwright (University of California, Davis). While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, financial support, technical instruction and editorial assistance.

Financial support for the project was provided by the Australian Coral Reef Society, Lizard Island Reef Research Foundation, James Cook University, and my supervisor Prof. David Bellwood. Stipend support was provided by an Australian Postgraduate Award, and James Cook University.

Acknowledgements

I wish to say a special thanks to the people who gave me sound advice during the course of this project. I am particularly grateful to my supervisor, David Bellwood, who never failed to provide thought-provoking conversations, personal encouragement and insightful comments with just the right balance of criticism and praise. A special thanks also to Peter Wainwright for his perceptive advice and helping me to develop a deeper understanding of the principles of ecomorphology. I also benefited from the helpful advice and comments of Howard Choat and John Steffensen. Thanks to Mark Westneat, Jeff Walker and Rebecca Fisher for constructive comments on flow tank design and performance protocols, and to Peter Ridd, Thomas Stieglitz and Severine Thomas for invaluable advice on the wave energy assessments. Comments from my supervisor, Amara Thomas, colleagues in the Reef Fish Lab, and several anonymous reviewers on the published components benefited me greatly during the writing of this thesis.

I also owe a debt of gratitude to the many people who provided assistance with the practical aspects of this project. Thanks to Andrew Harvey, Andrew Hoey, Nicolai Konow, Peter Wruck and Amara Thomas for providing assistance with flow tank construction. Thanks also to Denis Hakansan from Townsville Bureau of Meteorology for providing wind data. Such a field-intensive project would not have been possible without helpful field assistance from John Ackerman, Lachlan Barnes, Katherine Dunn, Neal Cantin, Andrew Hoey, Nicolai Konow, David Wakelin, Tony Sunderland and Amara Thomas. Many thanks to the staff of Lizard Island Research Station, Lyle Vail, Anne Hoggett, Lance & Marianne Pearce, and Robert & Tanya Lamb who provided invaluable field support. Thanks also to my friends down south who provided equipment and logistic support during my temperate field trips: John Simm for the generous use of his time and boat, Terry Fulton for accommodation and Pro-Dive Nelson’s Bay for equipment.

Last and far from least I am thankful for those whose friendship has helped me along the way and made this journey an enjoyable one. My sincere thanks to David & Orpha Bellwood, Neal Cantin, Martial Depczynski, Monica Gagliano, Helen Gilbert, Pernille Hansen, Andrew & Jessica Hoey, Nicolai Konow, Charmaine Read, Thomas Stieglitz and Guthrie Fulton for their personal encouragement and support. Finally, to those who played the largest role in shaping, guiding and supporting me, Mum, Dad, my brother [redacted] and my partner [redacted] whose consistent love and faith gave me the confidence to pursue my passion.

Abstract

Although functional explanations for the influence of wave energy on marine communities have been well reported for sessile taxa, the underlying mechanisms in highly mobile organisms such as reef fishes have remained largely unexplored. The present study compared levels of wave-induced water motion among reef habitats with the swimming mode and performance of resident reef fishes. Encompassing ten families (Acanthuridae, Chaetodontidae, Labridae, Lutjanidae, Nemipteridae, Pomacanthidae, Pomacentridae, Serranidae, Siganidae and Zanclidae), the generality of this functional relationship was examined both among and within swimming modes, and across tropical and temperate reef fish assemblages.

Wave-induced water motion was quantified using Lagrangian and Euler measures of flow across five habitat zones and four exposure regimes commonly found on coral reefs. Significant spatial variations in net flow velocity (7.4 - 43.2 cm s^{-1}) and rates of flow direction change (0.06 - 0.66 Hz) were found among habitats of different depth. Water motion within the crest and flat habitats was largely wave-driven, as rates of flow direction change (0.63 - 0.66 Hz) corresponding closely with surface wave periodicity, with relatively little contribution (14 - 16%) from drift (tidal) flow velocities. Similar spatial variation in wave-induced water motion was found amongst reefs of different exposure (6.2 - 59.5 cm s^{-1}), with exposed and oblique reef crests displaying greater temporal variation in wave height and water motion compared to the relatively static sheltered and lagoonal sites. Overall, average levels of wave energy produced substantial variations in water motion over spatial scales relevant to the distribution and abundance of reef taxa.

Fin use censuses of 5,230 individuals from 117 species revealed three primary modes of swimming: pectoral (labriform, 70 spp.), pectoral-caudal (chaetodontiform, 29 spp.), and caudal (subcarangiform, 18 spp.). Experimental trials of critical swimming speed (U_{crit}) indicated that labriform taxa displayed the highest average speeds in absolute terms (82.4 cm s^{-1}), although considerable overlap was found in the range of experimental speeds displayed among the three modes (9.2 - 82.4 cm s^{-1}). Whilst body shape varied substantially among taxa within the three modes, variations in body depth and cross-sectional profile were not significantly correlated to swimming speed performance. However, direct comparisons between experimental and field speeds revealed a striking separation in performance amongst swimming modes: field speeds in labriform taxa were 83 ± 4 % (mean ± 1 SE) of their experimental speed, whereas field speeds in chaetodontiform and subcarangiform species were 44 ± 2 % and 49 ± 4 % of their experimental speeds, respectively.

Ecological arrangement of these functional attributes in relation to wave-induced water motion was similarly striking among swimming modes. Labriform fishes were the most abundant group, predominating in areas with high levels of water motion, whereas pectoral-caudal and caudal-swimming fishes displayed the opposite trend. These differences reflected the relative swimming performance of the three modes, with most labriform fishes displaying field speeds that matched or exceeded the water flows recorded in wave-swept habitats, compared to the considerably slower speed performances in chaetodontiform and subcarangiform fishes. Further examination of the extensive within-mode variation in labriform taxa revealed an ecomorphological basis in pectoral fin shape. Pectoral fin aspect-ratio (AR) was strongly correlated with swimming speed performance in a similar linear relationship across all three labriform families (Acanthuridae, Labridae and Pomacentridae): species with higher AR fins attained faster size-specific swimming speeds using lift-based thrust. Congruent ecological relationships of increasing pectoral fin AR with increasing water motion in all three families indicated that wave energy has shaped labriform fishes from at least two distinct evolutionary lineages into a common ecomorphological form.

Comparisons between tropical (Great Barrier Reef) and temperate (Port Stephens, New South Wales) labrid assemblages revealed two alternate strategies for occupying wave-swept habitats. Variation in pectoral fin shape in temperate labrids was strongly correlated with swimming speed in a relationship similar to tropical labrids. However, the reduced diversity of pectoral fin AR of temperate labrids (aspect ratios of 0.52 - 1.43) compared to the tropical labrids (0.90 - 2.08) indicated a lack of lift-based swimming taxa in the temperate assemblage. Although fin shape provided some explanation for the distribution of temperate labrids in relation to wave energy, increased swimming speeds through increased body size appeared to be the dominant mechanism by which temperate species occupied wave-swept habitats. In contrast, coral reef labrids dominate wave-swept habitats using high AR pectoral fins and efficient lift-based kinematics, with no discernable difference in size among habitat zones.

Overall, this study found a consistent relationship between the swimming abilities of reef fishes and their distribution in relation to wave energy, with the fastest swimmers occupying the most wave-swept habitats. Biomechanical evidence suggests reef fishes that dominate these wave-swept habitats display high mechanical and energetic efficiency of locomotion. Encompassing fishes from several divergent perciform lineages, these links between swimming performance and wave energy were irrespective of phylogenetic or trophic status, suggesting a strong, overriding influence of wave energy on reef fish distributions. Ultimately, wave energy appears to have interacted in both ecological and evolutionary terms with the locomotor abilities of fishes to provide an underlying theme in reef ecosystems: biophysical interactions between wave energy and swimming performance shape reef fish assemblages.

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General Introduction

Physical factors often have an overriding influence on community composition in both terrestrial and aquatic systems, with the distribution and abundance patterns of species often being determined by interactions between their physiology and physical attributes of the environment. In marine systems, variables such as temperature, salinity, and water motion have been linked to the distribution of species from local to regional biogeographical scales (Beaugrand et al. 2002, Bellwood et al. 2002, Gray 2002, Chevaldonne & Lejeusne 2003). Physical factors can even override biological interactions such as competition and predation, where physical disturbances from extremes in water temperature or wave energy can cause mass mortality and major shifts in community structure (Dayton 1971, Menge 1978, Lassig 1983, Connell 1997, Booth & Beretta 2002). Given that such physical influences may be crucial for the maintenance of biodiversity in marine communities (Steneck & Dethier 1994, Knowlton 2004, McManus & Polsenberg 2004), it is critically important to determine the underlying mechanisms if we are to understand the potential ramifications of changes in these physical conditions.

Linking morphology and performance with ecology

Functional analyses provide a particularly useful means of revealing interactions between organisms and physical factors, as functional attributes are often shaped by environmental challenges (Wainwright & Reilly 1994). Central to this relationship between organisms and their environment are variations in morphology and performance: the ability to accomplish specific tasks or behaviours such as prey capture or predator avoidance (Garland & Losos 1994, Wainwright 1994). For example, predatory fishes require a specific muscle strength to produce the lethal crushing force necessary to consume robust prey (Wainwright 1988), while in birds and bats, flight in enclosed spaces requires short rounded wings versus soaring in open spaces using tapered wings (Norberg 1981, Norberg & Rayner 1987). In each case, measures of morphology and performance can be directly related to ecological parameters to reveal the underlying environmental factors shaping patterns of resource use.

Studies that provide application of such functional information to ecological patterns at the community-level have been particularly revealing. For example, patterns of prey use and foraging in freshwater sunfishes and coral reef fishes have been linked to oral and pharyngeal jaw morphologies (Osenberg & Mittelbach 1989, Huckins 1997, Wainwright & Bellwood 2002, Bellwood 2003). Similarly, patterns of habitat-use have been linked to differences in wing morphology and flight performance in birds and bats (Norberg 1981, 1994), and differences in body size, hindlimb morphology and locomotor performance in *Anolis* lizards (Losos 1992, Beuttell & Losos 1999). By examining communities as functional systems, we can overcome taxonomic limitations to provide crucial insights into ecosystem structure and function in response to both physical and biological challenges. The present study employs a functional approach to examine the interaction between reef fish assemblages and wave energy, a ubiquitous physical forcing agent present in all aquatic ecosystems.

Wave energy in shallow aquatic ecosystems

Wave energy effects are mainfest in all shallow aquatic habitats, with a large body of descriptive evidence linking patterns of community composition with levels of wave exposure in ecosystems such as freshwater lakes and streams (Jackson et al. 2001, Brind' Amour et al. 2005), temperate rocky shores (Lewis 1968, Denny 1994), and tropical coral reefs (Done 1983, Williams 1991). Much of our present knowledge on the nature and impact of wave energy has been provided by studies of rocky intertidal systems, where an early focus on community-level effects provided the first empirical evidence that wave energy plays a major role in shaping rocky intertidal communities by altering rates of predation and competition (Sousa 1979, Paine & Levin 1981). Extreme wave events have been a focal point, as it was believed that such extremes were required for the complete removal of individuals from habitats, creating a substantial disturbance that would ultimately affect patterns of community composition and diversity (Connell 1997, Hughes & Connell 1999). Accordingly, extreme wave events and the maximal velocities or forces needed to damage or dislodge individuals are often considered to be the most important measures of wave-induced water motion for sessile communities (Denny 1988, 1994, Bell & Denny 1994, Gaylord 1999).

Water motion appears to be the critical mediator by which wave energy directly influences benthic marine organisms. Indeed, variations in water motion have been linked with almost all aspects of the biology of benthic organisms, including rates of fertilisation (Denny & Shibata 1989), settlement and dispersal (Bertness et al. 1992, Gaylord et al. 2002), growth (Trussell 2002, Sebens et al. 2003), primary productivity (Klumpp & McKinnon 1992, Carpenter & Williams 1993) and mortality (Shanks & Wright 1986, Bodkin et al. 1987). While extreme wave events and maximal forces have often been the focus of early studies on sessile organisms, daily levels of wave energy have the potential to create considerable levels of water motion. Quantitative measurements from rocky intertidal habitats have recorded daily wave-induced water speeds of up to 2.5 metres s^{-1}, which are equivalent in force to cyclonic wind strengths of over 200 kilometres hr^{-1} on land (Bell & Denny 1994, Denny & Gaylord 2002). Given that these wave forces are repeatedly impacting marine organisms on a daily basis, even average levels of wave energy can impose substantial physical challenges for the occupation of shallow marine habitats.

Functional analyses have been particularly useful in identifying the underlying mechanisms that shape the distribution patterns of species through direct comparisons of wave-induced forces with the functional attributes of organisms. Such studies on rocky intertidal shores have provided our best understanding of the relative abilities of organisms to withstand wave-induced water motion, identifying morphologies that reduce drag and lift forces in echinoderm tests and mollusc shells (Denny 1994, Denny & Gaylord 1996), and increased tensile tissue strengths and simpler branching in algal thalli (Koehl 1988, Gaylord et al. 1994, Friedland & Denny 1995). Species lacking such adaptations to the physical challenges of wave impacts are simply unable to persist under certain levels of wave energy. Consequently, the community composition and diversity of benthic organisms on rocky shores has been strongly linked to extreme levels of wave-induced water motion (Denny 1988, 1995, Koehl 1999, Denny & Gaylord 2002). Most importantly, these studies highlight the utility of functional analyses for understanding the specific impacts of wave energy on marine communities.

Wave energy effects in coral reef assemblages

On coral reefs, similar functional examinations for the impacts of wave energy have largely focused on differences in geomorphology and coral communities. Descriptive evidence indicated repeated variations in coral reef habitats across categorical variations in wave exposure, leading to the development of the exposed-sheltered paradigm according to habitat depth and aspect to prevailing winds (Geister 1977, Bradbury & Young 1981, Done 1983). Early examinations of coral communities focused on variations in skeletal morphology and breakage according to maximum levels of wave energy, identifying ‘wave-resistant morphs’ in shallow wave-swept habitats (Done 1983, Graus & MacIntyre 1989). More recent studies have focused on the importance of water motion for physiological processes in corals, identifying links between water motion and rates of primary production, respiration and calcification (Dennison & Barnes 1988, Patterson et al. 1991, Atkinson et al. 1994, Bruno & Edmunds 1998), capture of particulate matter (Sebens & Johnson 1991, Sebens et al. 1996), uptake of dissolved nutrients (Atkinson & Bilger 1992, Thomas & Atkinson 1997), growth and reproduction (Jokiel 1978) and enhanced recovery from bleaching (Nakamura et al. 2003).

Examination of these effects in an ecological context has been particularly effective for understanding how corals respond to variations in wave energy. Differences in polyp and skeletal morphology have been linked to the physiological performance and structural resilience required by different levels of wave-induced water motion among habitats (Sebens & Done 1992, Sebens 1997). For example, the dominance of tabular *Acropora* species in shallow windward habitats has been attributed to their faster growth due to hydrological conditions that maximise rates of respiration, capture of food particles and uptake of nutrients in these species (Dennison & Barnes 1988, Sebens & Done 1992, Sebens et al. 2003). Conversely, species occurring in sheltered and/or deeper habitats exhibit tolerance for very low flow conditions, whereas widespread coral species are often those capable of utilising a greater range of water flow speeds (Sebens & Done 1992, Sebens et al. 2003). Combined, this evidence has been used to demonstrate that a combination of both average and extreme levels of wave energy contribute to the distribution patterns of corals (Sebens & Johnson 1991, Sebens & Done 1992, Storlazzi et al. 2005).

Wave energy has repeatedly been suggested as a primary physical correlate to the long-term distribution and abundance of coral reef fishes (review Williams 1991). In contrast to sessile organisms, reef fishes appear to be relatively resilient to extreme levels of wave energy. While storms and cyclones have been found to displace some individuals from habitats (Lassig 1983), the vast majority of individuals either endure these short-term extremes or subsequently return from sheltered locations after such events have passed (Walsh 1983, Cheal et al. 2002). Given such tolerances to extremes and the extensive evidence linking the community structure of reef fishes with levels of wave exposure, it appears that average levels of wave energy may be the critical hydrological measure influencing the long-term distribution patterns of reef fishes.

Supply-side mechanisms may play an important role in shaping these variations in reef fish assemblages, with recruitment studies encompassing the same spatial scales identifying variations in larval supply among reefs and habitat-selectivity at settlement (Doherty 1991). Indirect wave energy effects acting through influences on habitat characteristics or trophic resources have also been a major focus in adult fish populations (Jones 1991). However, comparisons between adult fish distribution patterns and the availability of habitats or trophic resources have found mixed results, ranging from extremely high correlations to no discernible effect (e.g. Luckhurst & Luckhurst 1978, Williams et al. 1986, Green 1996, Ormond et al. 1996, Munday et al. 1997, Holbrook et al. 2000, 2002, Syms & Jones 2004). Nonetheless, descriptive evidence indicates that nearly all reef fishes display consistent and predictable variations in distribution patterns across prevailing wave energy gradients (e.g. Williams 1982, Russ 1984a, 1984b, Adjeroud et al. 1998, Gust et al. 2001, Lecchini et al. 2003), regardless of taxonomic affiliation or trophic group.

Could wave energy have a direct and overriding influence on the distribution patterns of reef fishes? Only recently has the possibility of direct wave energy effects on reef fishes been explored, where studies examining the fin morphology of coral reef wrasses revealed a consistent relationship between the inferred swimming abilities of taxa and their distribution across different wave exposures (Bellwood & Wainwright 2001, Fulton et al. 2001, Bellwood et al. 2002). These studies hypothesised that such a relationship was due to an interaction between wave-induced water motion and the differential swimming speed performance of taxa. However, due to a paucity of information on swimming performance and levels of wave-induced water motion at the appropriate scales, these examinations were limited to assumed differences in wave energy and functional predictions of swimming performance across a single family of reef fishes. Consequently, the generality of this relationship is yet to be explored using direct measures of swimming performance from the many fish families that characterise demersal reef fish faunas, and tested against a quantitative gradient of wave energy.

Aims and thesis outline

Using a functional approach, this thesis investigates the relationship between wave energy and the distribution patterns of reef fishes. Quantitative comparisons of wave energy and fish swimming capabilities are used to test the key hypothesis that *the distribution of reef fishes across gradients of wave energy are linked to differences in swimming morphology and performance*. Examining reef fishes from ten families that encompass over half the taxonomic diversity of visually apparent fishes found on coral reefs (Bellwood 1996), the four primary aims of this study were to: (1) quantify variations in wave-induced water movements on coral reefs across a range of habitats and exposures, (2) measure the morphology, swimming mode and performance of an entire assemblage of reef fishes, (3) evaluate the ecological arrangement of reef fishes according to their swimming abilities and levels of wave-induced water motion, and (4) establish if the same functional relationship between wave energy and swimming ability applies in both tropical and temperate reef fish assemblages.

These aims are addressed in a series of five seperate studies according to the chapters outlined below, which largely correspond to the publications derived from this thesis (see Appendix I for full list). **Chapter 1** presents results from a quantitative assessment of the nature and magnitude of water movements produced by wave energy across four exposures and five habitat zones commonly found on coral reefs. **Chapter 2** describes a field assessment of swimming modes in an assemblage of reef fishes, and compares the swimming speed performance of fishes using each mode through both field and experimental estimates of performance. **Chapter 3** combines information from the previous two chapters to provide a direct comparison of the swimming abilities of reef fishes with their distribution across gradients of wave-induced water motion. **Chapter 4** investigates the extensive variation in swimming ability within the diverse mode of labriform-swimming fishes; combining published kinematic analyses with new information on fin morphology and swimming speed performance, this chapter examines the functional basis for differences in performance and ecology within three labriform-swimming fish families. Finally, **Chapter 5** explores the generality of this relationship between morphology, performance and ecology in labriform fishes through comparisons of two taxonomically distinct labrid assemblages from a tropical (Great Barrier Reef) and temperate (Port Stephens) reef system.