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

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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.

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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.

Chapter 1: Wave-induced water motion on coral reefs.

Published in *Limnology & Oceanography* **50,** 255-264.

1.1. Introduction

Wave energy is a prominent physical factor in sub-tidal and intertidal marine ecosystems, where correlations between wave energy and the distribution patterns of species have been well documented (e.g. Lewis 1968, Denny et al 1985, Williams 1991). Functional analyses which have focused on the water movements produced by incident wave energy have been particularly useful for identifying the impacts of wave energy on patterns of distribution and abundance in shallow aquatic ecosystems. Previous examinations of hydrodynamic forces and the functional morphology of sessile organisms on temperate rocky shores have recorded flow velocities up to 25 metres s^{-1}, which have been directly linked to the functional attributes of algae (Gaylord et al. 1994, Koehl 1999, Denny & Gaylord 2002), echinoderms (Denny & Gaylord 1996), gastropods (Denny 2000, Denny & Blanchette 2000) and crabs (Martinez 2001, Lau & Martinez 2003). Community-level effects have also been documented, where the removal of sessile individuals from habitats by wave extremes have produced shifts in competitive interactions and predation rates in rocky intertidal communities (Paine & Levin 1981, Ebeling et al. 1985, Kawamata 1998, McQuaid & Lindsay 2000). Whilst extremes in wave energy can also displace mobile taxa from habitats (Lassig 1983), many either endure short-term extremes or subsequently return after such events have passed (Walsh 1983, Cheal et al. 2002), suggesting that average levels of wave energy may be the relevant hydrodynamic variable shaping the distribution of mobile taxa.

Similar quantitative examinations of the impacts of wave energy on coral reef assemblages have been rare, and predominantly focused on sessile taxa and biogeochemical processes. However, studies that have included quantitative estimates of wave energy have been particularly revealing for coral reef ecosystem function, demonstrating links between wave energy and the mass transfer of nutrients (Crossland & Barnes 1983, Thomas & Atkinson 1997, Hearn et al. 2001), deposition of sediments and detrital matter (Crossman et al. 2001, Purcell & Bellwood 2001) and productivity in algal turfs (Carpenter et al. 1991, Klumpp & McKinnon 1992, Carpenter & Williams 1993). In particular, clear links between the distribution patterns of functional traits in coral communities and levels of wave energy have been provided through direct comparisons with estimates of wave-induced water motion (Dennison & Barnes 1988, Sebens & Done 1992). Combined, these findings have demonstrated the importance of average levels of wave energy for shaping benthic coral reef assemblages according to variations in water motion and the physiological performance of taxa. While these and other wave energy assessments have identified flow velocities in the range of 3-140 cm s^{-1} across sheltered and exposed habitats (Young 1989, Kench 1998, Gourlay & Colleter 2005), estimates of wave-induced water motion specifically targeted to the major spatial variations in fish distribution patterns are yet to be quantified for coral reefs.

Therefore, this study combines five complementary measures to characterize wave-induced water motion across spatial scales relevant to the distribution of mobile organisms on coral reefs. For the first time, water motion produced by average levels of wave energy will be directly quantified for a range of habitats zones and exposures commonly examined in studies of fish distribution and abundance on coral reefs. Specifically, the aims were to: 1) quantify the water movements produced by wave energy on coral reefs over the two spatial gradients of depth and exposure to prevailing winds; and 2) examine the impact of temporal changes in sea conditions on these patterns of water movement.

1.2. Material and Methods

Calibration of gypsum dissolution technique

Gypsum balls were constructed from calcium sulphate hemihydrate (casting plaster manufactured by CSR Limited), mixed in the proportion of 470 g gypsum to 250 g cold water (6°C), and poured into spherical moulds made from rubber tennis balls. A piece of galvanised wire (210 mm long, 2.5 mm thick) embedded in each ball provided an attachment point. Gypsum balls were left to set in the mould for 2 h, then removed and allowed to dry in a low humidity (air-conditioned) room at 25°C until repeated daily weighing revealed a stable mass. Before deployment, the mass, and diameter across an axis parallel to the direction of flow (x-axis), and across axes perpendicular to the flow in the horizontal (y-axis) and vertical planes (z-axis), was recorded for each individually tagged ball. Pre-deployment gypsum balls were selected to be within the limits of 109.0 ± 1.0 g (excluding 8.1 g of wire) in weight, and 54.0 ± 1.0 mm in diameter (all axes). Plaster ball size and density was chosen so that all weight losses (excluding wire) remained within 65% of the original mass to maintain a linear relationship in gypsum dissolution over time, following Jokiel & Morrissey (1993).

Calibration of gypsum dissolution in a flow tank allowed us to convert gypsum dissolution from an overall measure of flow energy to a measure of linear flow velocity in units of cm s^{-1} (Dennison & Barnes 1988). Since gypsum dissolution is strongly related to water temperature (Jokiel & Morrissey 1993), the relationship between flow velocity and gypsum dissolution was examined for the two water temperatures recorded during the field deployments (28°C and 24°C). Dissolution of gypsum balls was examined for seven experimental flow speeds (0, 10, 20, 30, 40, 50, and 60 cm s^{-1}) in a 194 L recirculating flow tank (Fig. 1.1) with water replacement at the rate of 15 L min^{-1}. Each trial was conducted for 24 hours and repeated three times at each flow velocity

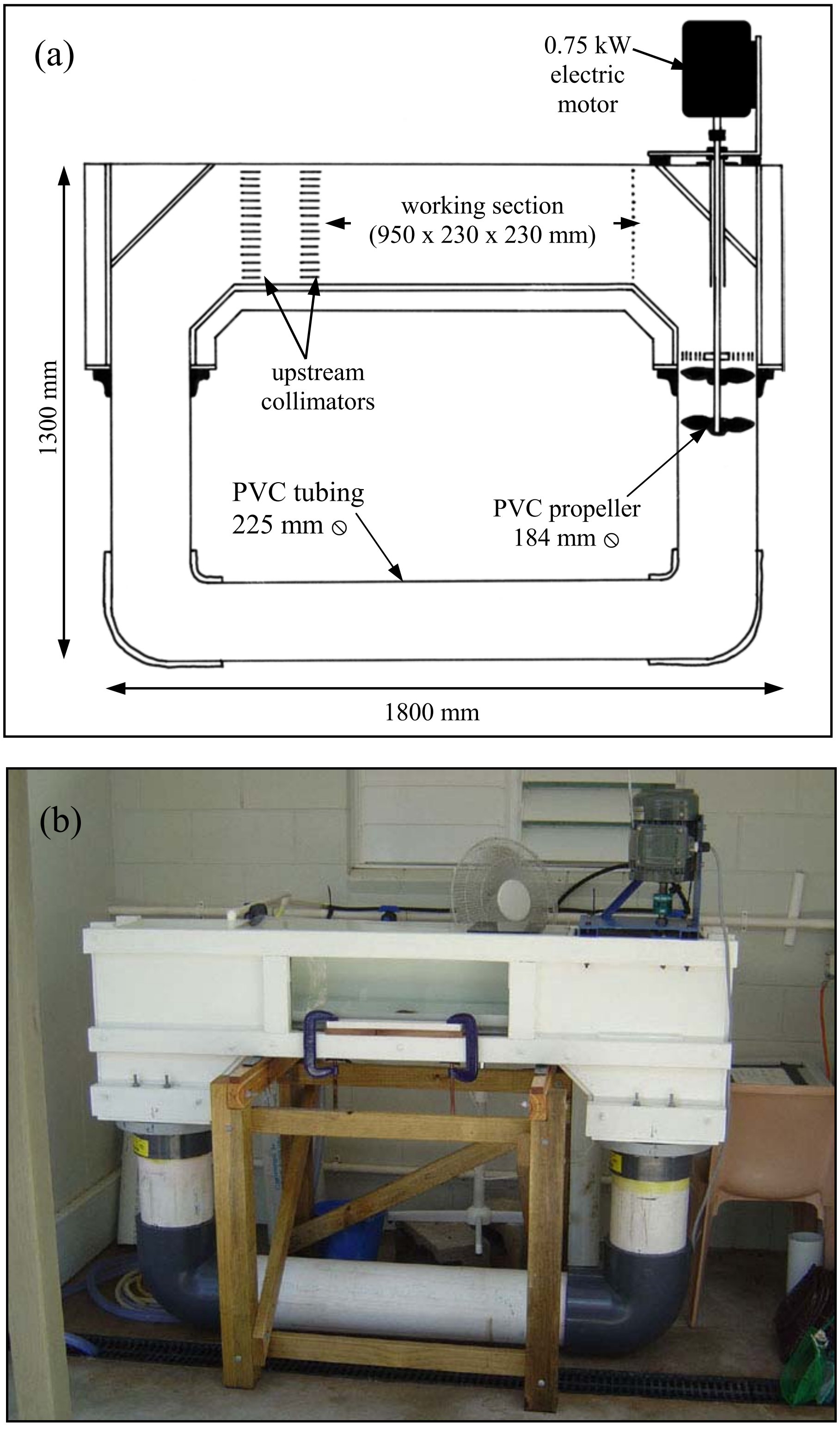

Fig. 1.1. (a) Cross-sectional diagram of 194 L recirculating flow tank used for gypsum calibration trials. (b) During operation the tank is oriented vertically with the working section open at the top. Design and construction followed Vogel & LaBarbera (1978).

and temperature. Salinity was maintained within the range 33.6 - 34.7, which coincides closely with the range of values found in the field (33.9 - 35.3).

Assessment of wave-induced water-motion

Five measures that encompassed both surface (wave height, wave period) and sub-surface conditions (net flow velocity, drift flow velocity, and rate of flow direction change) were used to simultaneously assess levels of water motion at 48 different locations across four exposure regimes (separated by 1-3 km) and five habitat zones (separated by 10 - 300 m). Net water motion was quantified using an enhanced plaster dissolution technique that has previously been successfully applied to sub-tidal ecosystems (Dennison & Barnes 1988, Jokiel & Morrissey 1993, Kawamata 2001, Sebens et al. 2003). In addition to the usual measure of plaster mass loss, multi-dimensional changes in the size of gypsum balls was also examined, in combination with rates of flow direction change, to evaluate the extent of laminar or mixed flow environments in each deployment location following Porter et al. (2000).

Field deployments of gypsum balls were made on the reefs surrounding Lizard Island (14°38’S, 145°26’E), Great Barrier Reef, Australia, across two spatial gradients of wave energy: habitats of different depth, and locations of different exposure (Fig. 1.2). Three replicate gypsum balls were deployed within the crest habitat (3 m depth) at two sites in each of four locations of different wave exposure (exposed, oblique, lagoon, and sheltered) according to their aspect to prevailing south-east trade winds. Within the exposed reef sites, among-habitat differences were assessed by placing three gypsum balls within the five habitat zones of base (15 m depth), slope (9 m), crest (3 m), flat (2 m), and back (3 m). Variations in sea conditions were also examined by repeating the gypsum deployments in each of the four wave exposure locations (crest habitat only)

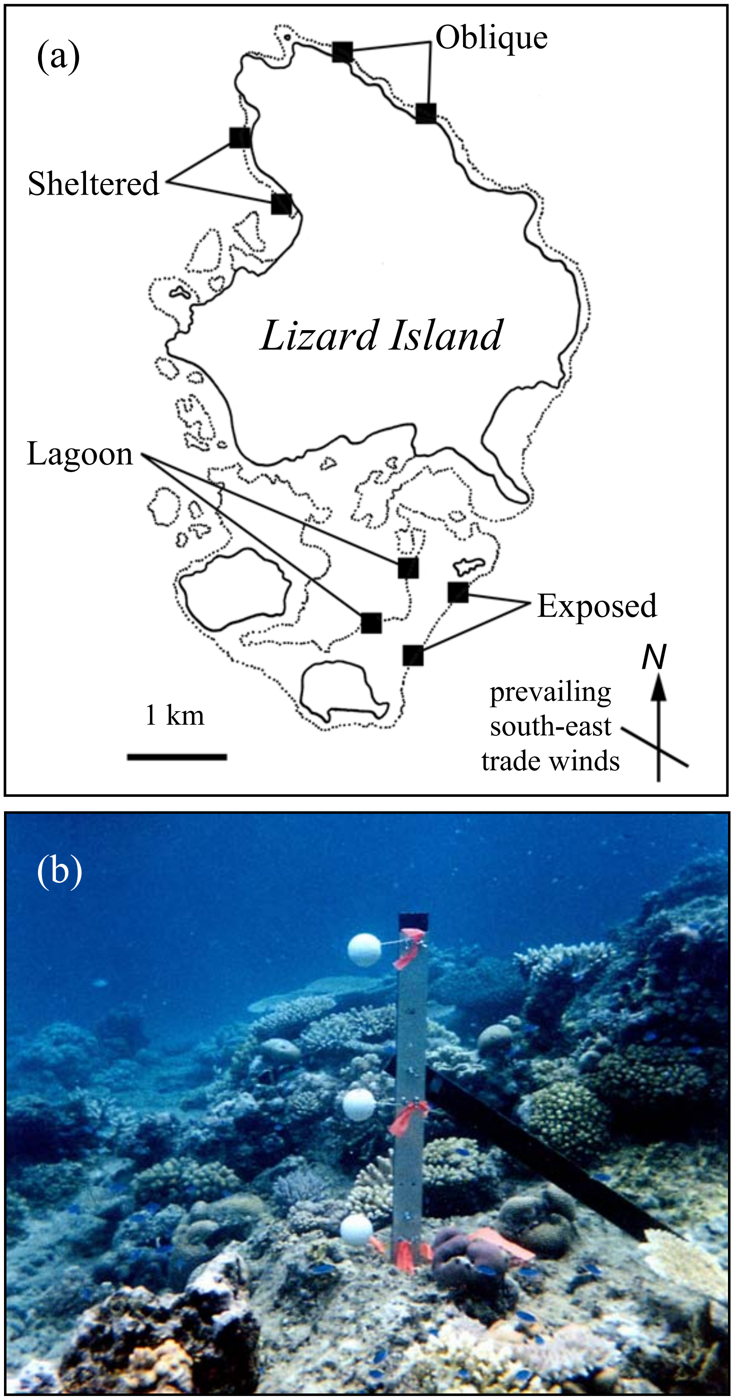

Fig. 1.2. (a) Location of study sites at four wave exposures around Lizard Island (14°38’S, 145°26’E), Great Barrier Reef, Australia. Depth profile of habitat zones within the exposed locations are presented in Fig. 1.4. (b) Plaster balls deployed on one of the three replicate stakes within the crest habitat of a windward reef site. Data is presented on the topmost plaster ball (60 cm from substratum) to match the average water-column position of reef fishes at these locations (Fulton et al. 2001).

during the different south-easterly wind strengths of ‘calm’ 6.0 ± 0.3 m s^{-1} and ‘rough’ 11.9 ± 0.5 m s^{-1} (average ± 1 SE for the region, for the 4 d leading up to and including the deployment days in January and July 2003, Bureau of Meteorology, Townsville). When deployed, each ball was mounted on a rigid metal frame 60 cm above the substratum (Fig. 1.2b) to match the average water column position of reef fishes at these locations (Fulton et al. 2001). The x-axis of each ball was orientated perpendicular to the incident wave fronts. A minimum of 50 m separated adjacent balls (stakes) within each site. Balls were deployed for a 24 h period (± 20 min) during neap tidal conditions (max tidal range 0.98 m) to minimise tidal effects. After retrieval, each ball was dried in a low-humidity room at 25°C where the mass and diameters were then remeasured.

Relationships between surface conditions and estimates of water motion were evaluated using two direct measures of surface wave motion, recorded three times in the crest habitat at each site (and back reef habitat at the exposed sites) by an observer on the surface: overall wave height (H), which was measured using a wave staff placed against the substratum and recording the distance between the highest crest and the lowest trough after 1 minute; and wave period (T), where the number of crests passing a fixed point (wave staff) per unit time was recorded. Furthermore, to examine the degree of laminar or mixed flow in the habitats and sites where gypsum balls were deployed (Porter et al. 2000), we used two parameters that were recorded three times within each habitat and site by an underwater observer on SCUBA: rate of flow direction changes per minute (Δv), which involved the underwater visual tracking of a passive particle released 60 cm above the substratum, noting the number of changes in direction over a 5 minute period; and drift velocity (v_{d}), which was measured as the horizontal distance travelled by the passive particle after a 5 minute period.

Statistical Analyses

After initial data exploration, all violations of normality and homoscedasticity were corrected using $\log_{10}(x + 1)$ transformations. Least-squares linear regressions were used to examine the relationship between gypsum dissolution and experimental flow velocity for each temperature. Variables measured during the among-habitat and among-exposure deployments were examined using two-way analysis-of-variance (ANOVA), with either habitat and site, or exposure and site as fixed factors. Net flow velocities during rough and calm deployments were compared using a three-way ANOVA, with sea condition, exposure and site as fixed factors. The relationship between net velocity and wave height was examined using Pearson's Correlation and least-squares linear regression. Wherever a result of no significant site effect was found, values were pooled at the level of the next highest factor (either habitat or exposure) for figure presentations.

1.3. Results

Calibration of gypsum dissolution

Weight loss (*WL*) of gypsum balls was found to display a strong linear relationship with experimental flow velocity (*v)* at both water temperatures (Fig. 1.3a), which allowed conversion of field values of mass loss into a measure of net flow velocity according to the temperature during deployment. Changes in ball diameter across the three measured axes differed according to orientation of the axes to the direction of experimental flow. Specifically, a greater reduction in diameter was displayed across the x-axis (parallel to flow direction) when compared with the y- and z-axes, which were perpendicular to the flow direction (Fig. 1.3b).

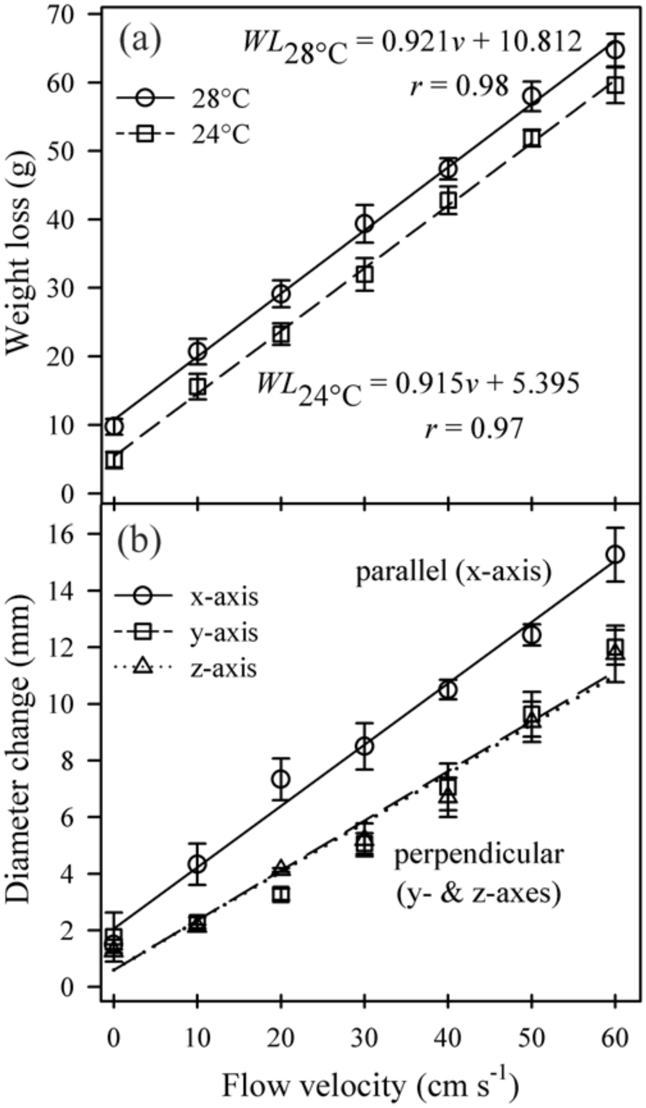

Fig. 1.3. Gypsum dissolution calibration. (a) Weight loss (*WL*) from gypsum balls after 24 hours exposure to seven flow velocities (v) at two water temperatures. (b) Diameter change across three axes after 24 hours exposure to seven flow velocities at 24°C. Error bars are standard errors of the mean.

Wave-induced water motion

Field deployments revealed statistically significant differences in net flow velocity amongst habitats ($F_{4,20} = 115.58$, $p < 0.001$), with no significant site effects ($F_{1,20} = 0.24$, $p = 0.630$) or interaction ($F_{4,20} = 2.45$, $p = 0.080$). Crest and flat habitats displayed the highest estimated net flow velocities (38.3 cm s^{-1} and 43.2 cm s^{-1}, respectively), with the drift velocities (5.3 cm s^{-1} and 6.9 cm s^{-1}) appearing to be a relatively minor contribution (14% and 16%) to total flow velocities in each habitat (Fig. 1.4a). Notably, the reduction in wave height on the shallow back reef (81%) corresponded with a marked reduction in net velocity (65%) when compared with the exposed reef crest of the same depth (Fig. 1.4a, 1.4d). Rates of flow direction change recorded underwater were significantly different among habitats ($F_{4,20} = 248.82$, $p < 0.001$), with no significant site ($F_{1,20} = 0.11$, $p = 0.748$) or interaction effects ($F_{4,20} = 1.08$, $p = 0.391$). Whilst the average rate of flow direction changes occurring in the crest, flat, and back habitats (0.63 - 0.66 Hz) were almost exactly double the wave period recorded on the surface (0.31 - 0.36 Hz), flow direction changes decreased with increasing depth, with very low average rates occurring in the reef base habitat (Fig. 1.4b). Diameter losses on balls deployed in the reef crest and flat differed amongst the three measured axes, with a markedly greater loss found across the x-axis in these shallow habitat zones (Fig. 1.4c). In contrast, diameter loss was relatively uniform amongst the three axes in the deeper habitats of the reef slope and base (Fig. 1.4c).

Significant differences in net flow velocities among reefs of different exposure were also apparent ($F_{3,16} = 76.16$, $p < 0.001$), with no site ($F_{1,16} = 1.79$, $p = 0.200$) or interaction effects ($F_{3,16} = 1.34$, $p = 0.298$). Variations in average net velocity among exposures (6.2 - 38.3 cm s^{-1}) were comparable to the among-habitat variations observed under the same calm conditions, with the greatest net velocities being recorded in the

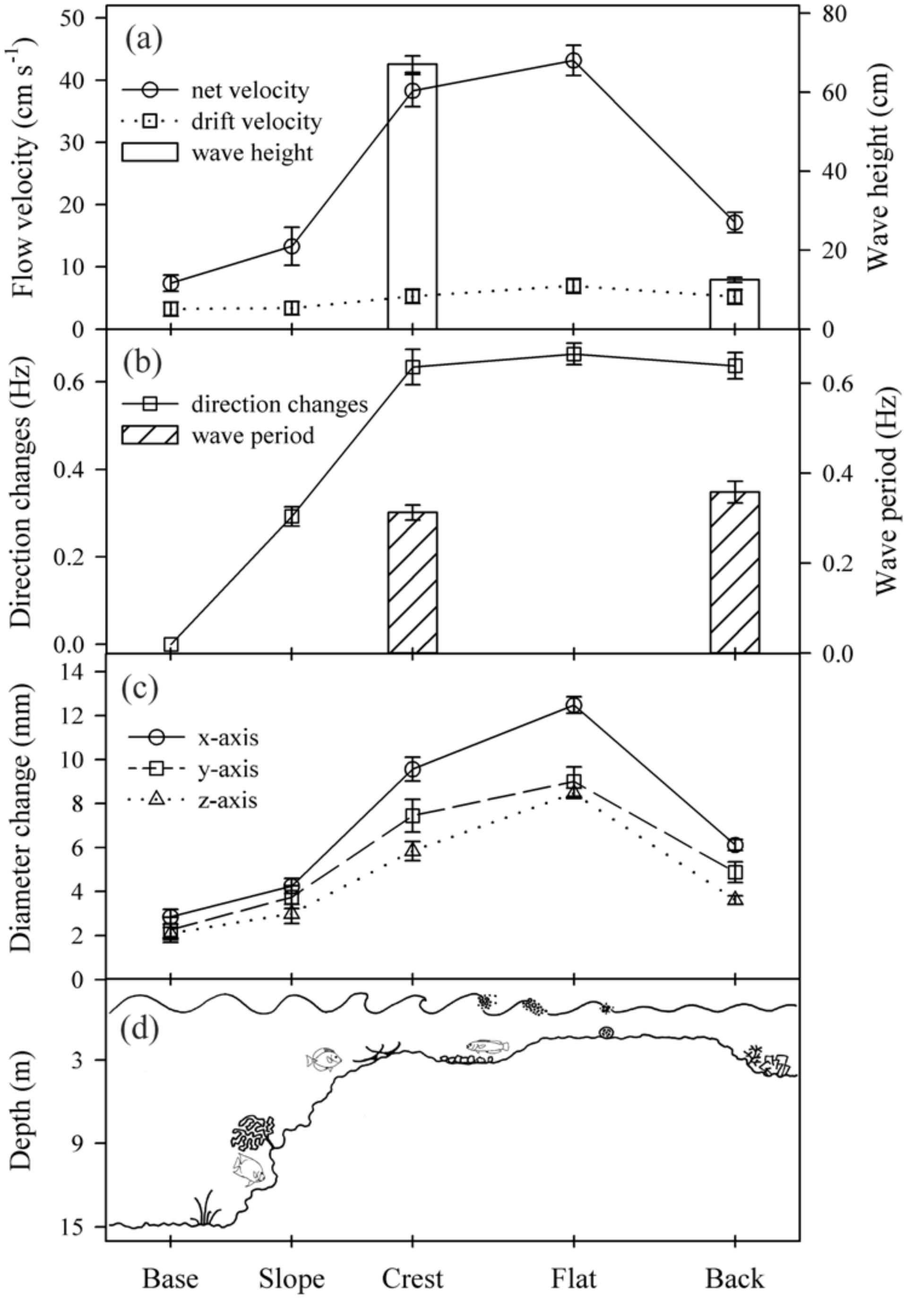

Fig. 1.4. Water motion assessments amongst five habitats on an exposed reef at Lizard Island. (a) Net flow velocities from gypsum dissolution, with drift velocities recorded for each habitat and incident wave heights on the front and back reef for this exposed location. (b) Wave period and rates of flow direction change recorded in each habitat. (c) Diameter change of gypsum balls across three axes. (d) Habitat depths on exposed reef profile. Error bars are standard errors of the mean.

exposed (38.3 cm s^{-1}) and oblique locations (24.4 cm s^{-1}); lagoon values (17.1 cm s^{-1}) were intermediate between these and the sheltered (6.2 cm s^{-1}) sites (Fig 1.5).

Comparison across a temporal change in sea condition ('calm' versus 'rough') indicated that increases in wind strength produced increases in incident wave height at the exposed (74%) and oblique locations (36%), with corresponding increases in net flow velocity at these exposures (Fig. 1.5a and 1.5b, Table 1.1). Conversely, this change in weather conditions produced relatively little or no increase in wave height within the sheltered and lagoonal sites and correspondingly minor increases in net flow velocity (Fig. 1.5a and 1.5b), which is the probable source of the significant interaction between sea condition and exposure (Table 1.1). Average wave periodicities across exposures were similar under calm and rough conditions for all habitats (0.31 Hz and 0.33 Hz, respectively), as were rates of flow direction change (0.61 Hz and 0.65 Hz), with the exception of the sheltered sites (wave periodicity 0.16 Hz, rate of direction change 0.06 Hz). Overall, a strongly significant correlation (Pearson's 0.956, $p < 0.01$, $n = 8$) was evident between wave height and net flow velocities measured by gypsum dissolution, in a linear relationship across the wave heights encountered (Fig. 1.6).

Table 1.1. Three-way ANOVA on mean net flow velocities taken under calm and rough conditions in the crest habitats from two reef sites at four exposures around Lizard Island. Sea condition, exposure, and site are fixed factors.

Source of variation	**df**	**SS**	**MS**	***F***	***p*-value**
Sea condition	1	1978.59	1978.59	81.02	<0.001
Exposure	3	10126.55	3375.52	138.22	<0.001
Site	1	27.52	27.52	1.13	0.296
Sea cond. × exp.	3	411.38	137.13	5.62	<0.01
Sea cond. × site	1	3.62	3.62	0.15	0.703
Exp. × site	3	75.93	25.31	1.04	0.390
Sea cond. × exp. × site	3	62.52	20.84	0.85	0.475
Error	32	781.46	24.42		
Total	47	13467.57			

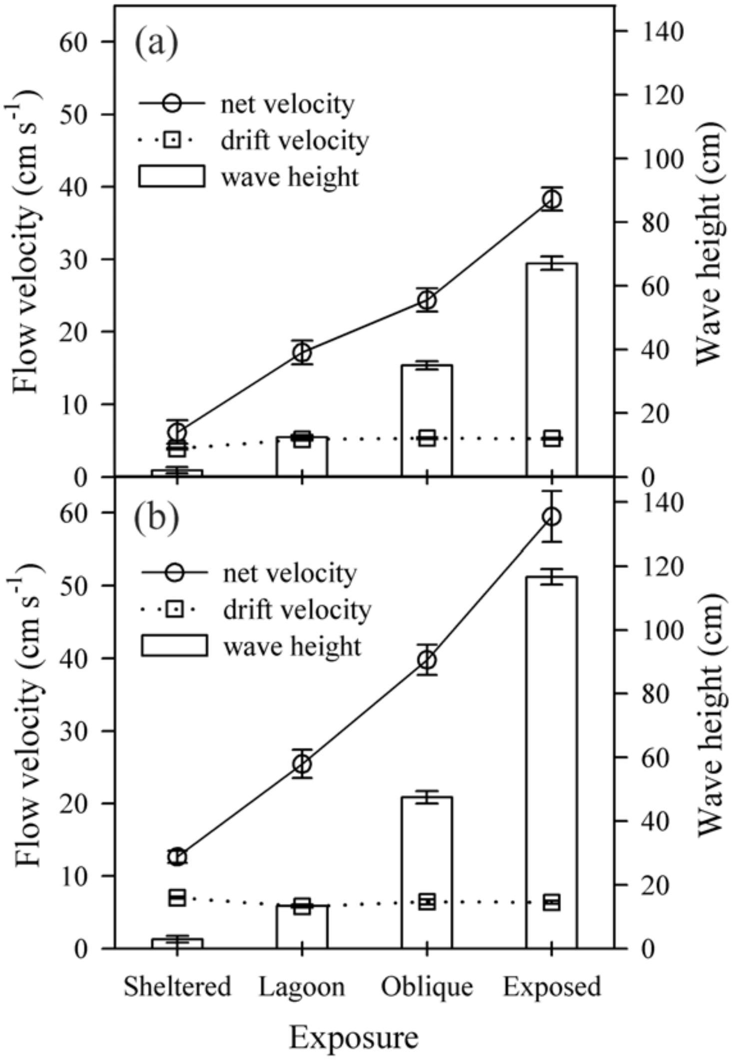

Fig. 1.5. Water motion assessments amongst four exposures around Lizard Island, with mean wave heights, net flow and drift velocities indicated. (a) ‘Calm’ sea conditions. (b) ‘Rough’ sea conditions. Error bars are standard errors of the mean.

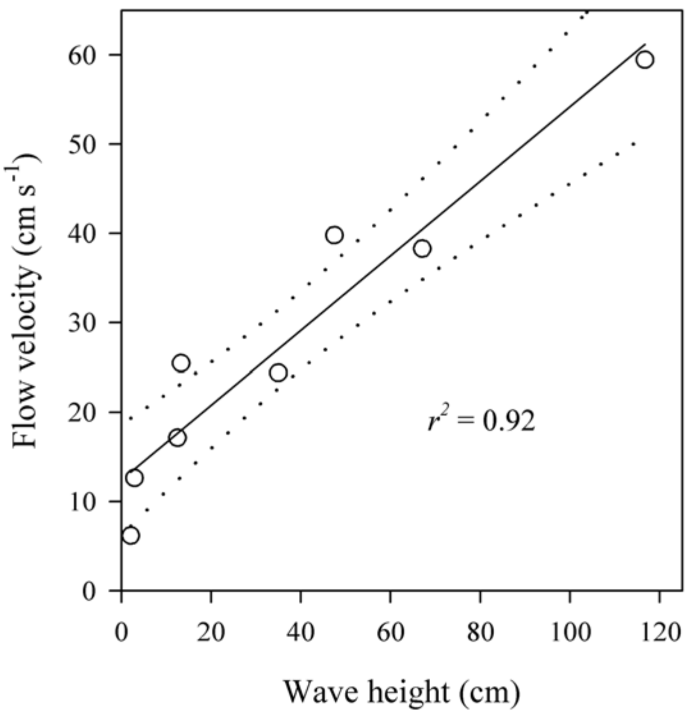

Fig. 1.6. Relationship between wave height and net flow velocity as measured by gypsum dissolution on reefs around Lizard Island. Values are means from each exposure for both 'calm' and 'rough' deployments. Dotted lines represent 95 % confidence limits.

1.4. Discussion

Spatial variations in wave energy have been examined categorically on coral reefs worldwide, leading to general paradigms concerning the level of wave energy in a location based on depth and aspect to prevailing winds (e.g. Geister 1977, Bradbury & Young 1981, Done 1983). Using a combination of several hydrodynamic measures, this study quantified marked variations in water motion across spatial gradients of depth and exposure that largely support these previous predictions. Exposed shallow habitats (reef crest and flat) displayed the highest overall flow velocities and rates of flow direction change, with the magnitude of water movements decreasing with increasing depth similar to previous findings on the Great Barrier Reef (Sebens & Done 1992, Young 1989). Using comparisons of surface and sub-surface measures we found that water motion within the shallow crest and flat habitats appeared to be largely wave-driven. Rates of flow direction change in these habitats coincided closely with the number of incident wave crests, suggesting that such flow direction changes are driven by the oscillatory water motion produced by incident waves (Denny 1988). Deviations in axial diameter loss only occurred in these shallow reef front habitats; greater diameter losses were found across the axis that was orientated into the direction of wave travel. Whilst oscillatory water motion from breaking waves can contain several directional components (Denny 1988, Vogel 1994, Gaylord 1999), such deviations in diameter loss suggest that the majority of flows in these habitats appear to alternate direction within a single axis perpendicular to the incident wave front. Although back reef habitats were of similar depth to the exposed crest, they displayed lower net flow velocities and deviations in axial loss, with reductions in wave height from wave attenuation across the reef flat (cf. Young 1989) corresponding closely with these decreases in water motion.

Spatial variations amongst reefs of different exposure were of a similar magnitude to those found amongst different depths within a single exposure. As can be expected, reefs directly exposed to prevailing winds were subject to the greatest wave heights and net flow velocities. Whilst the relative differences between exposures in our study largely correspond with previous appraisals (Geister 1977, Bradbury & Young 1981, Sebens & Done 1982, Done 1983), one notable exception was the lagoon. Although coral reef lagoons are generally considered to be sheltered from wave energy, our assessments indicate that lagoonal sites were intermediate between exposed and sheltered reefs. Wave attenuation over the exposed reef flat had reduced the incident wave energy reaching the lagoon by around 81%, which corresponds favourably with previous estimates of 75 - 90% that varied according to depth and incident wave height (Young 1989, Sebens & Done 1992, Hardy & Young 1996, Kench 1998). However, this reduced wave energy still produced water motion within lagoonal reefs that was similar in magnitude to obliquely exposed reefs under the same calm sea conditions, with relatively little contribution from drift velocities.

Temporal changes in sea conditions have been found to produce changes in wave-induced water motion of a magnitude comparable to variations over static spatial gradients of wave energy (Young 1989, Sebens & Done 1992, Kench 1998). Whilst published empirical information on wave climate within the northern Great Barrier Reef (GBR) lagoon is relatively scarce, previous studies indicate that the range of wind speeds and wave heights encountered in the present study agree with average values for a mid-shelf location on the GBR (Young 1989, Hardy & Young 1996, Crossman et al. 2001). A temporal change from calm to rough sea conditions in the present study produced shifts in wave height that were proportionally greater for the exposed and oblique reefs than for sheltered and lagoonal locations. Accordingly, lagoonal and sheltered sites remained relatively static in overall water motion, whereas net flow velocities increased markedly on reefs directly and obliquely exposed to the prevailing winds. Consequently, inhabitants of the lagoonal and sheltered back reef locations would experience relatively stable wave energy conditions over time, whereas front reef locations are more susceptible to temporal changes in wind strength and wave height.

Drift velocities were a relatively minor contribution to overall levels of water motion, with the exception of sheltered crests and reef base habitats where such flows constituted up to 60% of the total velocities encountered. Given that these drift velocities probably represent tidal flows, such low levels would be expected during the neap tidal periods when deployments occurred. Indeed, these flows (3.2 - 8.6 cm s^{-1}) that ran parallel to the reef face, correspond to the lower end of spring tidal flow values (0 - 20 cm s^{-1}) taken on a mid-shelf reef of the GBR (Leonard et al. 1988). In shallower habitats such as the crest, flat and back, however, these drift velocities flowed perpendicular to the reef face and would include a component of wave forced flows, with previous estimates from the GBR indicating wave-forced flows in the range of 5 - 22 cm s^{-1} (Symonds et al. 1995).

Given that water movements produced by waves are extremely complex in nature, our gypsum method provides a time-averaged estimate of the net flow velocities experienced under the low to moderately turbulent conditions in each habitat and location (Dennison & Barnes 1988, Denny 1988). When combined with the other parameters measured, this provides an overall picture of the nature of water movements encountered by mobile organisms in these locations. Concerns have been expressed that gypsum dissolution displays a weak relationship with water velocity under different flow conditions (Porter et al. 2000). However, simultaneous deployments of electromagnetic flow meters and gypsum blocks across wave energy gradients have empirically demonstrated a good relationship between flow velocity and gypsum dissolution across a range of velocities (2 - 38 cm s^{-1}) and depths (2 - 6 metres) comparable to the present study (Kawamata 2001). The strong relationship between wave height and flow speed in the present study suggests that the methodology employed was appropriate for the range of wave conditions encountered. Furthermore, the range of flow velocity values recorded in the present study (5 - 45 cm s^{-1}) appear to coincide closely with previous measurements taken using S4 flow meters deployed in similar depths at other coral reef locations (Sebens & Done 1992, Sebens et al. 2003, Gourlay & Colleter 2005).

Conclusions

Overall, these estimates indicate that even average levels of wave energy can produce substantial variations in water motion among habitats and exposures on shallow coral reefs. Moreover, these quantitative estimates now provide the opportunity to explore the implications of wave-induced water motion for mobile reef taxa distributed across the same spatial scales. Potentially, substantial variations in both flow velocity and periodicity (flow direction changes) could interact with the locomotor capabilities of mobile reef taxa. For coral reef fishes, the next step is to measure the range of swimming capabilities displayed by adult reef fishes, and directly compare these abilities with the observed environmental gradients.

Chapter 2: Swimming mode and performance in coral reef fishes.

To be submitted to *Journal of Experimental Biology*

2.1. Introduction

Swimming performance can be crucial for the survival of fishes by affecting their ability to avoid predators and acquire food. These essential daily tasks often require precise movements, bursts of speed, or prolonged periods of swimming depending on the habitat or predator-prey system involved (Videler 1993, Drucker 1996, Plaut 2001), and can consume substantial amounts of energy on a daily basis (Feldmeth & Jenkins 1973, Kitchell 1983, Boisclair & Tang 1993, Krohn & Boisclair 1994). Despite the potential importance, quantitative information on the swimming abilities of adult fishes remains relatively scarce, particularly for the vast diversity of fishes found on coral reefs. Previous studies have focused largely on a few freshwater or commercially important marine taxa (Beamish 1978, Hammer 1995, Plaut 2001, Blake 2004), with wide variations in methodology hindering direct comparisons among studies. Moreover, most estimates have been taken in laboratory settings where fishes are subjected to periods of captivity that may unpredictably affect their swimming performance (Hammer 1995, Plaut 2001). For the first time, this study will utilise field estimates of swimming speed in conjunction with laboratory trials of freshly caught individuals to directly compare the swimming capabilities of adult reef fishes from several diverse families.

Swimming behaviours can be categorized into modes or ‘gaits’ based on the particular body parts or fins used to produce thrust, with most mode categories in fishes being encompassed within the two main groups of Body and Caudal Fin (BCF) or Median and Paired Fin (MPF) propulsion (reviews by Webb 1994, Blake 2004).

Biomechanical examinations suggest that swimming modes are often associated with certain aspects of locomotor performance, such as continuous cruising or slow-speed manoeuvrability and stability, which match the particular pelagic, demersal or benthic lifestyle of the fish (Lindsey 1978, Webb 1994, 2002, Weihs 2002, Blake 2004). Mechanical efficiency may differ considerably between modes through the use of either an undulatory or rigid-body position and different muscle groups and fins, all of which can influence the comparative energetics of routine swimming activities using each mode (Wu 1977, Webb 1992, Videler 1993, Vogel 1994, Korsmeyer et al. 2002, Walker & Westneat 2002). Current evidence indicates that the use of particular fins and body regions during routine swimming largely differentiates among fish taxa at the family level (Webb 1994, Blake 2004). While most coral reef fishes are thought to use some form of MPF swimming with a limited representation of BCF modes (Lindsey 1978, Webb 1994, Blake 2004), this is yet to be verified through quantitative assessments of fin use, and the comparative performance of swimming modes explored.

Morphology can also play a central role in the swimming abilities of fishes. Body size has an overriding influence on swimming speed performance in a wide range of organisms, with larger individuals attaining faster absolute speeds, but slower speeds relative to their size (e.g. Bainbridge 1958, Wardle 1977, Bellwood & Fisher 2001). Consequently, size effects need to be minimised when comparing taxa of markedly different sizes through the use of body ratios or residualisation, depending on the variable of interest (Reist 1985, Wainwright et al. 2002). Body shape may also play a role in determining swimming performance. Early studies have indicated that body shape (in terms of body depth and cross-sectional profile) may be associated with certain aspects of swimming performance (Bainbridge 1960, Alexander 1967, Blake 1983, Webb 1984, Weihs 1989), leading to the paradigm that fishes with fusiform bodies are associated with fast continuous swimming, whereas laterally-compressed bodies are suited to slow-speed stability and manoeuvrability. However, more recent findings suggest that the relationship between body shape and these aspects of performance are complex, ranging from marked differences to little or no discernible influence (review by Blake 2004). While there have been empirical examinations of body shape effects on the stability, manoeuvrability or fast-start capabilities of different fish taxa (Webb 1978, Gerstner 1999, Schrank et al. 1999, Webb & Fairchild 2001, Eidietis et al. 2002), the relationship between body shape and prolonged swimming speed remains largely unexplored for the considerable diversity of fish body forms found on coral reefs.

Swimming speed performance in fishes has been studied using a wide variety of methods, ranging from short-term burst trials to incremental test of maximum critical speed and single-speed evaluations of long-term endurance. Critical swimming speed (U_{crit}) was first developed by Brett (1964) as a means of measuring speed performance by subjecting fishes to incrementally increased speeds until exhaustion under aerobic conditions. While U_{crit} estimates are sensitive to the magnitude of the speed and time increments employed (Farlinger & Beamish 1977, Willliams & Brett 1987), the use of small speed increments relative to fish length (less than 0.5 BL s^{-1}) and appropriately long time intervals (15-20 minutes) provides a U_{crit} estimate that is equivalent to maximum prolonged swimming speed (Wilson & Egginton 1994, Hammer 1995, Plaut 2001). Prolonged swimming performance can play an important role in the foraging and habitat-use of fishes over daily times scales (Videler 1993), and several studies have utilised such U_{crit} estimates to compare the swimming performance of fishes to several biological and ecological variables (Jones et al. 1974, Hartwell & Otto 1991, Kolok 1991, Hawkins & Quinn 1996, Lowe 1996, Myrick & Cech 2000, Fisher 2005). Critical swimming speed has also been correlated with other aspects of performance such as routine field speed (Plaut 2000, Fisher & Bellwood 2003, Leis & Fisher in press), sustained speed (Brett 1964, Fisher & Wilson 2004) and sprint speeds (Reidy et al. 2000) in a restricted range of fish taxa. While this suggests that the lab-based U_{crit} metric provides an effective measure of relative swimming speed performance that is relevant to the biology and ecology of fishes (Plaut 2001), this remains to be tested against field speeds in fishes using different swimming modes.

This study, therefore, utilises both experimental measures of critical swimming speed and *in situ* estimates of undisturbed field speed to evaluate the swimming capabilities of coral reef fishes within a diverse assemblage encompassing 52 genera from ten families. The main aims were to: (1) quantify fin use during routine swimming activities in an assemblage of coral reef fishes, (2) compare both the field and experimental swimming speed performance of reef fishes using different swimming modes, and (3) examine the relationship between body shape and swimming speed performance within and among modes.

2.2. Material and Methods

Swimming mode

Swimming mode was evaluated using an instantaneous census technique following Fulton et al. (2001), which involved swimming a non-overlapping path over the reef whilst recording the fins being used during the 3-second period following identification of each individual. These censuses encompassed species from ten families: the Acanthuridae, Chaetodontidae, Labridae, Lutjanidae, Nemipteridae, Pomacanthidae, Pomacentridae, Serranidae, Siganidae and Zanclidae (Fig. 2.1). Observations were taken from 117 species and recorded into three main fin-use

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Fig. 2.1. Representatives from the 10 reef fish families examined, indicating the range of body forms used in the assessment of morphology and swimming speed performance (photos: Fishbase 2005).

categories (solely pectoral, caudal, or simultaneous pectoral-caudal). Raw frequencies in each category were converted to proportional use per species to account for differences in the total number of observations recorded for each species (up to 151 observations per species, with an average of 45.2 ± 6.9 SE per species).

Swimming speed performance

Both field and experimental swimming speeds were used to evaluate swimming performance in species from the ten reef fish families (Fig. 2.2). Field speeds were measured by timing individual fish as they swam undisturbed on the reef in an approximately linear path. If an individual deviated markedly from a constant velocity or straight swimming path during an observation, the trial was discontinued. The beginning and end of each trial was marked by stopwatch as the fish travelled past noted landmarks on the reef. Immediately after each trial the distance between each landmark was measured to the nearest 5 cm and recorded, along with the travel time, species and estimated TL of the individual. These field observations were taken under calm weather conditions to minimise the effects of water motion on swimming speeds. A minimum of 10 individual observations were taken for each species, with the average travel distance and duration of each field trial being 244 cm and 7.5 seconds, respectively.

Experimental speed trials involved an incremental velocity test following Brett (1964) to measure critical swimming speed (U_{crit}), which estimates maximum prolonged swimming speed under aerobic conditions (Hammer 1995, Plaut 2001). This was done using a 194 L re-circulating flow tank (described in Chapter 1) in the field setting of the Lizard Island Research Station (LIRS), so that fishes could be swum soon after capture to minimise captivity effects. Fishes were collected using barrier nets from the reefs surrounding Lizard Island and provided with a minimum 2 h still-water stabilisation

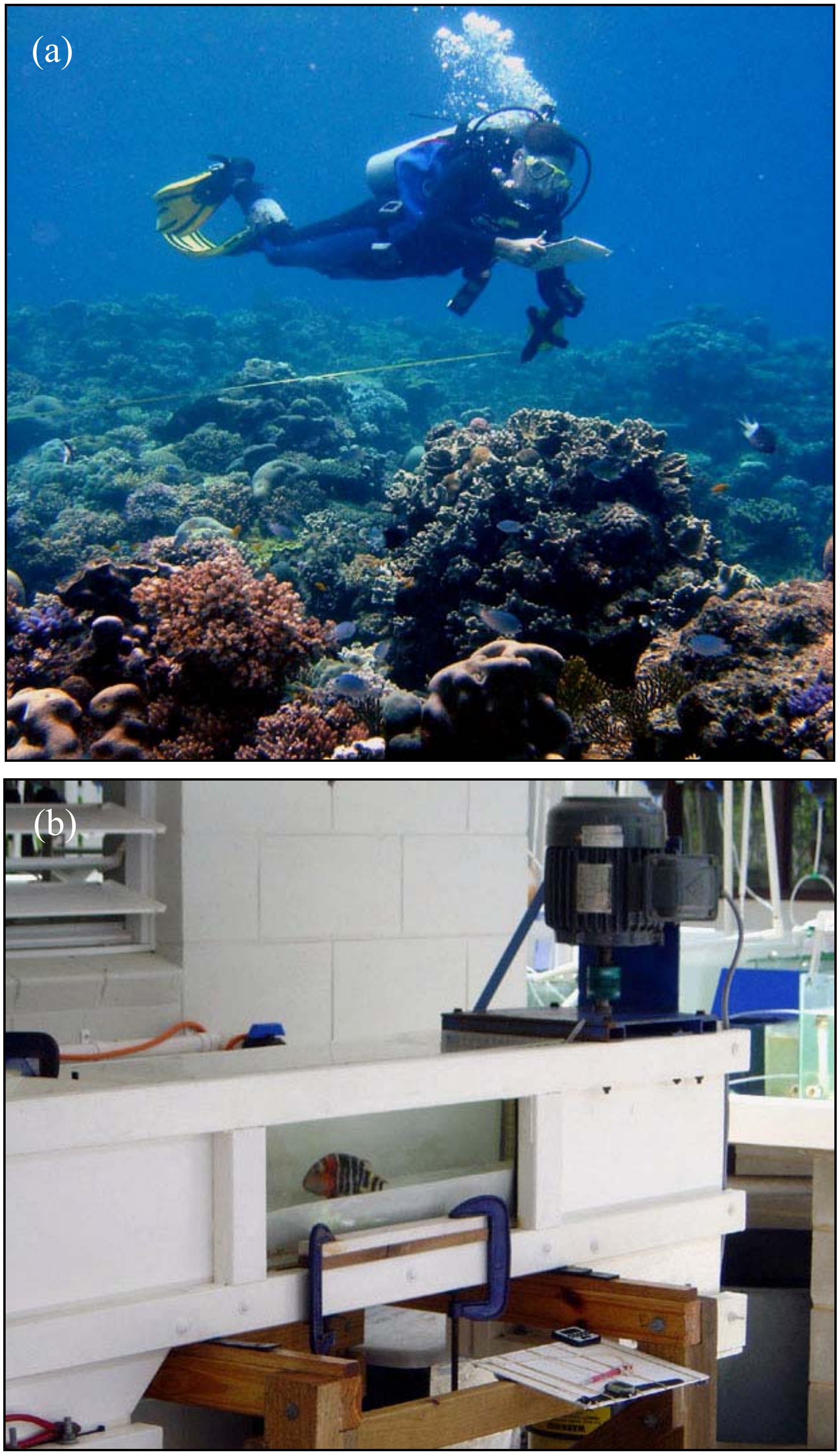

Fig. 2.2. (a) Fin use and field speeds were recorded from *in situ* observations of fishes swimming on the reef. (b) Critical swimming speed (U_{crit}) trials were conducted at Lizard Island Research Station using the recirculating flow tank.

period, with all individuals being tested within 36 h of capture. Only individuals that displayed adult colouration and were of a size (<16 cm TL) that minimised the possibility of hydrodynamic interaction with the walls of the flow tank (i.e. individuals with dimensions of less than one third the width and half the height of the working section) were used in the experimental trials. Each individual was allowed to acclimatise to the flow tank under an initial flow speed of 15 cm s^{-1} for 30 mins. Any individuals that displayed abnormal behaviour or symptoms of stress during this period were removed. Flow velocity was then increased in sequential increments of approximately 0.5 TL s^{-1}, with each interval being of 15 minutes duration; these incremental changes were continued until the individual could no longer hold position in the working section and became impinged on the downstream mesh, whereupon the time swum into that interval and the penultimate speed was recorded. Each individual was tested only once, with an average trial duration of 138 minutes. Seawater used in the experimental trials was taken from the flow-through aquarium system at LIRS, which draws water from reefs adjacent to where specimens were captured. Individual U_{crit} values were calculated using the formula of Brett (1964): $U_{\text{crit}} = U + (t / t_{\text{i}} \times U_{\text{i}})$; where U = penultimate speed, t = time swum in final velocity increment, t_{i} = set time interval of each velocity increment (15 mins), and U_{i} = velocity increment (0.5 TL s^{-1}). Of the 117 species recorded in the instantaneous censuses of fin use, 73 species were included in both the field and experimental performance trials, with a minimum of 15 field and 3 experimental speed observations taken for each species.

Body morphology

All fishes used in the experimental performance trials were euthanased on completion of the trial for morphological examination. Additional individuals were also collected using spears or barrier nets and placed in an ice-water slurry within one hour of capture. Body size was measured in the form of total length (TL) to match the size estimates taken during field observations, which is also the size metric commonly used in the swimming performance literature (e.g. Beamish 1978, Hammer 1995, Plaut 2001). Body depth was measured at the deepest point on the body (excluding fins), and cross-sectional profile was taken by dividing body depth by width (also taken at the widest point on the body, excluding fins).

Statistical analyses

Patterns of fin use among species were examined by a Correspondence Analysis (CA) performed on the log transformed proportional fin use data for 117 species. Similarities in fin use among species were then examined by hierarchical clustering of the transformed fin use data using the unweighted pair group method of averaging (UPGMA), with the allocation of species into each of the major clusters being confirmed by non-hierarchical k-means clustering.

Body size effects were minimised in all swimming performance measures by calculating swimming speed residuals from the linear regression of speed against TL, using mean values of speed and TL from each species (Reist 1985, Wainwright et al. 2002). The relationship between field and experimental swimming speed performance was then examined for each swimming mode through linear regressions of field against experimental speed residuals using the 73 species for which both field and experimental speeds were recorded. Species were grouped into swimming modes according to the outcomes from the fin use analyses outlined above. Linear regressions of field versus experimental speed were compared between modes using an F-test analysis and GT2 multiple comparison of regression coefficients following Sokal & Rohlf (1995).

Relationships between body shape and performance were examined through bivariate plots of body ratio means and speed residuals in the same 73 species described above. Where ratios taken from body lengths did not adequately remove allometric effects from a particular body shape variable, residuals were calculated from the linear regression of the variable against total length using mean values for all 73 species following Reist (1985).

2.3. Results

Swimming mode and performance

Three main modes of fin use were recorded from a total of 5,285 field observations across the ten families – pectoral, simultaneous pectoral-caudal, and caudal swimming (Table 2.1). Correspondence Analysis revealed a major separation of taxa according to either proportion of pectoral fin use (CA1), or proportion of caudal fin use (CA2, Fig. 2.3). Non-hierarchical (k-means) cluster analysis confirmed the species groupings found in the three main clusters from a UPGMA hierarchical analysis of proportional fin use, which grouped 70, 29, and 18 species into each of the pectoral, pectoral-caudal and caudal modes, respectively (Fig. 2.3). With only one exception (*Stegastes*, which was divided amongst the pectoral and pectoral-caudal groups), all 52 genera were assigned exclusively to a single mode category, which resulted in some families being divided amongst two modes (Table 2.1, Fig. 2.3). Examination of proportional fin use within each of these groups revealed they included taxa that used a particular fin category in more than half of the individuals observed (Table 2.1).

A wide range of field and experimental speed performances within and among the three swimming modes were revealed from 1,845 field and 291 experimental observations (Table 2.2, Fig. 2.4). In terms of absolute speed (in units of cm s^{-1}),

Table 2.1. Proportional frequency of fin use by coral reef fishes from ten families, arranged by genus within each family across the three main fin-use groups identified by UPGMA and k-means clustering (Fig. 2.3).

	pectoral	pectoral-caudal	caudal	n
(i) Pectoral				
Acanthuridae				
Acanthurus	**0.99**	0.01		290
Ctenochaetus	**1.00**			101
Zebrasoma	**1.00**			68
Labridae				
Anampses	**1.00**			38
Bodianus	**1.00**			61
Cheilinus	**1.00**			165
Choerodon	**1.00**			7
Cirrhilabrus	**1.00**			7
Coris	**1.00**			51
Epibulus	**1.00**			63
Gomphosus	**1.00**			136
Halichoeres	**1.00**			408
Hemigymnus	**1.00**			114
Hologymnosus	**1.00**			9
Labrichthys	**1.00**			34
Labroides	**1.00**			61
Macropharyngodon	**1.00**			55
Novaculichthys	**1.00**			43
Oxycheilinus	**1.00**			82
Pseudocheilinus	**1.00**			11
Stethojulis	**1.00**			103
Thalassoma	**1.00**			347
Pomacanthidae				
Pomacanthus	**0.69**	0.31		104
Pomacentridae				
Abudefduf	**0.98**	0.01	0.01	91
Acanthochromis	**0.99**	0.01		151
Amblyglyphidodon	**1.00**			107
Amphiprion	**1.00**			31
Chromis	**1.00**			158
Chrysiptera	**0.95**	0.05		123
Dascyllus	**0.94**	0.06		31

Table 2.1. (cont.)

	pectoral	pectoral-caudal	caudal	n
(i) Pectoral (cont.)				
Pomacentridae (cont.)				
Neoglyphidodon	**0.64**	0.36		50
Neopomacentrus	**1.00**			74
Pomacentrus	**0.95**	0.05		457
Premnas	**1.00**			3
Stegastes (apicalis)	**0.75**	0.25		55
Zanclidae				
Zanclus	**1.00**			36
(ii) Pectoral-caudal				
Chaetodontidae				
Chaetodon	0.04	**0.90**	0.06	589
Chelmon	0.17	**0.83**		18
Heniochus	0.20	**0.80**		30
Nemipteridae				
Scolopsis	0.08	**0.64**	0.28	14
Pomacanthidae				
Centropyge	0.06	**0.89**	0.05	152
Pygoplites	0.43	**0.57**		30
Pomacentridae				
Dischistodus	0.22	**0.78**		9
Plectroglyphidodon	0.43	**0.55**	0.02	58
Stegastes (nigricans)	0.27	**0.55**	0.18	11
(iii) Caudal				
Acanthuridae				
Naso	0.01	0.01	**0.98**	157
Lutjanidae				
Lutjanus		0.07	**0.93**	13
Serranidae				
Cephalopholis	0.04	0.11	**0.85**	85
Epinephelus		0.07	**0.93**	15
Plectropomus	0.02	0.05	**0.93**	60
Variola			**1.00**	7
Siganidae				
Lo		0.02	**0.98**	42
Siganus	0.01	0.08	**0.91**	270

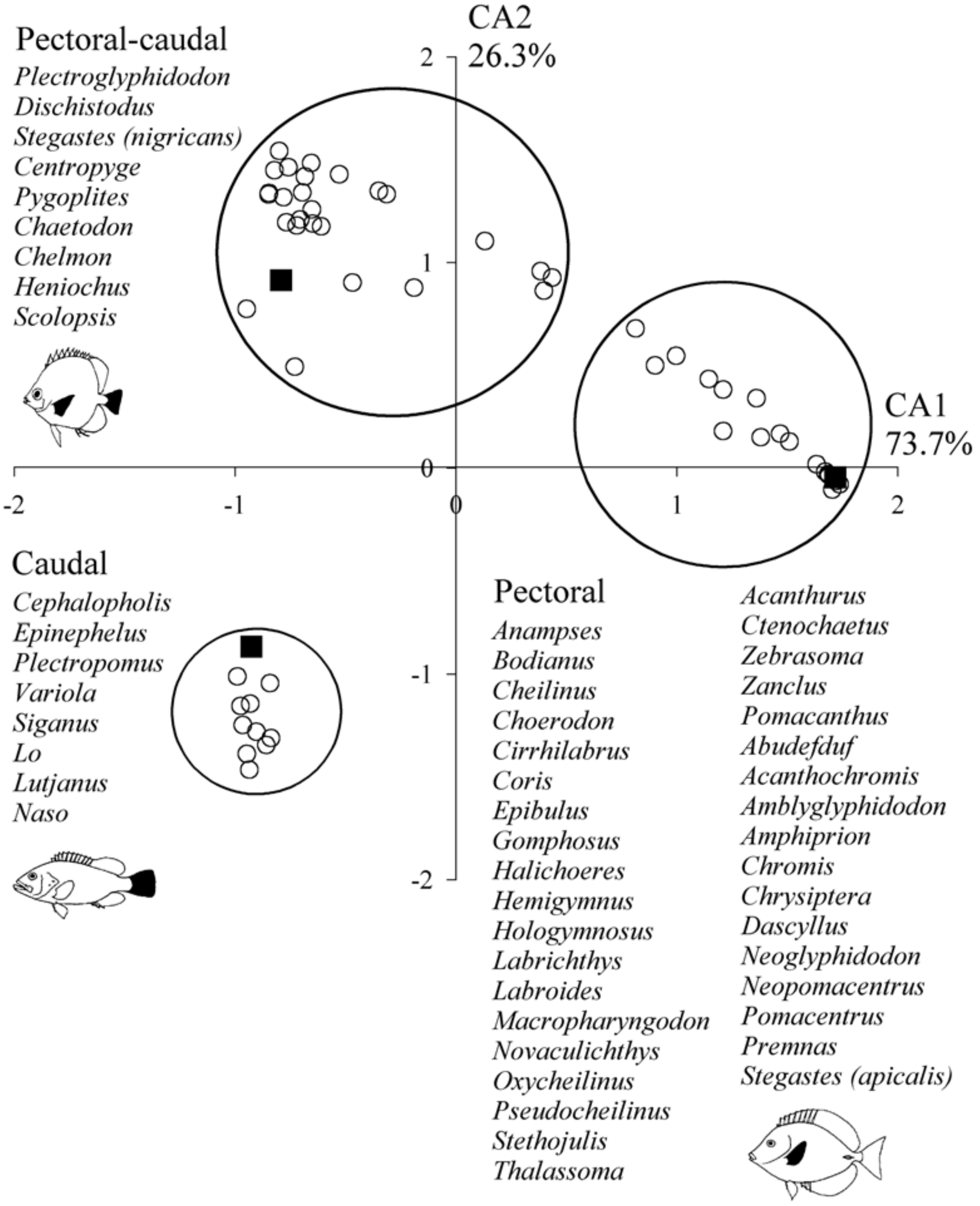

Fig. 2.3. Biplot of Correspondence Analysis on the fin use of 117 species of coral reef fishes from ten families. Filled squares represent the ordination of each of the three fin use categories; small open circles represent the vector position of each species. Larger circles are the grouping of species according to fin use as determined by both UPGMA hierarchical analysis and k-means clustering.

pectoral-swimming taxa displayed higher averages overall, with considerable overlap in the range of experimental speeds amongst the three modes (Table 2.2, Fig. 2.4). Under field conditions, however, pectoral- swimming taxa maintained a wide range of swimming speeds while the maximum field speeds of pectoral-caudal and caudal-swimming taxa was reduced below an absolute speed of 40 cm s^{-1} (Table 2.2, Fig. 2.4).

Table 2.2. Field and experimental swimming speeds and mean total length (TL) of species using each of three swimming modes, with the regression slope (*b*) and correlation (r) between field and experimental speed residuals indicated. Correlations were highly significant ($p < 0.01$).

	mean TL (cm)	mean ± se (cm s^{-1})	min - max (cm s^{-1})	*r*	*b*
(i) Pectoral					
Field speeds	11.3	31.7 ± 1.9	9.2 – 68.8		
Experimental speeds	10.7	56.0 ± 1.8	28.4 – 82.4	0.72	0.83
(ii) Pectoral-caudal					
Field speeds	10.6	25.9 ± 1.0	19.3 – 35.8		
Experimental speeds	9.8	52.8 ± 2.8	32.5 – 77.5	0.63	0.25
(iii) Caudal					
Field speeds	20.5	24.3 ± 1.9	14.7 – 39.0		
Experimental speeds	13.4	48.6 ± 4.5	24.0 – 59.3	0.49	0.22

Allometric relationships between the average total length and swimming speed performance of species (Fig. 2.5) were removed by residualisation, with no significant correlation between total length and the swimming speed residuals of species for both field (Pearson's 0.001, p = 0.99, n = 73) and experimental (Pearson's -0.01, p = 0.94, n = 73) measures. Differences in the comparative field-experimental performance of modes were confirmed by the relationships between residualised field and experimental speed for each mode (Fig. 2.6). While there was a strong correlation between residualised field and experimental speeds within all modes (Table 2.2), the linear

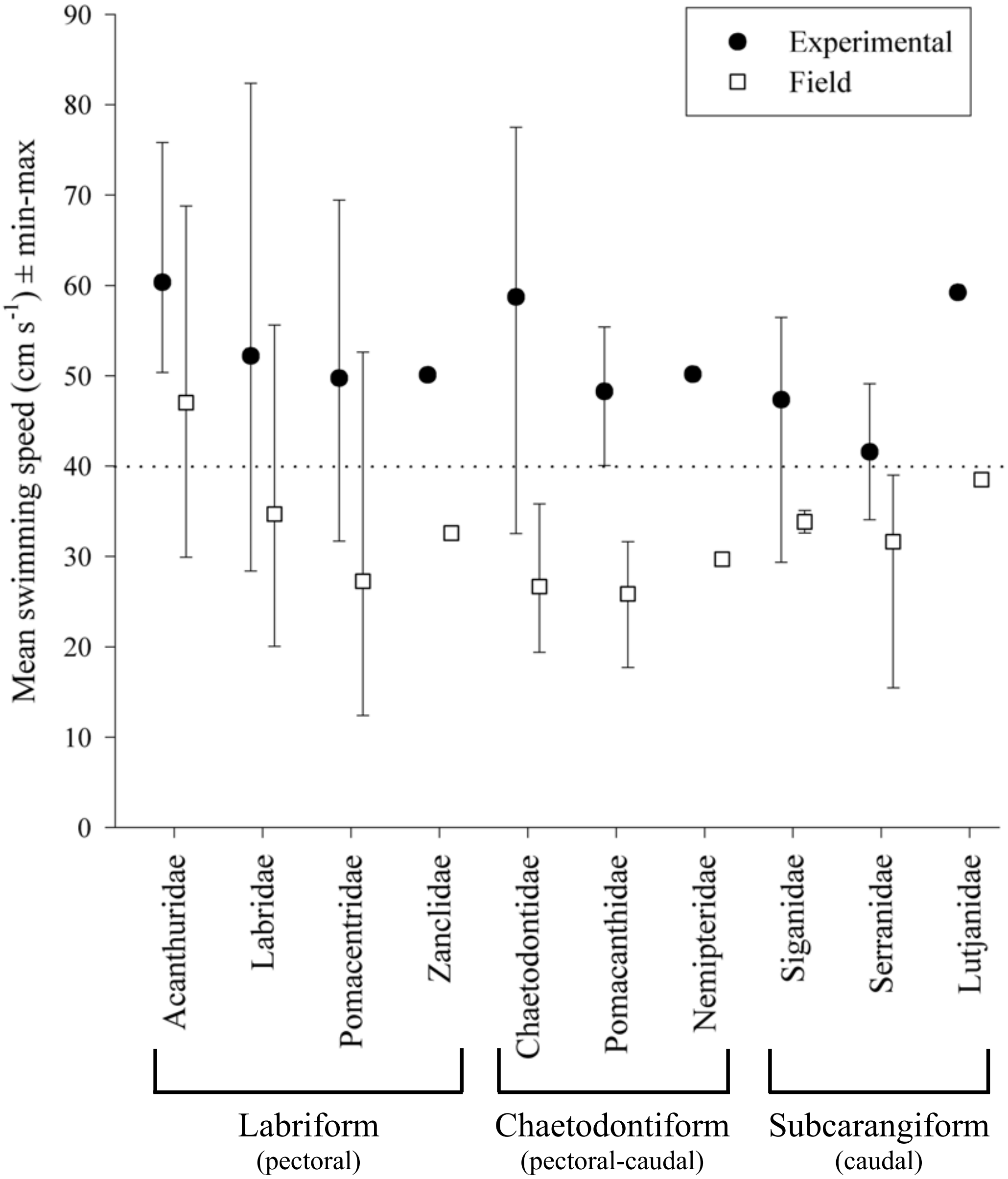

Fig. 2.4. Range of experimental (U_{crit}) and field speeds recorded in 10 reef fish families, arranged according to the predominant swimming mode. Each value is the overall mean swimming speed and the minimum and maximum average speed recorded for a species in each family, for both field and experimental performance trials. Note that only those families which have predominantly pectoral-swimming species display absolute field speeds that exceed 40 cm s^{-1} (dotted line).

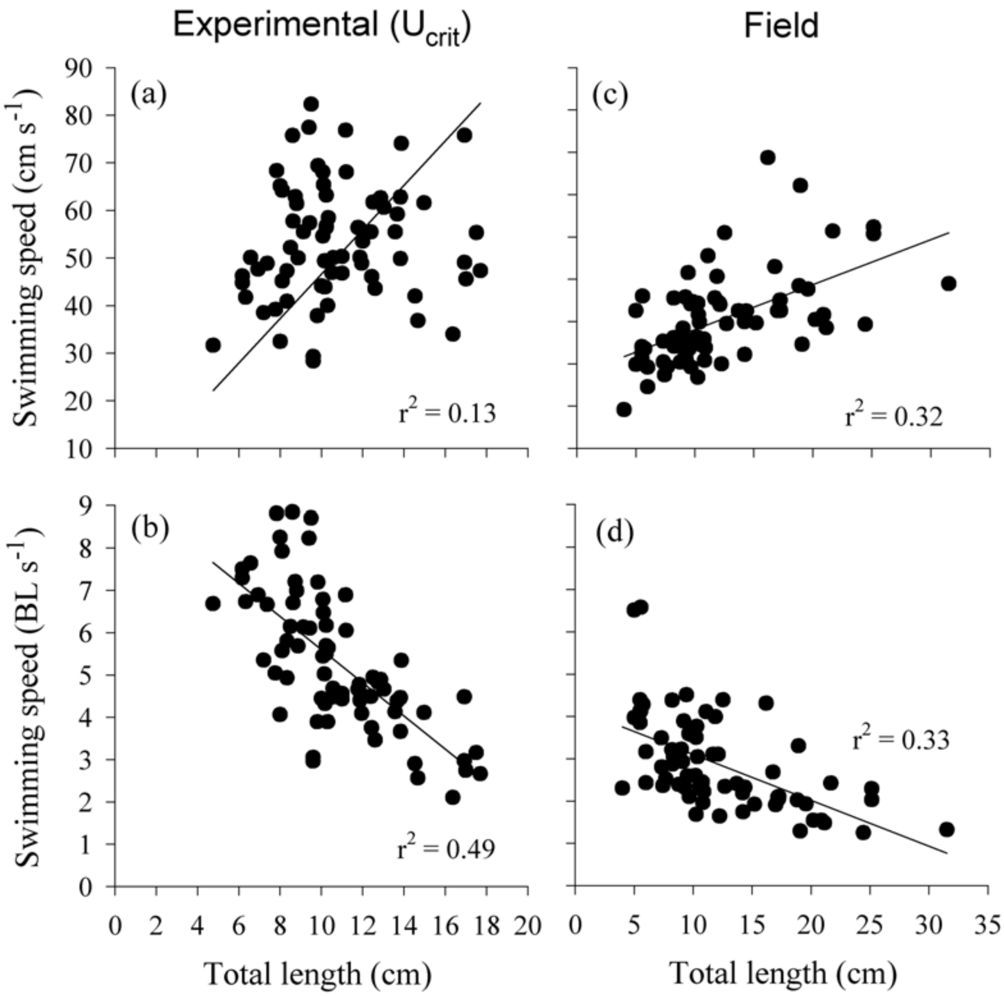

Fig. 2.5. Relationship between total length and swimming speed in terms of both absolute speed (cm s^{-1}) and body lengths per second (BL s^{-1}) under experimental (a, b) and field (c, d) conditions. Values are averages for 73 species of reef fishes from 10 families; experimental values are based on critical swimming speed (U_{crit}).

relationships were found to be significantly different between the three modes by an F-test comparing their slopes ($F_{2, 55} = 4.91$, $p < 0.02$). Post-hoc (GT2) comparisons grouped the regressions of pectoral-caudal and caudal-swimming taxa together, but separated the pectoral-swimming relationship from the other two modes (Fig. 2.6).

Direct comparisons between absolute field and experimental speeds revealed that pectoral-swimming species tended to display a field speed which was 83 ± 4 % (average ± 1 SE) of the speed attained under experimental conditions, whereas field speeds in pectoral-caudal and caudal-swimming species were an average of 44 ± 2 % and 49 ± 4 % of their experimental speeds, respectively. There were a number of significant positive outliers with the pectoral-swimming species *Acanthurus triostegus*, *A. lineatus* and *Chrysiptera rex*, and the pectoral-caudal species *Chaetodon trifascialis* displaying field performances that appeared to be considerably higher than expected from the general relationship for each mode (Fig. 2.6).

Body shape and performance

Body shape varied substantially among the 73 species of fishes examined (Fig. 2.7), although these variations in body depth and cross-sectional profile were not significantly correlated to experimental (Pearson's 0.119, $p = 0.32$, $n = 73$; Pearson's -0.118, $p = 0.31$, $n = 73$, respectively) or field (Pearson's -0.084, $p = 0.48$, $n = 73$ and Pearson's 0.046, $p = 0.70$, $n = 73$) swimming speed performance. When swimming mode was taken into account, the linear relationships of depth against cross-section ratio were not significantly different between modes ($F_{2, 55} = 1.85$, $p = 0.166$); although the majority of deep-bodied, laterally-compressed taxa appeared to be pectoral-caudal swimmers (Fig. 2.7). Whilst there was considerable overlap between modes in terms of body depth and cross-section ratios against experimental speed (Fig. 2.8a & Fig. 2.9a),

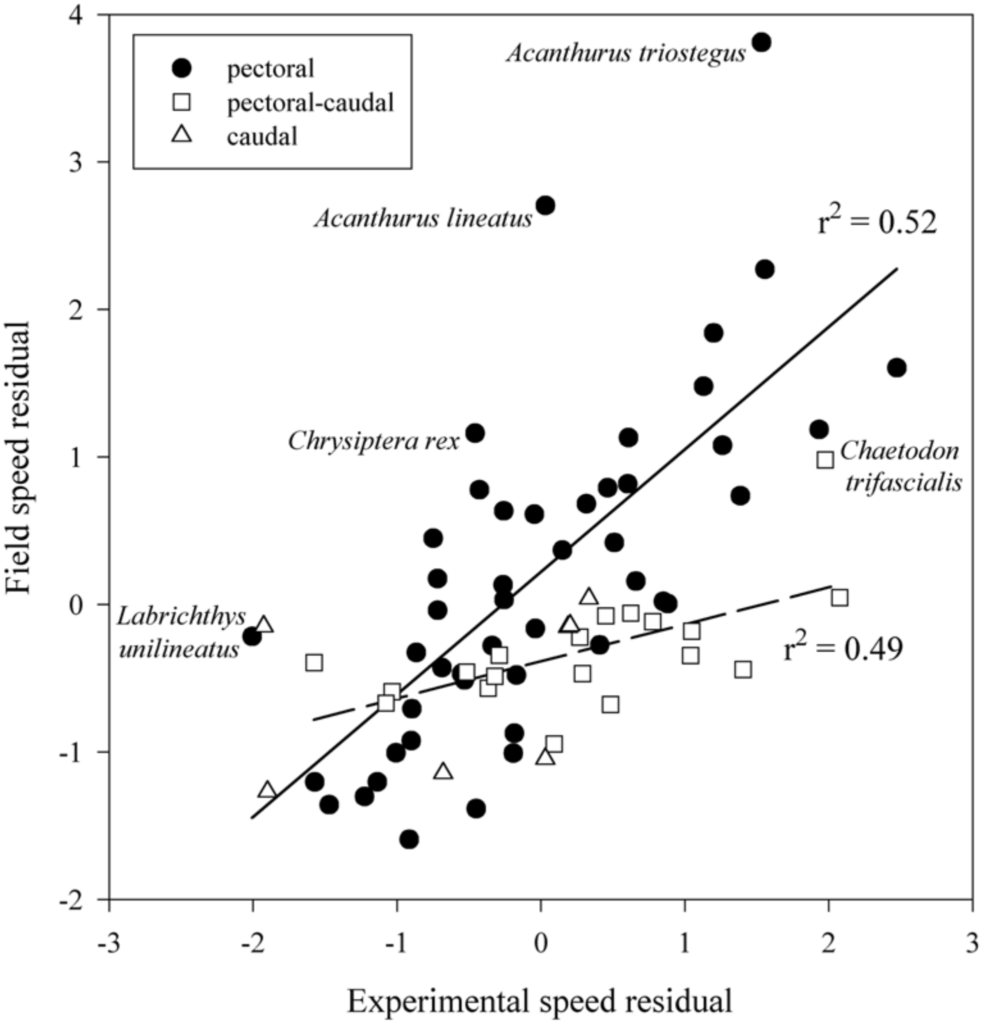

Fig. 2.6. Relationship between field and experimental speed performance in 73 species of coral reef fishes. Both axes have been corrected for body size; high positive residuals represent high speeds for a given size. Solid line represents the linear relationship for pectoral-swimming taxa; dashed line represents the pooled linear relationship (grouped by GT2 post-hoc analysis) for the pectoral-caudal and caudal-swimming taxa.

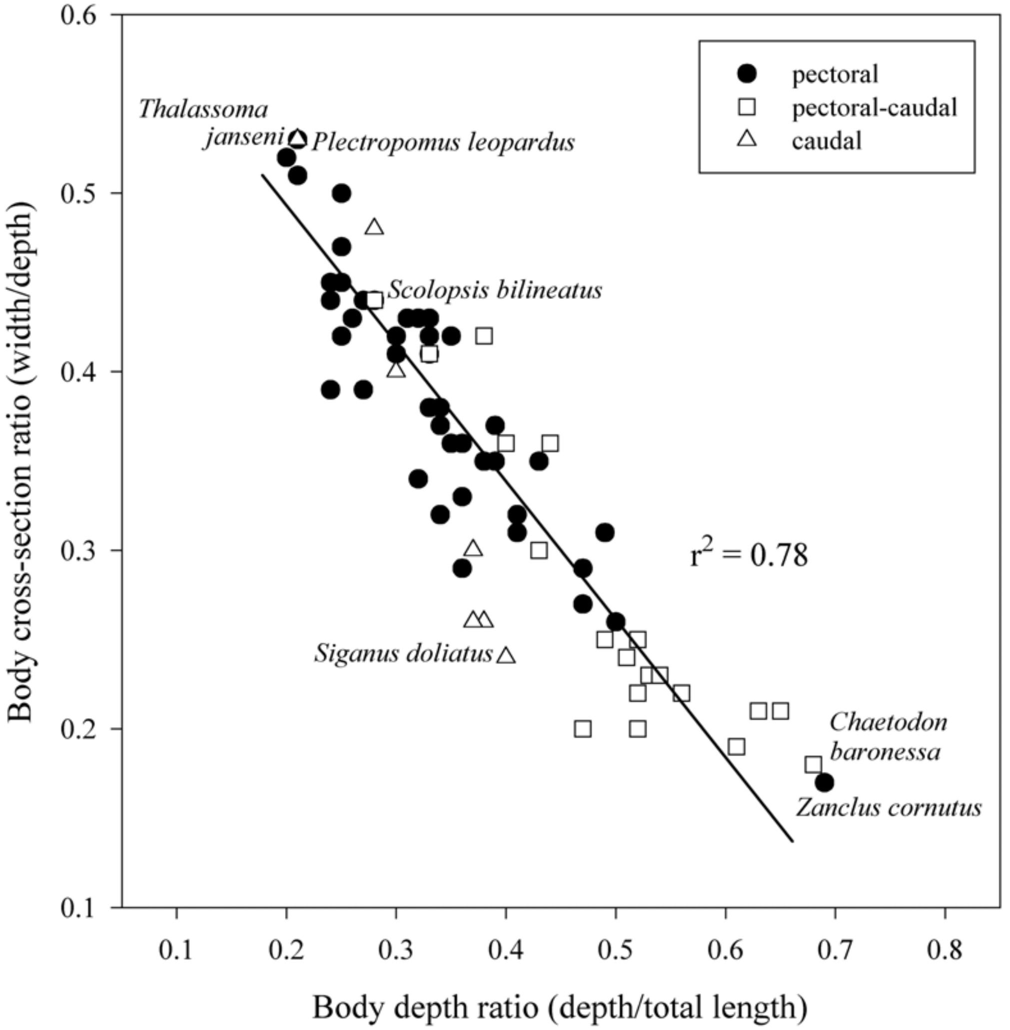

Fig. 2.7. Relationship between body depth and cross-sectional profile in 73 species of coral reef fishes. Solid line represents the pooled linear relationship for taxa across all swimming modes. Species occupying the body shape extremes from each mode are indicated.

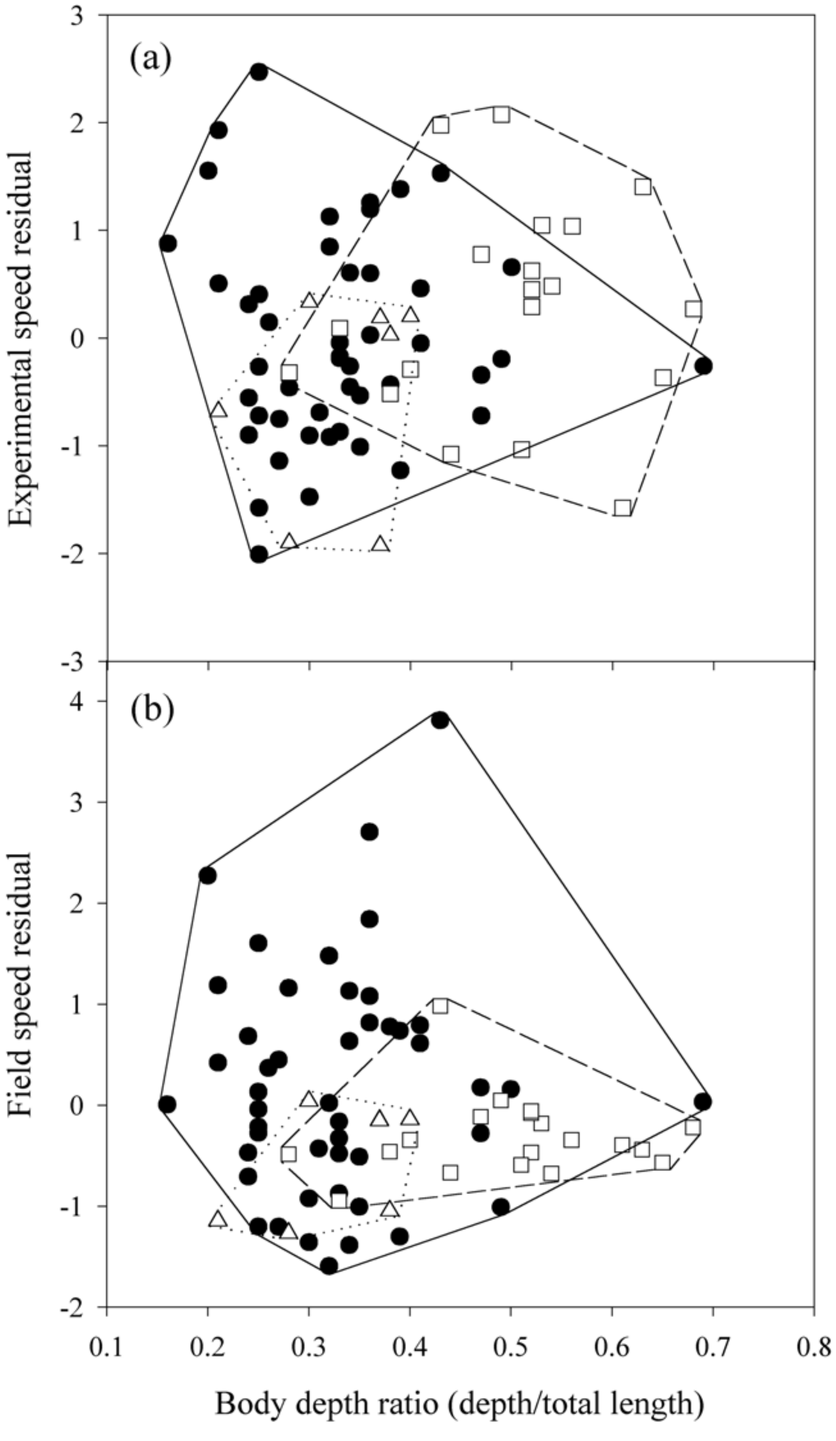

Fig. 2.8. Relationship between body depth and (a) experimental swimming speed, and (b) field swimming speed in 73 species of coral reef fishes. Solid, dashed and dotted lines represent the boundaries for pectoral (circles), pectoral-caudal (squares) and caudal-swimming (triangles) taxa, respectively. Vertical axes have been corrected for body size; high positive values represent high speeds for a given size.

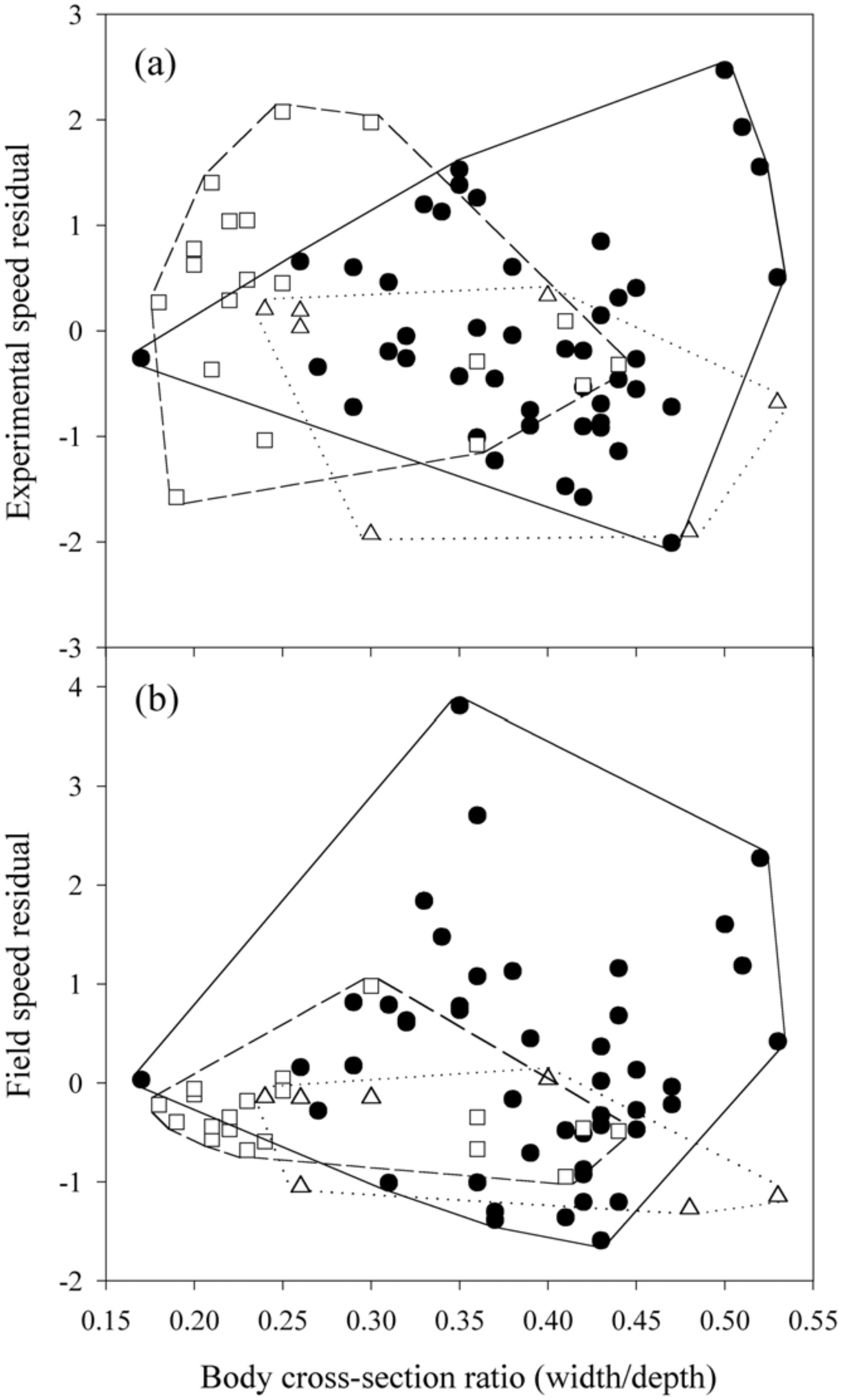

Fig. 2.9. Relationship between body cross-section profile and (a) experimental swimming speed, and (b) field swimming speed in 73 species of coral reef fishes. Solid, dashed and dotted lines represent the boundaries for pectoral (circles), pectoral-caudal (squares) and caudal-swimming (triangles) taxa, respectively. Vertical axes have been corrected for body size; high positive values represent high speeds for a given size.

pectoral-swimming taxa maintained a wider range of field speed performances across the range of body depth and cross-section ratios when compared with the other two modes (Fig. 2.8b & Fig. 2.9b).

2.4. Discussion

Previous examinations of swimming behaviour in adult fishes have identified a range of swimming modes within the MPF and BCF forms of propulsion, with biomechanical evaluations indicating that fundamental differences in these forms of propulsion may have significant implications for several aspects of swimming performance (Alexander 1967, Weihs 1989, Webb 1994, Blake 2004). This study identifies three primary swimming modes in an assemblage of coral reef fishes encompassing over 100 species from 10 families, and provides the first empirical comparison of speed performance amongst swimming modes using both field and laboratory estimates. While lab-based critical swimming speeds (U_{crit}) were strongly correlated with field speeds in these reef fishes, the relationship between potential (U_{crit}) versus realised (field) swimming speed performance differed markedly according to the swimming mode employed. Conversely, the wide range of body shapes found in this reef fish assemblage appeared to have no direct influence on swimming speed performance.

Swimming mode and performance

Based on *in situ* observations of the propulsors used during daily swimming activities, this study confirms previous predictions that pectoral-swimming is the predominant form of locomotion in coral reef fishes (Breder 1926, Lindsey 1978, Webb 1994). While differences in swimming mode were largely a family-level phenomenon, a species-level analysis indicated that taxa were more accurately allocated to a particular mode at the genus-level. Each of the 52 genera were assigned exclusively to a single swimming mode, with only one exception (*Stegastes*). The defining characteristic by which taxa were allocated to a particular mode was the use of a specific fin category in more than 50% of observed individuals. Whilst this resulted in most species within a family being assigned to a single mode, some families were split amongst modes. For example, the Pomacanthidae contained both pectoral-caudal (*Centropyge* and *Pygoplites*) and pectoral-swimming (*Pomacanthus*) taxa. Of the three main swimming modes identified, two corresponded with the traditional classifications of Labriform (pectoral) and Subcarangiform (body-caudal) swimming (sensu Webb 1994, Blake 2004). A third intermediate mode involved subcarangiform swimming augmented by pectoral fin strokes (simultaneous pectoral-caudal). This pectoral-caudal mode was used widely within the chaetodontoids (with the exception of *Pomacanthus* and *Hemitaurichthys*, pers obs), and may therefore be referred to as Chaetodontiform swimming following Webb (1984). Overwhelmingly, the labriform mode was used by the greatest number of coral reef fish taxa, with 70 species from 36 genera using this mode, most (96%) of which were from the three families Acanthuridae, Pomacentridae and Labridae.

Functionally, these three swimming modes may be separated amongst the two realms of Median and Paired-Fin (MPF) and Body Caudal-Fin (BCF) propulsion. Labriform swimming using solely the pectoral fins represents an MPF form of propulsion where thrust is produced by the oscillation of discrete fin appendages without substantial body undulation. Conversely, the chaetodontiform and subcarangiform modes are essentially BCF in nature, using primarily the caudal fins and some degree of body undulation to produce thrust (Lindsay 1978, Webb 1994, Blake 2004). In terms of thrust exploitation, the two BCF forms of propulsion used by reef fishes in the present study are most likely to be associated with drag-based thrust, whereas taxa using the labriform mode may use oscillatory fin kinematics to exploit either drag- or lift-based forces (Webb 1988, Walker & Westneat 2000, Blake 2004, but see Lauder 2000). Such differences in thrust exploitation may ultimately have consequences for the swimming speed performance of taxa, with lift-based thrust the most effective form of propulsion for maintaining high speeds, versus acceleration and slow sustained speeds using drag-based thrust (Vogel 1994, Walker & Westneat 2000).

Striking differences were found in the swimming speed performance of taxa using different swimming modes, with labriform taxa displaying much higher field speeds than fishes using a BCF mode. In terms of absolute speed, labriform (MPF) fishes displayed average field speeds of up to 70 cm s^{-1}, whereas fishes of similar size using either of the BCF modes did not exceed average speeds of 40 cm s^{-1} in the field. Undoubtedly, BCF swimming fishes are capable of attaining high swimming speeds, as is evident from the considerable overlap in experimental speed performance among the three modes in the present study. Chaetodontiform taxa using augmented BCF propulsion attained close (78 cm s^{-1}) to the maximum experimental speeds displayed by labriform taxa (82 cm s^{-1}). Moreover, inclusion of pelagic and anadromous fishes in this comparison indicates that BCF fishes often attain faster speeds than MPF taxa of the same size (Walker & Westneat 2002). However, such capabilities were not reflected in the field performances of BCF taxa. Comparisons of field-experimental performance at the species-level indicated that field speeds in labriform fishes were an average of 80% of their maximum capabilities (based on critical swimming speed estimates), whereas species using a BCF mode maintained field speeds at less than 50% of the speed attained under experimental conditions.

Comparisons of swimming capabilities in reef fishes at different life history stages also suggests an overriding influence of swimming mode on speed performance. Previous examinations of critical swimming performance in reef fishes at the settlement stage (total lengths 10 - 36 mm) have revealed average and maximum swimming speeds of 38 cm s^{-1} and 101 cm s^{-1}, respectively (Fisher et al. 2000, Bellwood & Fisher 2001, Fisher et al. in press). Family-level comparisons indicate that such settlement-stage swimming speed performances are equivalent to around 73 % of the speeds attained as adults (Table 2.3). While these comparisons should be interpreted with caution due to the different swimming trial methodologies used in each study (Table 2.3), they suggest that reef fishes attain a large proportion of their swimming speed capabilities at a very early stage. Most intriguing, however, is the fact that larval fishes have been found to maintain field speeds at around 50% of their critical swimming speed (Leis & Fisher in press), which is a similar figure to that found in adult reef fishes using BCF propulsion

Table 2.3. Comparison of critical swimming speeds between settlement-stage and adults from 7 reef fish families, with settlement-stage performance indicated as a percentage of adult U_{crit} speed. Note settlement-stage values taken from Fisher et al. (in press) were based on U_{crit} trials with 2 min time intervals and 3 BL s^{-1} increments, versus 15 min and 0.5 BL s^{-1} increments used in the present study.

Family	mean U_{crit} ± SE (cm s^{-1})		mean TL ± SE (mm)		% adult performance at settlement
	settlement	adult	settlement	adult	
Acanthuridae	50.5 ± 1.4	60.4 ± 2.5	35.4 ± 0.5	152.6 ± 11.0	83.6
Chaetodontidae	48.8 ± 2.3	58.8 ± 3.4	15.5 ± 0.7	99.1 ± 4.6	83.0
Lutjanidae	49.4 ± 2.0	59.3	26.2 ± 0.8	136.7	83.3
Nemipteridae	34.3 ± 2.3	50.2	16.5 ± 0.7	118.7	68.3
Pomacanthidae	20.7 ± 3.1	48.3 ± 4.5	16.4 ± 0.2	136.0 ± 34.5	42.9
Pomacentridae	37.6 ± 0.9	49.8 ± 2.4	15.7 ± 0.3	87.1 ± 5.4	75.5
Serranidae	31.5 ± 3.2	41.6 ± 7.5	21.4 ± 0.6	166.5 ± 2.8	75.7
Overall mean	**38.9 ± 4.2**	**52.6 ± 2.7**	**21.0 ± 2.8**	**128.1 ± 10.7**	**73.2 ± 5.5**

in the present study. Could this similarity in field-experimental performance between early life history stages and adults be due to overriding limitations according to the form of propulsion? Indeed, it appears that larval fishes at this size generally use BCF propulsion, where viscous and drag-based forces predominate at these low Reynold's numbers (Webb & Weihs 1986, Webb 1988). Such parallels in the comparative speed performance of settlement-stage and adult reef fishes suggests some overriding limitations to BCF propulsion that restricts realised swimming speeds in the field to half their potential speed, regardless of life-history stage.

Energetics may be a key factor underlying these differences in comparative field-experimental performance amongst swimming modes. Whilst there is a paucity of empirical information on the comparative energetics of swimming modes, relationships between cost-of-transport and speed in some representative MPF and BCF taxa provide some insight. Reef fishes using a labriform (MPF) swimming mode have been found to display minimum costs of transport across a broad range of swimming speeds (1.5 - 4.0 BL s^{-1}), whereas salmon using a subcarangiform (BCF) mode display a narrow minima at a relatively low speed (0.8 -1.5 BL s^{-1}) and steep increases in cost-of transport with increasing speed (Korsmeyer et al. 2002, Tolley & Torres 2002, Lee et al. 2003). Furthermore, labriform swimmers have been found to have a higher than average energetically optimum swimming speed (Korsmeyer et al. 2002), and empirical swimming evidence on labriform taxa confirms a wide range of swimming speed performances and a propensity for higher field speeds than BCF taxa of the same size (Wainwright et al. 2002, Walker & Westneat 2000, this Chapter). Based on rates of oxygen consumption, these cost of transport relationships provide a relative measure of energy consumption during continuous swimming at various speeds, for a set distance or period of time. Therefore, these relationships suggest that the labriform mode provides a particularly efficient means of swimming continuously over a broad range of high speeds, whereas fishes of a similar size using a subcarangiform (BCF) mode would incur comparatively greater energetic costs at high speed. Given that high energetic costs would prohibit the maintenance of high speeds over the substantial time periods involved in daily swimming activities (Boisclair & Tang 1993, Videler 1993, Pettersson & Hedenström 2000), this may explain why subcarangiform and chaetodontiform fishes in the present study displayed slower field speeds than labriform swimmers of the same size. Overall, it appears that labriform swimming provides the most versatile form of propulsion for demersal reef fishes, facilitating the maintenance of a wide range of swimming speeds through mechanical and energetic efficiency.

Body morphology and performance

Contrastingly, there appeared to be very little influence of body shape on swimming speed performance among fishes from this morphologically diverse coral reef assemblage. Considerable overlap in body shapes were found amongst modes, although there were indications that chaetodontiform swimmers were largely deep-bodied and laterally-compressed due to the predominance of chaetodontoid fishes in this mode. Such a wide range of body shapes and overlap between modes provided an ideal opportunity to examine the implications of body shape for swimming speed performance both among and within modes. Despite hydromechanical considerations suggesting that body form may be related to swimming performance (Alexander 1967, Webb 1984, Blake 2004), this study found that body shape was not predictably linked to routine swimming speeds in this assemblage of coral reef fishes. Species spanning a wide range of body depths and cross-sectional profiles displayed a similar range of critical swimming speeds, regardless of swimming mode employed.

Other aspects of swimming performance, however, such as manoeuvrability and stability, may be more closely linked to body shape. Indeed, manoeuvrability is a crucial aspect of swimming performance that complements speed performance during daily activities such as foraging and refuging (Webb 1983, 1994, Gerstner 1999, Webb 2002, Weihs 2002). While swimming manoeuvrability in fishes has been problematic to quantitatively define, a number of studies examining turning radii and the ability to negotiate tunnels have been particularly effective in examining the swimming capabilities of fishes spanning a range of gaits and body forms. Such empirical examinations have indicated that body shape may be less important for swimming performance than features such as fin morphology and behaviour (Webb 1978, Gerstner 1999, Schrank et al. 1999, Webb & Fairchild 2001, Eidietis et al. 2002). Ultimately, it appears that the ramifications of body shape for aspects of swimming performance remain unclear due to a complex interplay of several factors.

Conclusions

Swimming mode appears to have an overriding influence on the swimming performance of demersal reef fishes. Direct comparisons between laboratory and field estimates of performance were particularly useful for highlighting differences in swimming performance among modes, providing insights that were not immediately apparent from experimental measures taken alone. Labriform-swimming taxa were the dominant group in terms of diversity and performance, displaying a striking level of field speed performance at around 80% of their experimental capabilities, compared to less than 50 % in the other two swimming modes. Such differences appeared to be reflections of the fundamental differences between modes, in that the chaetodontiform and carangiform modes were largely BCF in nature, whereas the labriform mode is an exclusively MPF form of propulsion. While there are other aspects of swimming that are important measures of performance in fishes, such as manoeuvreability, evidence presented herein suggests that labriform swimming appears to be the most functionally versatile mode of swimming in terms of field performance and efficiency. Given the wide range of swimming speed performances observed in this assemblage and the striking separation amongst modes, there is considerable potential for interactions between swimming ability and spatial variations in wave energy on reefs.

Chapter 3: Wave energy and the role of swimming mode and performance in reef fish ecology

Published (in part) in *Limnology & Oceanography* **50,** 255-264.

3.1. Introduction

Most examinations of fish ecology in shallow aquatic habitats have incorporated wave exposure as a major physical factor. Consequently, numerous studies have found correlations between the distribution patterns of fishes and levels of wave exposure across multiple spatial scales, from among habitats zones, to among reefs located on a gradient from near shore to the open ocean (Williams 1982, Russ 1984a, 1984b, Green et al. 1987, Gust et al. 2001). Previous examinations of this relationship in adult reef fish populations have focused on the availability of resources, theorising that wave energy may indirectly affect fishes through concurrent influences on habitat characteristics and food availability. While some of these studies have been successful in documenting the relative habitat specificity of species or certain trophic groups, many studies have also found little or no effect. For example, the distribution of herbivores and detritivores closely matches the biomass or primary production of their benthic food resources among habitats (Williams et al. 1986, Klumpp & McKinnon 1992, Wilson et al. 2003), whereas the cross-shelf biomass of planktivorous fishes is poorly correlated with the availability of planktonic prey (Williams et al.1986). Similarly, while the distribution patterns of habitat-selective cryptic fishes have been found to display strong links with microhabitat availability (Munday et al. 1997, Depczynski & Bellwood 2004), highly conspicuous fishes such as wrasses display no consistent correlations between habitat characteristics and the distribution of species (Green 1996). Similar spatial variations in sessile taxa such as corals and algae have been directly linked to wave energy through differences in their morphology and physiology (Dennison & Barnes 1988, Sebens & Done 1992, Denny & Gaylord 1996, 2002). However, the possibility of direct wave energy effects on reef fishes has remained largely unexplored. This study, therefore, will utilise recent quantitative examinations of wave-induced water motion and reef fish swimming performances to investigate if these highly mobile coral reef organisms are responding directly to variations in wave energy.

Wave energy may directly impact on mobile organisms through interactions between wave-induced water movements and the locomotor performance of taxa. Wave-induced water motion has been found to affect locomotion in mobile invertebrates such as crabs and echinoids, where pedestrian movement during wave action can produce dislodgement from the substratum (Kawamata 2001, Martinez 2001, Lau & Martinez 2003). Accordingly, functional adaptations that reduce drag and dislodgement, such as modifications to echinoid tests and gastropod shells (Denny et al. 1985, Denny & Gaylord 1996, Denny 2000, Denny & Blanchette 2000) or changes in crab running posture (Martinez 2001), have been found in taxa that occupy the most wave-swept habitats. In highly mobile organisms such as fishes, experimental simulations of turbulent water movements have been shown to affect the swimming performance of fishes of different fin use and orientation (Webb 2004). Recent examinations of swimming speed performances in a demersal reef fish assemblage have revealed a wide range of swimming modes and capabilities, which manifest most strongly under field conditions (Chapter 2). Given the similarly wide variations in wave-induced water motion found among habitats and exposures on coral reefs (Sebens & Done 1992, Gourlay & Colleter 2005, Chapter 1) there is considerable potential for interactions between wave energy and swimming performance to shape the distribution and abundance of coral reef fishes.

Indeed, recent studies on a single family of coral reef fishes have revealed a strong correlation between relative levels of wave energy and the distribution of swimming abilities in wrasses (Fulton et al. 2001, Bellwood et al. 2002). Whilst promising, these studies were restricted to just one reef fish family and swimming mode, and based on comparisons across qualitative predictions of wave exposure. Given the availability of quantitative information on the wave-induced water movements in coral reef habitats (Chapter 1) and the relative swimming performance of fishes using three different swimming modes (Chapter 2), we are now in a position to test this hypotheses across an entire reef fish assemblage encompassing several diverse families and swimming modes. Specifically, it could be predicted that exposed reef flat and crest habitats will be characterised by fishes that use labriform swimming and/or maintain high swimming speeds for their size. Therefore, this study will compare the distribution of reef fish swimming modes and performances across gradients of wave-induced water motion that encompass a range of habitats zones and exposures. The main aims were to: (1) examine the spatial variation in reef fishes across four exposures and five habitat zones commonly found on coral reefs, and (2) determine the distribution of reef fish swimming modes and speed performances with variations in wave-induced flow velocity and periodicity.

3.2. Material and Methods

Spatial variation in swimming abilities and water motion

The distribution and abundance of seven diverse reef fish families (the Acanthuridae, Chaetodontidae, Labridae, Pomacanthidae, Pomacentridae, Serranidae, and Siganidae) and *Zanclus cornutus* were quantified during January 2003 using a visual census technique following Fulton et al. (2001) on reefs around Lizard Island, Great Barrier Reef, Australia. Censuses were made at 3 metres depth within each of two sites at four reef locations of different exposure to prevailing SE winds and incident wave energy (exposed, oblique, lagoon and sheltered). Within exposed sites, censuses were also conducted in several habitat zones of different depth: base (15 metres), slope (9 m), crest (3 m) and flat (2 m). All fish individuals within the seven families were identified to species and counted within 50 m x 5 m belt-transects, repeated three times within each habitat at each site. These habitats and sites were chosen to maximise the range of wave-induced water motion encountered in coral reef habitats of both similar and different depths, and matched exactly the locations where water motion had previously been assessed (Chapter 1). Distribution of swimming modes was examined by assigning each species to one of the three swimming modes, according to the designations in Chapter 2. Distributions of body shapes, field and experimental swimming speed performances were examined in a subset of this assemblage by applying the morphometrics and speed residuals taken for the 71 species in this assemblage that were assessed for field and experimental performances in Chapter 2.

Statistical analyses

Distributions of species per swimming mode (from all seven families) were examined using habitat and site as fixed factors and the three swimming modes as variables in a two-way multivariate ANOVA. Pearson's correlations were used to determine the significance of relationships between swimming mode and habitat flow velocity and periodicity. Principal Component Analyses on a covariance matrix of the distribution and abundance of reef fishes was conducted on the subset of 71 species for which swimming speed performances were also examined in Chapter 2. Ordination plots were optimised with flow velocities, and the swimming modes and body shapes of each species to examine the distribution of swimming characteristics among habitats and exposures.

Differences in the swimming speed performance amongst habitats and exposures were examined at the species-level by optimisation of PCA plots (described above) with speed residuals for each species. Relationships at the individual-level were also examined by calculating the mean swimming speed residual (for both field and experimental metrics separately) for all individuals from the 71 species within each habitat at each site (based on 3 transects from each site). Among-habitat distributions of these individual swimming speed performances were examined using habitat and site as fixed factors and the two swimming speed metrics (field and experimental residuals) as variables in a two-way multivariate ANOVA, after $\log_{10}(x+1)$ transformation of the swimming speed residuals to correct departures from normality and homoscedasticity of variances (Sokal & Rohlf 1995). Relationships between mean individual swimming speed residuals and habitat flow velocity and periodicity were then examined using Pearson's correlations and least-squares linear regressions.

3.3. Results

Visual censuses recorded a total of 66,027 individuals and 156 species (52 genera) from the seven families. Significant differences were found in the distribution of species per swimming mode amongst habitats (Pillai's trace 1.67, $F_{12,60} = 6.27$, $p < 0.001$) and exposures (Pillai's 1.86, $F_{9,48} = 8.68$, $p < 0.001$), with no significant site (Pillai's 0.04, $F_{3,18} = 0.24$, $p = 0.867$ and Pillai's 0.08, $F_{3,14} = 0.42$, $p = 0.739$, respectively) or interaction effects (Pillai's 0.37, $F_{12,60} = 0.37$, $p = 0.741$ and Pillai's 0.28, $F_{9,48} = 0.55$, $p = 0.830$, respectively). Whilst there was no significant correlation between mean species richness and either flow velocity or periodicity across all sites

(Pearson's correlation –0.14, $n = 14$, $p = 0.64$, Pearson's correlation –0.08, $n = 14$, $p = 0.78$), species per mode and habitat flow velocity were strongly correlated in all three modes, which displayed divergent linear relationships across the range of flow velocities examined (Fig. 3.1). Conversely, relationships between species per mode and flow periodicity were found to be non-significant (Pearson's 0.47, $n = 14$, $p = 0.09$, Pearson's -0.22, $n = 14$, $p = 0.45$, Pearson's -0.46, $n = 14$, $p = 0.10$, for labriform, chaetodontiform and subcarangiform modes, respectively).

Labriform swimming was the dominant mode in terms of the proportion of species using this mode in each habitat (more than 65% of species across all habitats), with increases in habitat flow velocity being associated with an increasing proportion of labriform species in each habitat (Fig. 3.1); species using modes of swimming that utilised the caudal fin displayed the opposite trend (Fig. 3.1). The Principal Component Analysis on the distribution and abundance of species confirmed these trends, identifying a major separation in the fish communities of the wave-swept crest and flat habitats from those in more sheltered habitats across both PC1 and PC2, with very little separation among sites within each level of habitat and exposure (Fig. 3.2a). The crest and flat habitats were characterised almost solely by labriform taxa (Fig. 3.2b), whereas chaetodontiform and subcarangiform taxa are predominantly associated with more sheltered habitats (Fig. 3.2b).

While there was no distinct separation amongst habitats and exposures in terms of either the body depth (Fig. 3.2c) or cross-sectional shape of species (Fig. 3.2d), the differential distribution of modes among habitats was reflected in the distribution of taxa according to their swimming speed performance. Significant differences were found in the distribution of swimming speed performances (field and experimental residuals) among habitats (Pillai's trace 1.64, $F_{2,19} = 23.06$, $p < 0.001$), with no

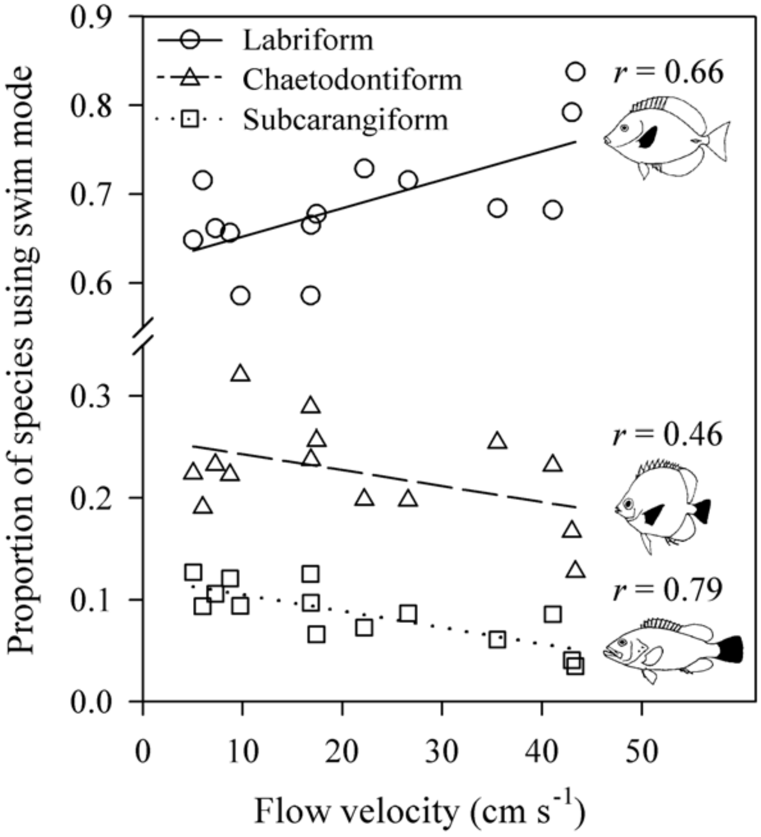

Fig. 3.1. Distribution of reef fishes (156 species) using each of three swimming modes against wave-induced flow velocities in each habitat at Lizard Island. Values are presented as a proportion of the total number of species in each habitat using each mode. Significance of regressions were $p < 0.01$ for the labriform and subcarangiform swimming modes, and $p < 0.05$ for the chaetodontiform mode.

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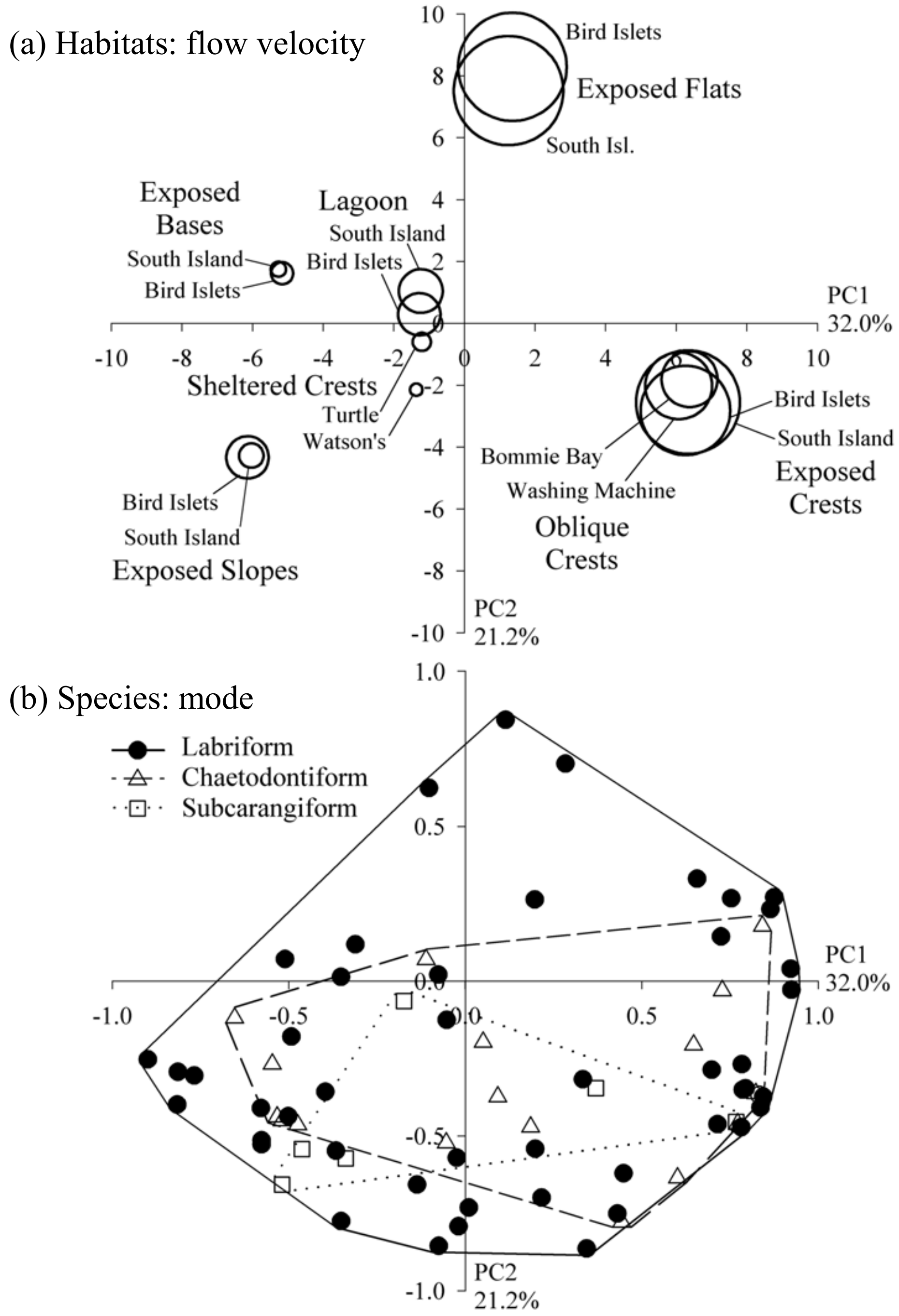
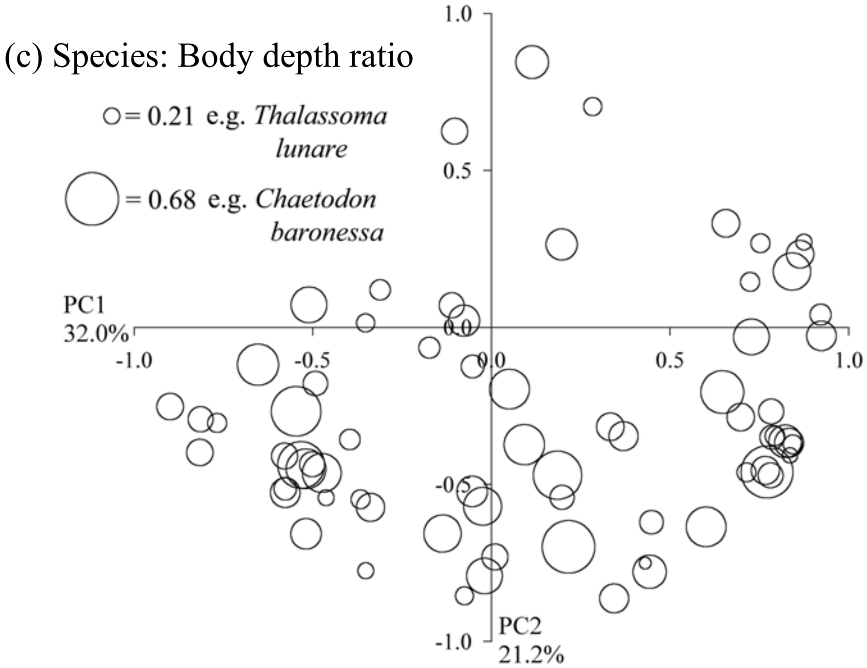


Fig. 3.2. Principal Component Analysis of the distribution and abundance of 71 reef fish species at Lizard Island. (a) Habitat ordination plot with average wave-induced flow velocities indicated (proportional to bubble size). (b) Species vector plot optimised with the swimming mode used by each species. Note the Euclidean space occupied by labriform taxa encloses (solid line) all habitats censused, whereas chaetodontiform and subcarangiform taxa largely characterise sheltered, low-flow habitats.



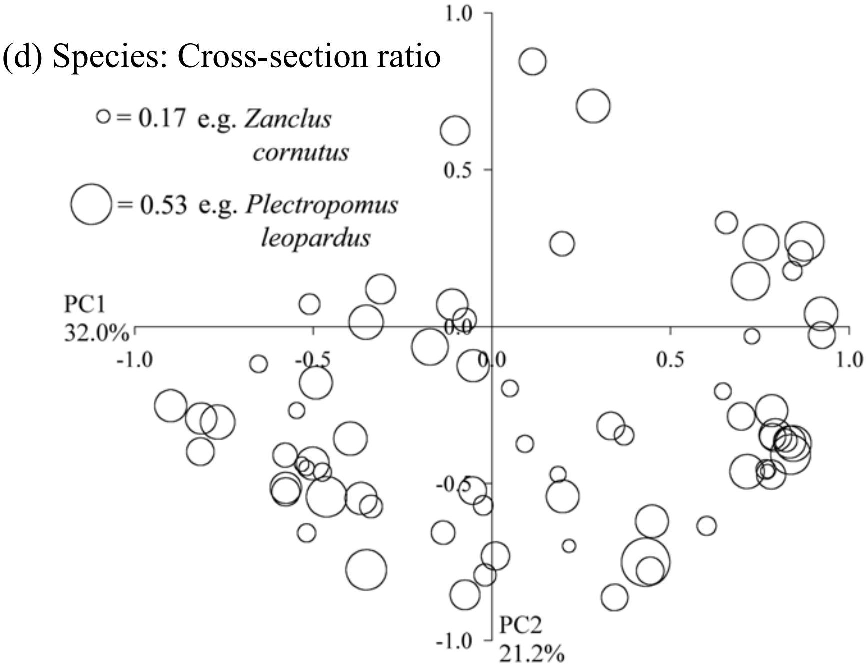
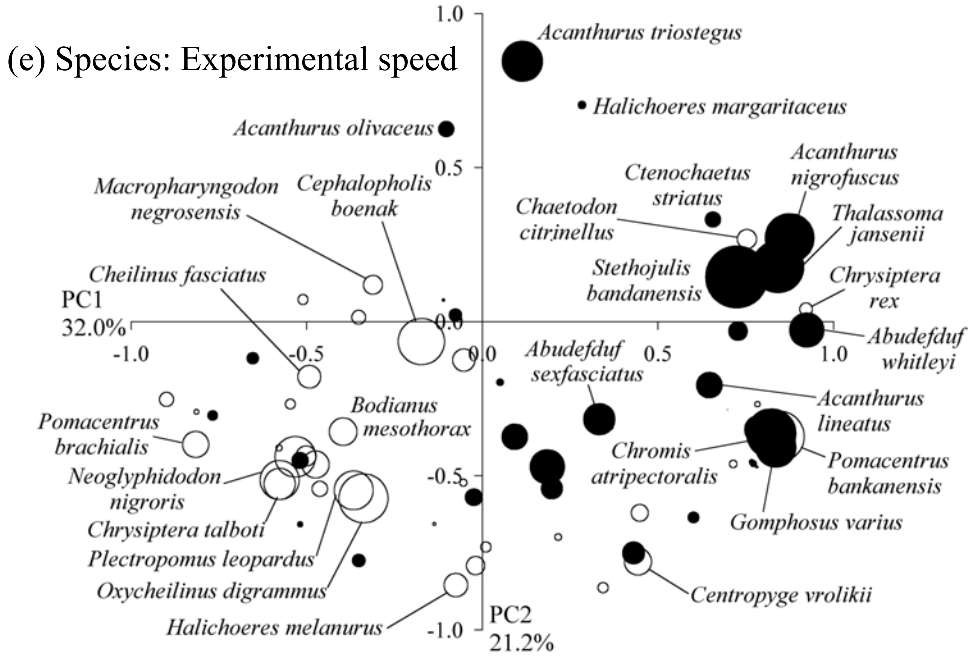


Fig. 3.2 (continued). Principal Component Analysis of the distribution and abundance of 71 reef fish species at Lizard Island. Species vector plots optimised with body shape ratios for each species in terms of body (c) depth ratio and (d) cross-section ratio. Circle size is proportional to either body depth or cross-section ratio, with examples of species displaying minimum and maximum values indicated.



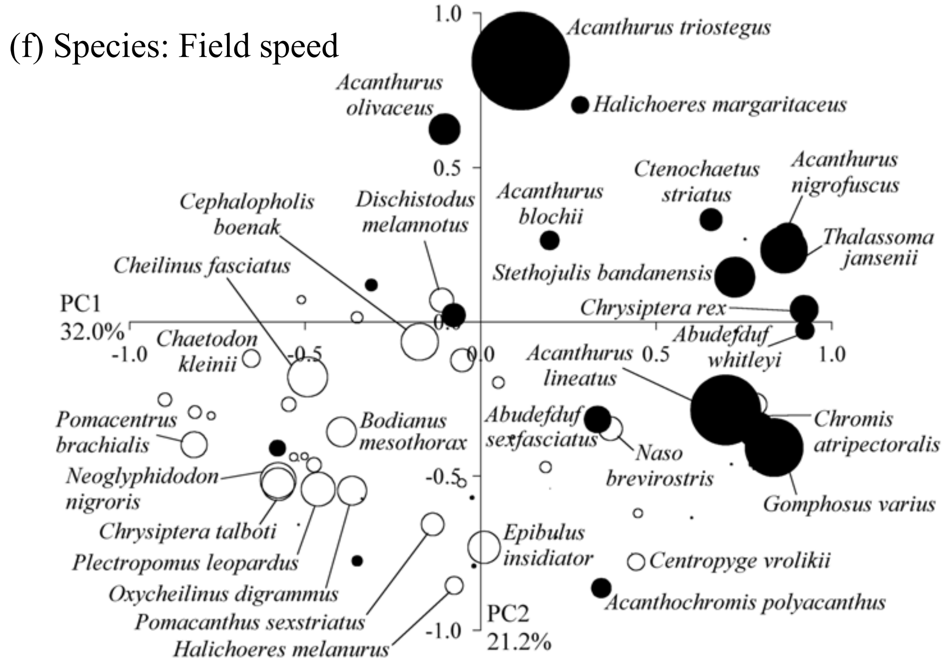


Fig. 3.2 (continued). Principal Component Analysis of the distribution and abundance of 71 reef fish species at Lizard Island. Species vector plots optimised with the swimming speed residuals of each species for both (e) experimental (U_{crit}) and (f) field swimming speed performance. Open circles represent negative residuals and slow speed performance for a given size; closed circles represent positive residuals and high performance.

significant site (Pillai's trace 0.25, $F_{2,19} = 3.23$, $p = 0.062$) or interaction effect (Pillai's trace 0.32, $F_{2,19} = 0.96$, $p = 0.484$). Species that dominated high-flow crest and flat habitats were predominantly those with high swimming speed performances for their size (high positive residuals), whereas taxa that characterised sheltered habitats were those of poor speed performance for their size (Fig. 3.2e & f). Furthermore, direct comparisons between swimming speed performances and levels of water motion in each habitat revealed strong correlations between flow velocity and the average swimming speed residual of individuals in terms of both field (Pearson's 0.78, $n = 14$, $p = 0.001$) and experimental speed performance (Pearson's 0.71, $n = 14$, $p = 0.004$). Least-squares linear regressions indicated that the average speed residual of individuals in each habitat displayed a positive relationship with flow velocity in terms of both field (Fig. 3.3a) and experimental speed performance (Fig. 3.3b).

3.4. Discussion

Reef fish distribution patterns in this assemblage appear to be closely linked to the wave-induced water motion within habitats and the swimming mode and performance of species. Previous studies on wrasses indicated that a major separation in the distribution of swimming abilities occurs among habitat zones of different wave energy (Fulton et al. 2001, Bellwood et al. 2002). Evidence from the present study indicates that this relationship is a general phenomenon in coral reef fishes. There is a clear and consistent link between variations in wave-induced water motion and the swimming abilities of fishes from several divergent perciform lineages using three different modes of swimming. Labriform fishes were the ecologically dominant functional group, with the prevalence of labriform species increasing in habitats of high flow velocity, whereas taxa using chaetodontiform and subcarangiform swimming

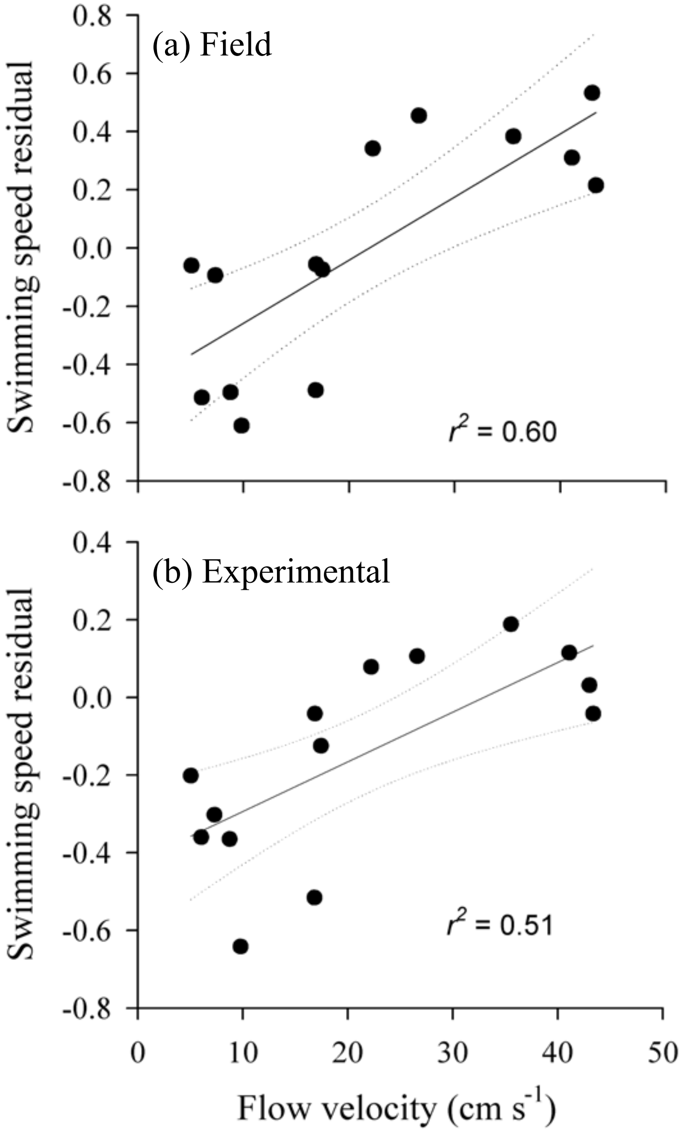


Fig. 3.3. Relationship between swimming performance of individuals against wave-induced flow velocity for a reef fish assemblage at Lizard Island. Values are average speed residuals of all individuals in each habitat against the mean flow velocity of each habitat for both (a) field and (b) experimental (U_{crit}) measures of speed performance.

modes displayed the opposite trend. Flow velocity appeared to be the relevant hydrological measure with strong correlations and direct linear relationships between flow velocity and the swimming speed performances; whereas either non-significant or poor correlations were found between the same swimming attributes and flow periodicity (rate of flow direction changes per minute). Interestingly, chaetodontiform and subcarangiform taxa were either entirely absent or in low abundance in the most wave-swept reef flat habitats where flow velocities exceed 40 cm s^{-1}, which is also the upper limit of field swimming speeds observed in fishes using these two modes (Chapter 2). Whilst experimental measures suggest that taxa using all three modes may be able to attain the speeds necessary to occupy these wave-swept habitats, realised field speeds indicate that only labriform taxa maintain speeds necessary for the occupation of the most wave-swept habitats.

Equivalent relationships between water motion and the swimming capabilities of adult fishes have been found in studies of freshwater systems. Relationships between flow velocity and habitat-use in freshwater fishes have been relatively well documented, identifying links between swimming capabilities and the position of fishes in the water-column, or amongst high- and low-flow habitats (Chipps et al. 1994, Sagnes et al. 1997, Heinimaa & Erkinaro 1999, Rosenfeld et al. 2000, Haro et al. 2004, Bhat 2005, Kodric-Brown & Nicoletto 2005). While the use of pool versus riffle habitats have often been attributed to lower predation risk (Power 1984, Gilliam & Fraser 1987, Lonzarich & Quinn 1995), differences in the size and growth of freshwater fishes amongst these habitats have led to examinations of the energetic implications of habitat-use according to water flow. Bioenergetic cost-benefit analyses based on swimming costs and energy intake from invertebrate drift have indicated that avoidance of high-flow riffle habitats may be entirely accounted for by locomotor energetics under different flow conditions, without having to invoke predation risk (Hughes & Dill 1990, Hill & Grossman 1993, Nislow et al. 2000, Rosenfeld & Boss 2001). Similar bioenergetic analyses have also indicated that many freshwater fishes choose an energetically optimal speed during upstream migrations (Hinch & Rand 1998, Haro et al. 2004, Castro-Santos 2005).

Could the energetic cost of locomotion be a determining factor in the distribution of swimming modes amongst coral reef habitats of varying water motion? Quantitative estimates of water motion across coral reef habitats and exposures highlight the potential for significant variations in the energetic costs of habitat utilization for coral reef fishes. Theoretical and empirical examinations in adult reef fishes have indicated that for a given size, energetic costs of swimming increase exponentially with speed at a rate of 1.7 - 2.3 (Beamish 1978, Korsmeyer et al. 2002, Lee et al. 2003). Taking the two extremes in flow velocity recorded at Lizard Island, inhabitants of exposed reef crests may be subjected to up to 5.2 times greater flow speeds than inhabitants of sheltered locations. If an individual fish of 10 cm length were to station-hold against these average flow velocities at each location, daily energy use associated with such swimming behaviour on exposed reefs could be up to 45 times greater than station-holding in a sheltered reef habitat. Given that this estimate is outside the 15-fold increase in metabolic rate that has previously been seen during swimming trials in many fishes (Beamish 1978), such differences in energetic demand between habitats could be beyond the capacity of many taxa. Indeed, fish faunas within the most wave-swept habitats on reefs are often characterised by a few abundant species (Fulton et al. 2001, Bellwood et al. 2002). Although these estimates incorporate simplifying assumptions and do not take into account behavioural modifications such as flow-refuging (Hill & Grossman 1993, Gerstner 1998, Fulton et al. 2001, Fulton & Bellwood 2002) and the effects of turbulence on locomotor costs (Enders et al. 2005, Alexander 2005), they suggest that increased energetic costs of locomotion may be a considerable barrier to the occupation of wave-swept habitats by fishes.

Biomechanical advantages associated with each locomotor mode in terms of stability, manoeuvrability and energetic efficiency could, therefore, play a major role in shaping the distribution of swimming modes across gradients of water motion. For example, the dominance of labriform taxa in wave-swept locations may be linked to the low costs of transport and higher than average energetically optimum swimming speeds exhibited by fishes using this swimming mode (Korsmeyer et al. 2002, Chapter 2). Maintenance of high swimming speeds with efficiency would provide a considerable competitive advantage to fishes occupying habitats of high flow velocity (Videler 1993), and may explain why labriform taxa dominate wave-swept habitats and locations. Moreover, efficiency in labriform locomotion may be further enhanced through the use of lift-based thrust (Vogel 1994, Walker & Westneat 2000), and previous studies on wrasses have demonstrated that taxa which dominate wave-swept habitats predominantly use lift-based thrust (Bellwood et al. 2002, Wainwright et al. 2002). A similar relationship may be expected for the other labriform taxa in this study, and a detailed comparison of interspecific patterns of fin shape, performance and distribution in relation to water motion will provide further insight (Chapter 4).

Manoeuvrability may also be an important variable shaping the relative distribution of swimming modes across gradients of wave energy. Fishes using a labriform mode (and other forms of rigid-body MPF propulsion in general) have been found to display high manoeuvrability (in terms of turning radius) and stability (Lindsey 1978, Gerstner 1999, Webb 2002, Webb & Fairchild 2001, Weihs 2002, Blake 2004). Given that wave-swept habitats are often associated with high rates of flow direction change, good manoeuvreability and stability would be advantageous for fishes interacting with a complex substratum to obtain food and shelter (Videler 1993). Indeed, fine-scale water movements such as turbulence and boundary layer effects may play an important role in shaping the distribution patterns of fishes at smaller scales than those examined in the present study (Fulton et al. 2001, Fulton & Bellwood 2002). While the caudal-swimming modes seen in these demersal reef fishes may be associated with a capacity for slow-speed power and acceleration, they may lack efficiency at high swimming speeds and exhibit larger turning radii than taxa using MPF forms of propulsion (Webb 1994, Weihs 1989, Gerstner 1999, Korsmeyer et al. 2002, Weihs 2002, Blake 2004). Consequently, subcarangiform fishes could be at both an energetic and biomechanical disadvantage to their labriform counterparts in high wave energy habitats. Notably, the intermediate prevalence of chaetodontiform taxa in wave-swept habitats may reflect the incremental benefits of using pectoral augmentation during caudal locomotion.

Despite previous suggestions that spatial variations in reef fish assemblages with wave energy may be due to the influence of wave energy on the availability of trophic resources (review Williams 1991), the above links between wave energy and the swimming performance of species appeared to be largely independent of trophic group. For example, planktivorous fishes distributed among different habitats displayed swimming abilities that were congruent with the level of wave-induced water motion in the habitat occupied. The most abundant planktivores on the relatively calm reef slope, *Pomacentrus brachialis* and *Cirrhilabrus punctatus*, displayed average field speeds of 14.6 cm s^{-1} and 20.6 cm s^{-1} respectively, whereas *Chromis atripectoralis* and *Thalassoma amblycephalum* dominated the wave-swept crest and flat habitats with average speeds of 36.1 cm s^{-1} and 36.0 cm s^{-1}. A similar pattern was found in the more benthic-associated roving herbivores and detritivores, with *Ctenocheatus binotatus* occurring primarily on the reef slope and displaying a mean field speed of 35.1 cm s^{-1}, whereas *C. striatus* (43.1 cm s^{-1}) and *Acanthurus nigrofuscus* (45.6 cm s^{-1}) were most abundant on the crest, and *A. triostegus* (68.8 cm s^{-1}) dominated the wave-swept reef flat habitat. Thus, it appears that these patterns are largely independent of trophic status, providing further support for the hypothesis that wave energy is directly influencing reef fishes through their swimming mode and performance.

Conclusions

Using quantitative estimates of wave-induced water motion, this study was able to directly evaluate of the link between wave energy and the distribution patterns of a highly mobile group of coral reef organisms. A clear relationship between the swimming capabilities of fishes and wave-induced water motion was found over a continuous gradient of water motion, regardless of habitat-type, and encompassed fishes from several divergent perciform lineages using three different modes of swimming. Furthermore, these patterns appeared to be largely independent of the trophic status of taxa, supporting the hypothesis that wave energy directly influences the distribution and abundance of reef fishes. Energetic and biomechanical considerations indicate that wave-swept habitats pose substantial challenges to locomotion that can shape broad-scale patterns of habitat utilization by reef fishes according to their locomotor performance. Fishes using the functionally versatile labriform swimming mode dominated this coral reef assemblage, particularly in wave-swept habitats were wave energy exerts the greatest influence. Whilst these among-mode comparisons highlight the importance of the labriform mode in patterns of reef fish ecology, extensive within-mode variation within this group would benefit from further examination.

Chapter 4: Ecomorphology of labriform swimming in coral reef fishes.

Published in *Proceedings of the Royal Society London: B* **272,** 827-832.

4.1. Introduction

Swimming using solely the pectoral fins for the production of thrust (labriform swimming, *sensu* Webb 1994) is the dominant swimming mode in coral reef fishes, with over 65% of taxa in any given habitat utilising this mode during daily activities (Chapter 2). Functional analyses have indicated that a diversity of pectoral fin shapes and kinematics may exist among labriform-swimming fishes, extending along a continuum from the extremes of drag-based rowing using rounded fins to lift-based flapping with tapered fins (Blake 1981, Drucker & Jensen 1997, Walker & Westneat 2002). This morphological diversity has been linked to differences in swimming performance among taxa (Wainwright et al. 2002). Major trade-offs appear to exist between manoeuvrability and acceleration at low speeds using rowing fin strokes, against efficient maintenance of high speeds using flapping lift-based thrust (Blake 1981, Vogel 1994, Drucker & Lauder 2000, Walker & Westneat 2000, 2002, Wainwright et al. 2002). Accordingly, this has led to the suggestion that a general relationship may exist in labriform swimmers: species with tapered fins exploit lift-based thrust to maintain higher swimming speeds than species with rounded fins that predominantly use drag-based thrust (Drucker & Lauder 2000, Wainwright et al. 2002, Thorsen & Westneat 2005).

Application of these functional characteristics to ecological patterns in a single family of labriform-swimming reef fishes, the wrasses (f. Labridae), have revealed strong correlations between the field-based swimming abilities of species and their distribution across habitats of varying wave energy at several coral reef locations in the Indo-Pacific and Caribbean (Bellwood & Wainwright 2001, Bellwood et al. 2002). Specifically, fishes that utilised lift-based locomotion where found to be highly abundant in wave-swept habitats and locations, whereas species using drag-based thrust during swimming were almost entirely restricted to more sheltered locations (Bellwood et al. 2002). Based on the available biomechanical evidence, these studies suggested this relationship may be the result of an interaction between wave-induced water motion and the relative efficiency of the two thrust types at high sustained swimming speeds (Wainwright et al. 2002, Walker & Westneat 2000, 2002).

Whilst promising, the generality of these relationships are yet to be examined for the majority of reef fishes that use labriform propulsion, and tested against a quantitative gradient of wave-induced water motion. Using three diverse families of labriform-swimming fishes (the Acanthuridae, Labridae, and Pomacentridae) that encompass almost half of the taxonomic diversity and two-thirds of the total number of visually apparent fishes commonly found on coral reefs (Bellwood 1996), the two specific aims were to: (1) determine if a general functional relationship between pectoral fin shape and swimming speed, both in the field and laboratory, exists in labriform swimming fishes from several independent evolutionary lineages, and (2) identify if these functional traits are linked to the distribution patterns of species according to the level of wave-induced water motion among habitats.

4.2. Material and Methods

Fin morphology and swimming performance

Pectoral fin morphology was examined in 111 reef fish species from the Great Barrier Reef. These fishes from the families Acanthuridae (16 species), Labridae (49) and Pomacentridae (46) use a labriform gait during locomotion (Chapter 2). Pectoral fin shape was quantified in terms of an aspect ratio (AR), which indicates a tendency towards either rounded (low AR) or tapered (high AR) fins (Wainwright et al. 2002). Fishes were collected using hand spears or barrier nets, placed in an ice-water slurry within one hour of capture, and their total length (TL) measured prior to dissection. The pectoral fin was removed from an individual at the base of the fin, spread on a sheet of foam, pinned, and then fixed in position using concentrated formalin solution (39% formaldehyde). Once fixed, a digital image was taken and the length of the leading edge and total fin area measured using Scion Image v4.0.2 (Scion Corporation). Aspect ratio was then calculated as the length of the leading edge squared, divided by total fin area. Mean AR was calculated from a minimum of 3 adult individuals for each species in the assemblage.

Both field and experimental swimming speeds were used to evaluate the relationship between fin shape and swimming performance in the three families. Field speeds were measured by timing individual fish as they swam undisturbed on the reef in an approximately linear path using the same protocols outlined in Chapter 2. A minimum of 10 individual observations were taken for each species, with the average travel distance and duration of each field trial being 248 cm and 7.2 seconds, respectively. Experimental speeds were measured in a 194 L re-circulating flow tank of the same design outlined in Chapter 1. Each incremental velocity trial measured the maximum prolonged swimming speed reached using solely the pectoral fins for locomotion (U_{pc}), following Drucker (1996) and Walker & Westneat (2002). This was repeated for a minimum of 3 individuals per species, with the average experimental trial duration being 138 minutes. While pectoral fin AR was measured for all of the species censused in the three families, just over 75% of these species were included in these field and experimental speed performance trials, with an overall total of 1,293 field and 194 experimental trials (Table 4.1).

Spatial variation in fish assemblages and water motion

Distribution patterns of the three families were quantified during January 2003 using a visual census technique following Fulton et al. (2001) on reefs around Lizard Island, Great Barrier Reef, Australia. All fish individuals within the three labriform-swimming families (Chapter 2) were identified to species and counted within 50 m x 5 m belt-transects, following the same census protocols outlined in Chapter 3. Habitats and sites were chosen to maximise the range of wave-induced water motion encountered in coral reef habitats of both similar and different depths, and matched exactly the locations where wave-induced water motion was previously quantified (Chapter 1).

Statistical analyses

All performance measures were corrected for differences in body size by calculating swimming speed residuals from the linear regression of speed against TL; this was done separately for each family using the mean values of speed and TL from each species (Reist 1985, Wainwright et al. 2002). Field and transitional (U_{pc}) speed residuals were compared by Pearson's correlation and least-squares linear regression using the 44 species for which both performances measures were recorded. Relationships between swimming speed residual and pectoral AR were then examined concurrently for each family using Pearson's correlations and linear regressions.

Differences in mean fin aspect ratio among habitats were examined for each family by calculating the average aspect ratio for all individuals of that family within each habitat and site (based on 3 transects from each site). Relationships between mean aspect ratio and water motion for the exact same habitats and sites were examined for each family using Pearson's correlation and linear least-squares regressions, with water motion values being taken from previous estimates (Chapter 1).

4.3. Results

Fin morphology and swimming performance

Pectoral fin shape varied considerably among species in all three families, with average aspect ratios in the range of 1.15 - 1.98 (Acanthuridae), 0.90 - 2.08 (Labridae), and 0.63 - 1.67 (Pomacentridae). This diversity of pectoral fin morphology was reflected in the range of swimming speeds observed (Table 4.1). Field and experimental (U_{pc}) speeds were strongly correlated, exhibiting an almost isometric linear relationship (Fig. 4.1). Strong correlations were also found between fin aspect ratio and swimming speed (Table 4.1), with all three families displaying a similar linear relationship between the two metrics (Fig. 4.2). Under both experimental and field conditions, species with higher aspect ratio fins attained faster swimming speeds (Fig. 4.2).

Table 4.1. Range of field and experimental speeds observed in each of three labriform reef fish families, with the number of species, mean total length (TL), and correlations (r) between pectoral fin aspect-ratio and swimming speed performance indicated. All correlations were highly significant ($p < 0.01$).

	species	mean TL (cm)	min - max (cm s^{-1})	min - max (TL s^{-1})	r
(i) Acanthuridae					
Field speeds	15	19.5	29.9 - 68.8	1.02 - 4.32	0.76
Experimental speeds	10	12.8	18.8 - 61.9	1.37 - 4.78	0.82
(ii) Labridae					
Field speeds	39	14.5	20.3 - 55.6	0.74 - 6.76	0.63
Experimental speeds	17	11.4	19.3 - 71.6	1.91 - 7.39	0.92
(iii) Pomacentridae					
Field speeds	20	8.9	10.2 - 36.1	1.69 - 6.59	0.78
Experimental speeds	29	9.2	15.0 - 47.7	1.83 - 5.49	0.83

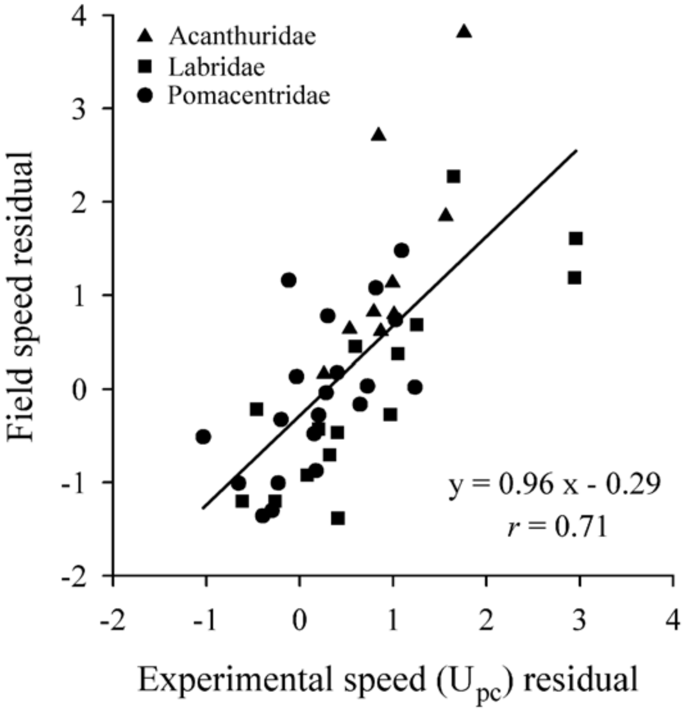


Fig. 4.1. Relationship between field and experimental swimming speed in 44 species of labriform-swimming fishes. Both axes have been corrected for body size; high positive residuals represent high speeds for a given size. Note that the linear regression is close to isometric (slope = 1.0).

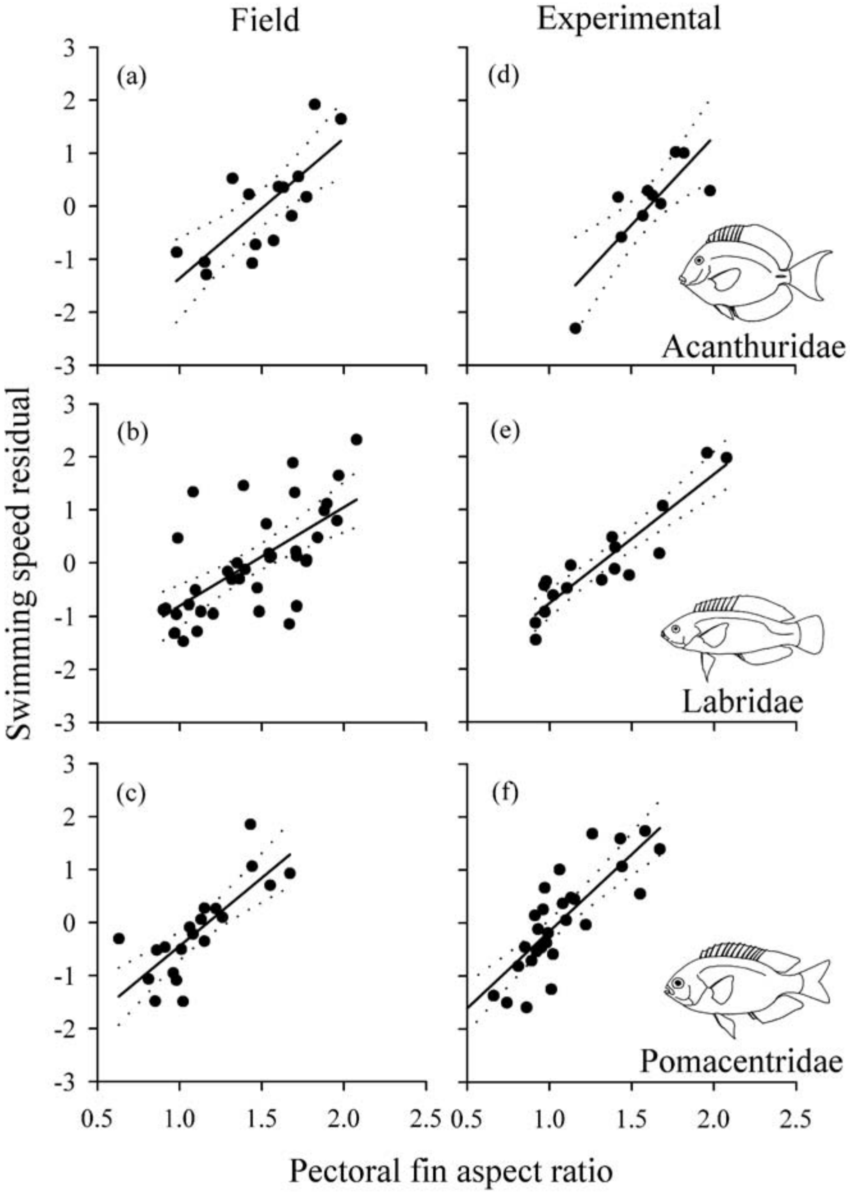


Fig. 4.2. Pectoral fin morphology and swimming performance in the field (a, b, c) and under experimental conditions (d, e, f) for three reef fish families (the Acanthuridae, Labridae and Pomacentridae, respectively). Experimental speeds are the maximum speeds reached using pectoral fins only (U_{pc}). Vertical axes have been corrected for body size; high positive values represent high speeds for a given size. The range of absolute speeds and correlations are given in Table 4.1. Dotted lines indicate 95 % confidence limits.

Distribution of fin morphologies and water motion

The distribution of fishes with different pectoral fin shape among habitat and exposures of different water motion was highly congruent among families (Fig. 4.3). Strong positive relationships between the mean fin aspect ratio of individuals and the water velocity of habitats were displayed in all three families (Fig. 4.3). In particular, crest habitats from different wave exposures with varying flow velocities displayed a corresponding variation in mean fin aspect ratios (Fig 4.3). Notably, the range of actual swimming speeds (cm s^{-1}) observed in the swimming performance trials appeared to span the range of flow velocities in the habitats examined (Table 4.1, Fig. 4.3).

4.4. Discussion

Among-mode comparisons of swimming performance indicated that labriform swimming may be a particularly efficient mode for maintaining high swimming speeds, with extensive within-mode variation in swimming speed performance and ecology (Chapter 2). Recent studies on wrasses (f. Labridae) have indicated that swimming morphology may be linked to performance and play a major role in shaping distribution patterns across a range of wave exposures (Fulton et al. 2001, Bellwood et al. 2002, Wainwright et al. 2002). The present study considerably expands on these findings, demonstrating that the functional relationship between fin morphology and swimming performance is a general phenomenon amongst labriform-swimming fishes in three families from at least two distinct evolutionary lineages. Furthermore, for the first time, a direct comparison between the distribution of these functional traits and quantitative values of wave-induced water movement revealed congruent ecomorphological patterns in all three families.

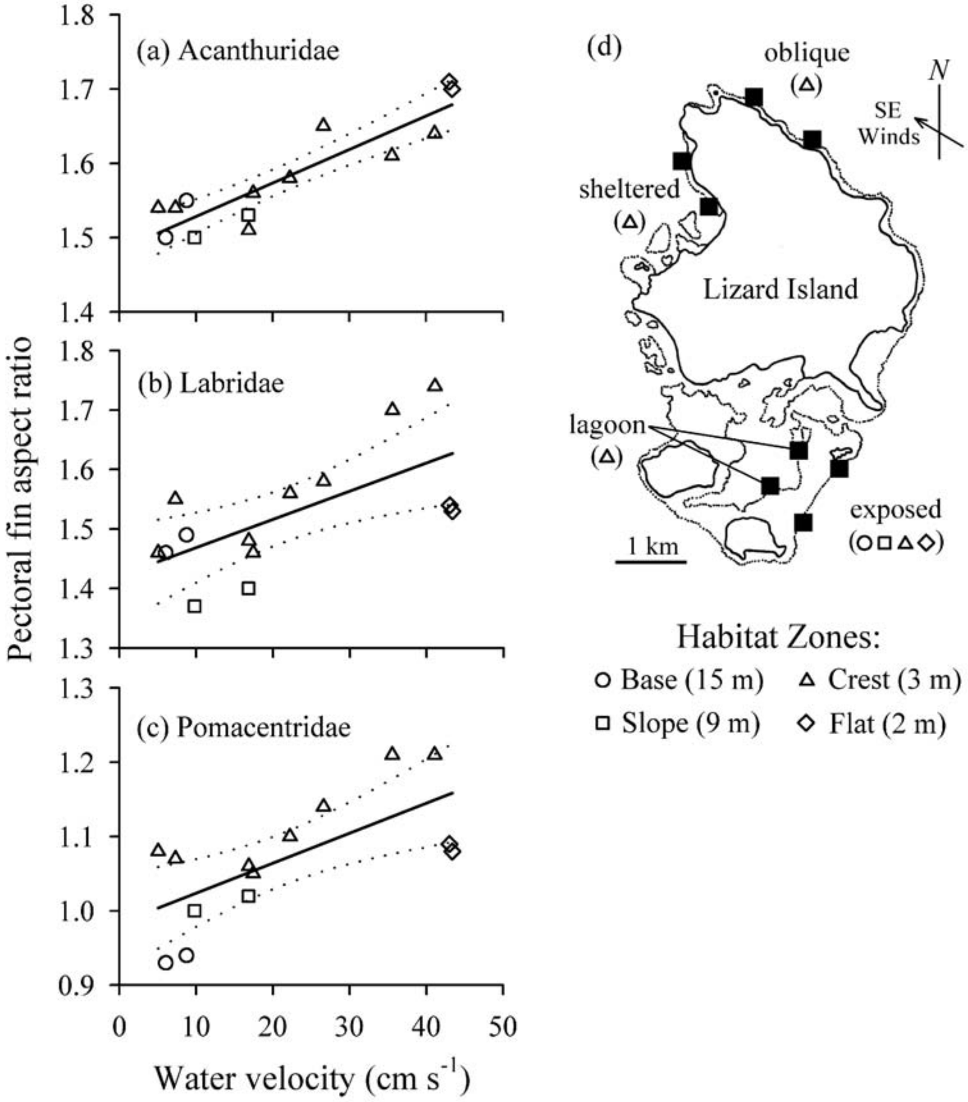


Fig. 4.3. Relationship between pectoral fin aspect ratio and net water velocity for each of the families (a) Acanthuridae ($r = 0.901, p < 0.01$), (b) Labridae ($r = 0.656, p < 0.05$) and (c) Pomacentridae ($r = 0.689, p < 0.01$). Fin aspect ratio values were calculated as the average of all individuals of that family within each habitat. Dotted lines indicate 95 % confidence limits. (d) Location of censused habitats amongst four different exposures around Lizard Island (filled squares), with the different habitat zones indicated by the symbols in parentheses.

Fin morphology and swimming performance

Fin morphology appears to be a powerful predictor of at least one aspect of locomotor performance in labriform-swimming fishes. All three families in the present study displayed a positive relationship between pectoral fin shape (AR) and swimming performance, regardless of motivation. Whether swimming undisturbed on the reef or pushed to maximum capabilities in a laboratory flow tank, labriform-swimming fishes with tapered fins (high AR) attained faster swimming speeds for their size. Biomechanical analyses suggest that the critical mechanism underlying this relationship between fin shape and performance is the differential use of thrust; fishes with tapered pectoral fins predominantly use lift-based flapping that produces more downstream-directed thrust to attain higher speeds, than taxa with rounded fins that solely use drag-based rowing fin strokes (Drucker & Lauder 2000, Walker & Westneat 2000, 2002, Wainwright et al. 2002, Thorsen & Westneat 2005). Interestingly, this lift-based flapping mechanism appears to have arisen independently in reef fishes from at least two major evolutionary lineages: the Acanthuroidei and Labroidei. Furthermore, available evidence suggests that within these two lineages there are repeated origins of high AR fins, with up to three independent origins in the Pomacentridae (*Abudefduf, Chromis*-*Dascyllus* and *Neopomacentrus*-*Pomacentrus*; Quenouille et al. 2004), five in the Labridae (*Cirrhilabrus*, *Halichoeres*, *Labroides*, *Thalassoma*-*Gomphosus* and *Stethojulis*; Wainwright et al. 2002), and at least one in the Acanthuridae (*Acanthurus*-*Ctenochaetus*, Clements et al. 2003). There appears to be no pronounced influence of trophic biology on these relationships, with taxa at the upper extremes in all three families ranging from roving herbivores and detritivores to benthic carnivores and planktivores (Randall et al. 1997). Fin morphology and swimming performance appear to be inexorably linked in labriform fishes due to fundamental biomechanical constraints and trade-offs, regardless of taxonomy or trophic biology.

Distribution of fin morphologies and water motion

Ecological arrangement of functional characteristics along a gradient of water motion was highly congruent among families. Positive relationships between wave-induced water motion and pectoral fin aspect ratio were apparent in all families, regardless of the habitat type examined. For example, crest habitats censused at different exposures (and consequently different levels of water motion, Fulton & Bellwood in press) displayed marked differences in the mean fin aspect ratio of individuals. Similar to the among-mode trends in performance and ecology examined in the previous two chapters, these within-mode variations appear to be linked to differences in mechanical efficiency according to fin morphology. Average aspect ratios of all labriform-swimming fishes found in each habitat indicated that taxa with a fin morphology that facilitates efficient maintenance of high speeds (tapered fins of high AR, Blake 1981, Vogel 1994, Walker & Westneat 2002) were the dominant occupants of locations with high water flow velocities.

Congruence in these relationships among the three families lends support to the hypothesis that fishes occurring in wave-swept habitats with high water motion may need to maintain high sustained swimming speeds or at least manoeuvre at high speeds on a daily basis (Bellwood & Wainwright 2001, Fulton et al. 2001). Indeed, the range of absolute swimming speeds (in terms of cm s^{-1}) displayed in each of the three families appeared to span the range of water motion values within habitats, suggesting a close match of swimming capabilities to environmental characteristics. Mean flow appears to be the relevant hydrological measure, as oscillatory flow conditions do not correspond with differences in the assemblage structure of these fishes. For example, crest habitats in the exposed and lagoonal locations display similar oscillatory flow conditions (0.63 and 0.66 changes in flow direction s^{-1}, respectively), but have markedly different fish assemblages and mean flow velocities (38.3 and 17.2 cm s^{-1}, Chapter 1). Given the similarity among families in the form and magnitude of these relationships, it may be hypothesized that the physical demands imposed by wave energy on fishes occupying these habitats has shaped reef fishes from independent lineages into a common ecomorphological form.

Conclusions

Within pectoral-swimming fishes, fin morphology appears to provide a powerful tool for understanding ecomorphological relationships between diverse reef fish assemblages and the physical characteristics of reefs. Given the applicability of this relationship among several families in the present study and in labrid assemblages at several coral reef locations around the globe (Bellwood et al. 2002), it is likely that this functional relationship is a widespread phenomenon that applies to the majority of coral reef systems. Further examination of the evolutionary origins and implications of labriform diversity should prove fruitful when adequate phylogenies become available. While it appears that the functional link between fin shape and performance is widespread in tropical reef systems, the extent to which this relationship applies in temperate reef fish assemblages remains to be examined.

Chapter 5: Wave energy, swimming performance and the structure of tropical and temperate reef fish assemblages.

Published in *Marine Biology* **144,** 429-437.

5.1. Introduction

On coral reefs, fin morphology and swimming performance appear to be particularly useful for understanding the assemblage structure of reef fishes in relation to wave exposure. But what of rocky reef systems in temperate latitudes? Whilst wave energy has been noted as an important physical factor for the community composition of both coral and rocky reefs (Ebeling & Hixon 1991), they are characterised by very different benthic communities and taxonomically distinct ichthyofaunas (Ebeling & Hixon 1991, Meekan & Choat 1997). Very little is known of the swimming abilities of temperate reef fishes. Could the same functional systems be operating in these two distinct reef ecosystems? This study examines the swimming capabilities of temperate reef fishes distributed across a range of wave exposures, and using comparisons with previous functional analyses of a tropical coral reef system, explores the extent to which common functional constraints may be operating in two taxonomically distinct reef fish assemblages.

Labrids are one of the most diverse and abundant components of the reef fish community in both tropical and temperate localities (Ebeling & Hixon 1991, Bellwood & Wainwright 2002). Using solely the pectoral fins for sustained swimming, recent examinations of labrid assemblages on the Great Barrier Reef identified a considerable diversity of pectoral fin shapes among taxa, which was reflected in a similarly diverse range of swimming performances (Wainwright et al. 2002, Chapter 4). Fin morphologies in tropical wrasses were spread along a continuum between the two extremes of rounded (low aspect-ratio) and tapered (high aspect-ratio) fins, corresponding to aspect ratios ranging from 0.56 to 2.1, respectively. Application of this functional information to aspects of their ecology revealed consistent links between fin morphology, swimming performance and habitat-use patterns (Bellwood & Wainwright 2001, Fulton et al. 2001, Chapter 4). Species that displayed a high pectoral fin aspect-ratio and faster sustained swimming speeds were the most abundant in wave-swept habitats, whilst the slower swimming (low fin aspect-ratio) species were either rare or absent from such habitats (Bellwood & Wainwright 2001, Fulton et al. 2001, Wainwright et al. 2002). Although allometric effects also had an influence on the overall swimming speeds produced by individuals (Walker & Westneat 2002, Wainwright et al. 2002, Chapter 2), size appeared to be relatively unimportant for differences in the among-habitat distributions of these tropical species when compared to differences in fin morphology (Wainwright et al. 2002).

Given this detailed information on the swimming abilities and habitat-use patterns of tropical labrid fishes, it could be predicted that the distribution of temperate labrids across a range of wave exposures will be correlated to their swimming performances. It may be anticipated that temperate labrids which exhibit higher swimming speed performance will occupy the most wave exposed habitats in greater abundance than their slower-swimming counterparts. To test this prediction, the specific aims were to: (1) determine if temperate labrids display distinct patterns of distribution and abundance amongst rocky reef habitats of different wave exposure, (2) establish if differences in pectoral fin morphology and swimming performance exist among temperate labrids, and (3) evaluate the extent to which the distribution of species across habitats of different wave exposure conform with differences in their sustained swimming performance. Overall, these aspects will be compared to patterns previously reported for a tropical coral reef assemblage to evaluate the wider utility of swimming abilities for explaining the distribution patterns of reef fishes in relation to wave exposure.

5.2. Material and Methods

Study sites

The study was conducted between February and November 2001 at Port Stephens (32°43'S, 152°11'E), New South Wales, Australia. Study sites were located on the reefs surrounding two offshore islands (Broughton Island and Cabbage Tree Island), and were either exposed or sheltered in relation to incident SE wave energy (Fig. 5.1). Southeast is the prevailing wave direction in the region for much of the year (Short & Trenaman 1992), and there are indications that average levels of wave energy in this region are of comparable magnitude to that incident on outer-shelf reefs of the Great Barrier Reef (Young 1989). These sites were chosen for their similar bathymetry, substratum complexity, and orientation to prevailing winds. Both exposed sites consisted of a steep rock face off the island, very large boulders (>3 metres diameter) forming a patchy reef flat in shallow water (1-5 metres depth), interspersed with medium (1-3 metres diameter) to small (<1 metre diameter) boulders which continued down on a moderately steep slope to sand at 14-18 metres depth. Sheltered sites were composed of a conglomeration of large, medium and small boulders on a rock shelf at 1-6 metres in depth, which then dissipated to sand at 6-9 metres depth. Benthic flora largely comprised encrusting and turfing algae in the shallow habitats (both exposed and sheltered), with patchy areas of large laminarian algae spread amongst each of the censused depths.

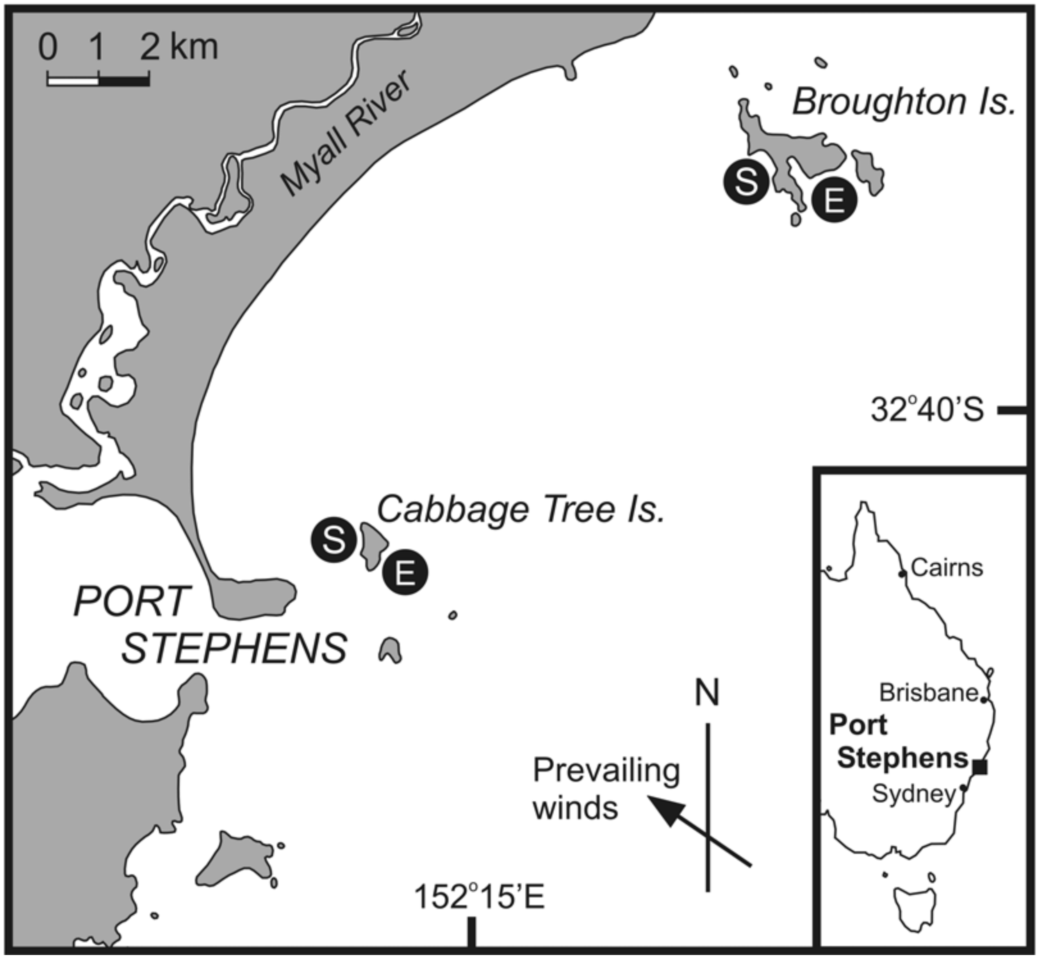


Fig. 5.1. Map of study sites located around the two offshore islands off Port Stephens, New South Wales, Australia. Each of the exposed (E) and sheltered (S) study sites are indicated.

Among-habitat reef fish distributions

Visual censuses of among-habitat distributions were conducted in three different habitats at each of the two island sites: exposed deep (9 metres depth), exposed shallow (4 m) and sheltered (4 m). These habitats were chosen to approximate the depth, aspect to prevailing winds, and gross geomorphology of the slope, crest and back reef zones commonly found on coral reefs (Bellwood & Wainwright 2001). Each census consisted of a 10 minute timed swim, recording all labrid individuals above 5 cm total length (TL) within a 5 metre wide linear transect which was run parallel to the low tide mark in each habitat. Fish total lengths were estimated and placed into 5 cm TL size classes. This procedure was repeated three times within each habitat, with a minimum of 20 metres separating adjacent censuses.

Fin morphology and swimming performance

Pectoral fin morphology was examined in all of the temperate species recorded in the distribution censuses. Fishes were collected using hand spears or barrier nets, placed in an ice-water slurry within one hour of capture, then TL and body mass taken prior to dissection. Pectoral fins were removed at the base and processed according to the fin morphology protocols outlined in Chapter 4. This procedure was repeated for at least 3 adult individuals of each species. Swimming speeds attained by each species were estimated in the field following the protocols outlined in Chapter 2. This procedure was repeated for a minimum of 6 adult individuals from each species, with the average travel distance and duration of each field trial being 304 cm and 10.3 seconds, respectively. Where possible, additional observations on an expanded size range of individuals were also conducted to examine the effects of size on speed.

Statistical analyses

After initial data exploration, all departures from normality and homoscedasticity were corrected using $\mathrm{Log}_{10}(x + 1)$ transformations. Among-habitat distributions were examined using principal component analysis on a covariance matrix of the transformed species abundances within each of the three habitats at each of the two sites. Differences in the mean abundance of species among habitats and sites were tested using a three-way analysis of variance (ANOVA), with site, habitat and species as fixed factors. Size distribution of individuals among habitats were also examined through size-frequency plots, where individuals from all species were pooled into six size classes for each habitat, at each of the two sites.

Differences in pectoral fin shape among temperate species were examined using a one-way ANOVA comparing mean pectoral fin AR, with species as a fixed factor. Sources of variation in pectoral fin shape were examined further using Pearson's Correlation Coefficient to compare mean values of fin AR with fin leading edge, and fin AR with fin area. Average absolute swimming speeds (cm s^{-1}) were calculated for each species, and found to display a strong correlation with mean size (Pearson Correlation 0.867, $n = 10$, $p < 0.01$). Consequently, speeds were converted to body lengths sec^{-1} (BL s^{-1}), which minimised these body size effects (Pearson Correlation 0.596, $n = 10$, $p > 0.05$). Differences in mean swimming speed (BL s^{-1}) among species were tested using a one-way ANOVA, with species as a fixed factor. Correlations between fin morphology and swimming performance were then assessed using Pearson's Correlation Coefficient comparing the mean values of pectoral fin AR and swimming speed (BL s^{-1}) from all temperate species. Relationships between size and swimming performance were examined further through least-squares linear regression of absolute speed against total length for each species.

4.3. Results

Among-habitat reef fish distributions

Labrid assemblages censused on the two offshore rocky reefs were dominated by temperate taxa (10 species, 83.5% of all individuals), with six predominantly tropical species also occurring on these reefs in low numbers. Distinct trends were evident in the distribution of species among the three habitats censused (Fig. 5.2). In particular, a marked reduction in the number of species (78.6%) was evident in the exposed shallow habitats when compared to the other habitats censused (Fig. 5.2). Principal component analysis highlighted this general trend, with the first principal component (explaining 59.8% of the variation in species distributions) indicating a major separation between the exposed shallow habitats and all other habitats censused (Fig. 5.3a), most likely as a consequence of the absence of species in shallow exposed habitats (Figs. 5.2 & 5.3b). A division was also evident between the exposed deep and sheltered habitats along the second principal component (Fig. 5.3a). This appeared to be largely due to the restriction of a few species to either exposed or sheltered locations (Fig. 5.2), particularly *Eupetrichthys angustipes* and *Pictilabrus laticlavius* in the sheltered habitats (Fig. 5.3b). Three-way analysis of variance indicated a significant difference among habitats and among species, a significant interaction between species and habitats, but no significant interactions between any other combination of factors (Table 5.1). Given that the mean abundances of the widespread species remained relatively constant among habitats, this significant interaction between species and habitats was most likely due to the restriction of a few species to either exposed or sheltered habitats, combined with the relative lack of species in the shallow exposed habitats (Fig. 5.2).

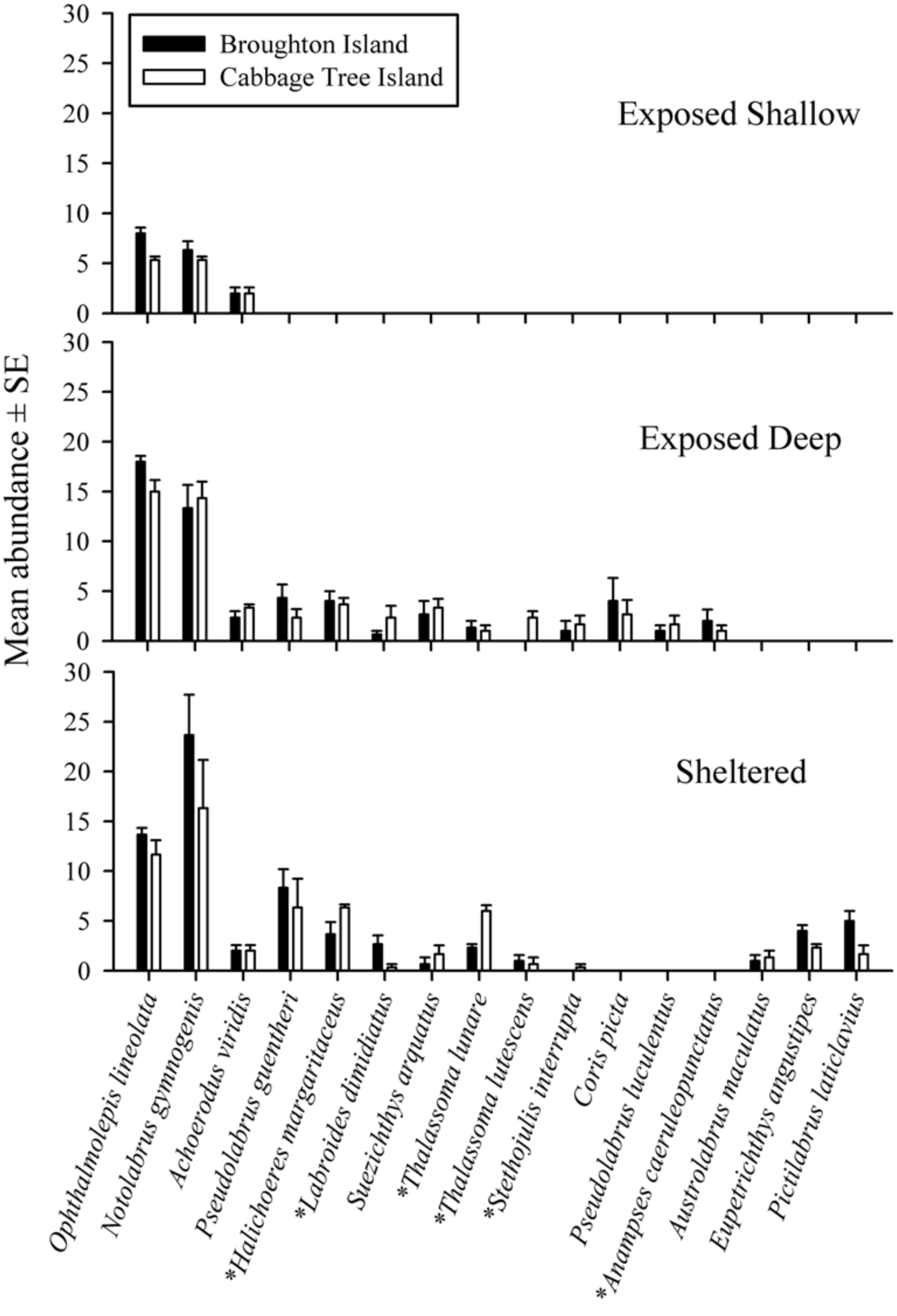


Fig. 5.2. Among-habitat distribution and abundance of labrid fishes at two offshore rocky reef sites off Port Stephens. Abundances are mean number of individuals per 10 minute timed swim (n=3). Asterisks (*) indicate predominantly tropical species.

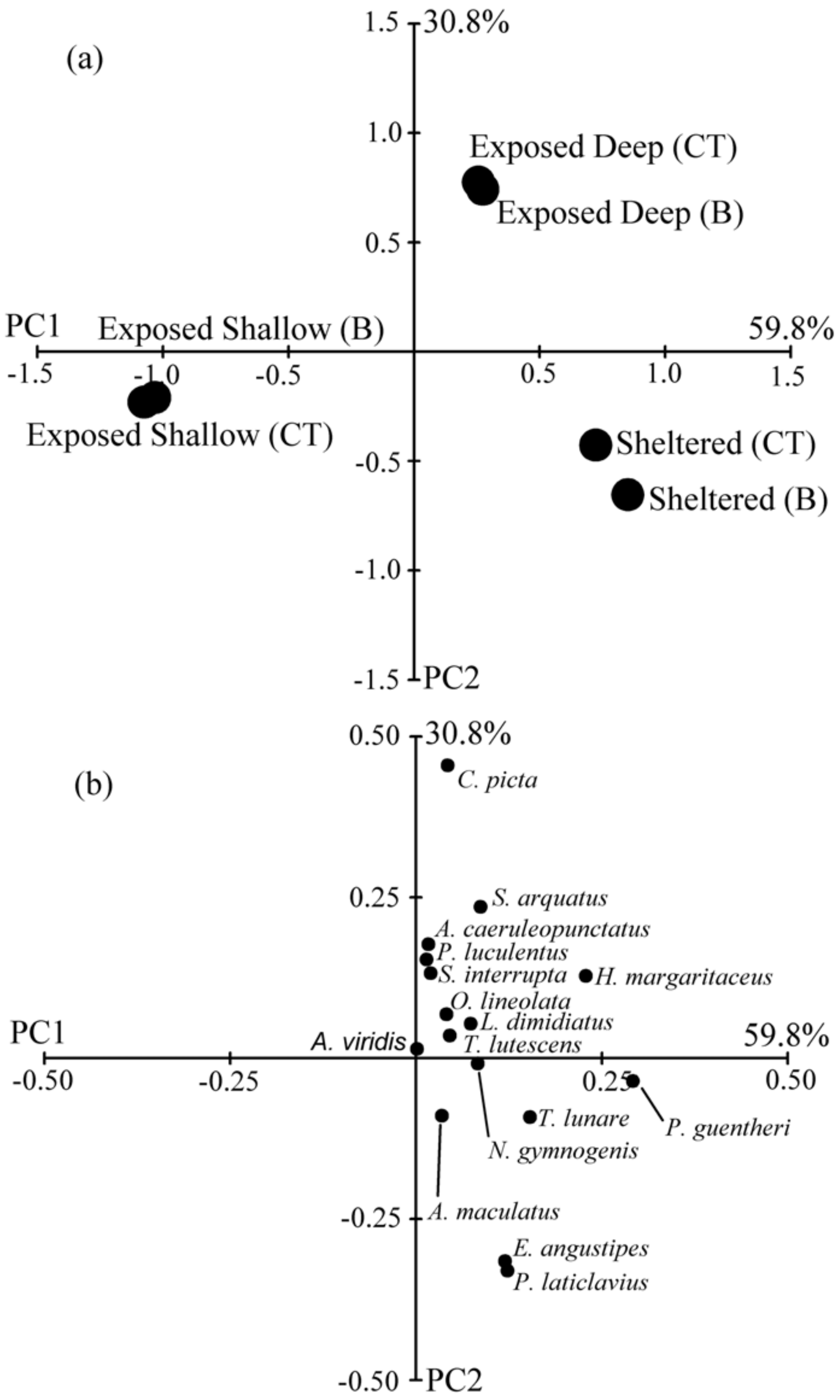


Fig. 5.3. Principal component analysis of mean abundance of labrid fishes across three habitats at the two rocky reef sites of Broughton Island (B) and Cabbage Tree Island (CT). (a) Ordination plot of habitat zones on principal components 1 (PC1) and 2 (PC2). (b) Species vector plot on principal components 1 (PC1) and 2 (PC2).

Table 5.1. Three-way ANOVA on mean abundance per habitat for sixteen labrid species across three habitats from two reef sites, with site, habitat and species as fixed factors.

Source of Variation	df	SS	MS	*F*	*p* value
Site	1	5.12×10^{-4}	5.12×10^{-4}	0.02	0.84
Habitat	2	6.53	3.27	114.40	<0.01
Species	15	27.64	1.84	64.57	<0.01
Site × Habitat	2	0.09	0.05	1.60	0.21
Site × Species	15	0.52	0.03	1.22	0.26
Habitat × Species	30	7.06	0.24	8.24	<0.01
Site × Habitat × Species	30	1.13	0.04	1.32	0.14
Error	192	5.48	0.03		
Total	287	48.45			

Apart from these differences in species composition, a distinct shift in the size frequency distribution of individuals between habitats was also evident (Fig. 5.4). Individuals occurring in the shallow exposed habitats at both sites were almost exclusively large (>25cm total length) (Fig. 5.4). Conversely, a bias towards smaller sizes (<15cm total length) was apparent in the exposed deep and sheltered habitats, most notably in the latter (Fig. 5.4).

Fin morphology and swimming performance

Pectoral fin shape, when expressed as an aspect ratio (AR), was found to be significantly different among the temperate species examined (Table 5.2). Mean pectoral fin AR for each species varied between a low of 0.52 in *Eupetrichthys angustipes* to a high of 1.43 in *Coris picta* (Fig. 5.5). A significant correlation between fin AR and fin leading edge (Pearson Correlation 0.695, n = 10, p < 0.02), but not between fin AR and fin area (Pearson Correlation 0.695, n = 10, p = 0.19), suggested that differences in pectoral fin AR among species were primarily due to variations in the length of the leading edge for a given fin area.

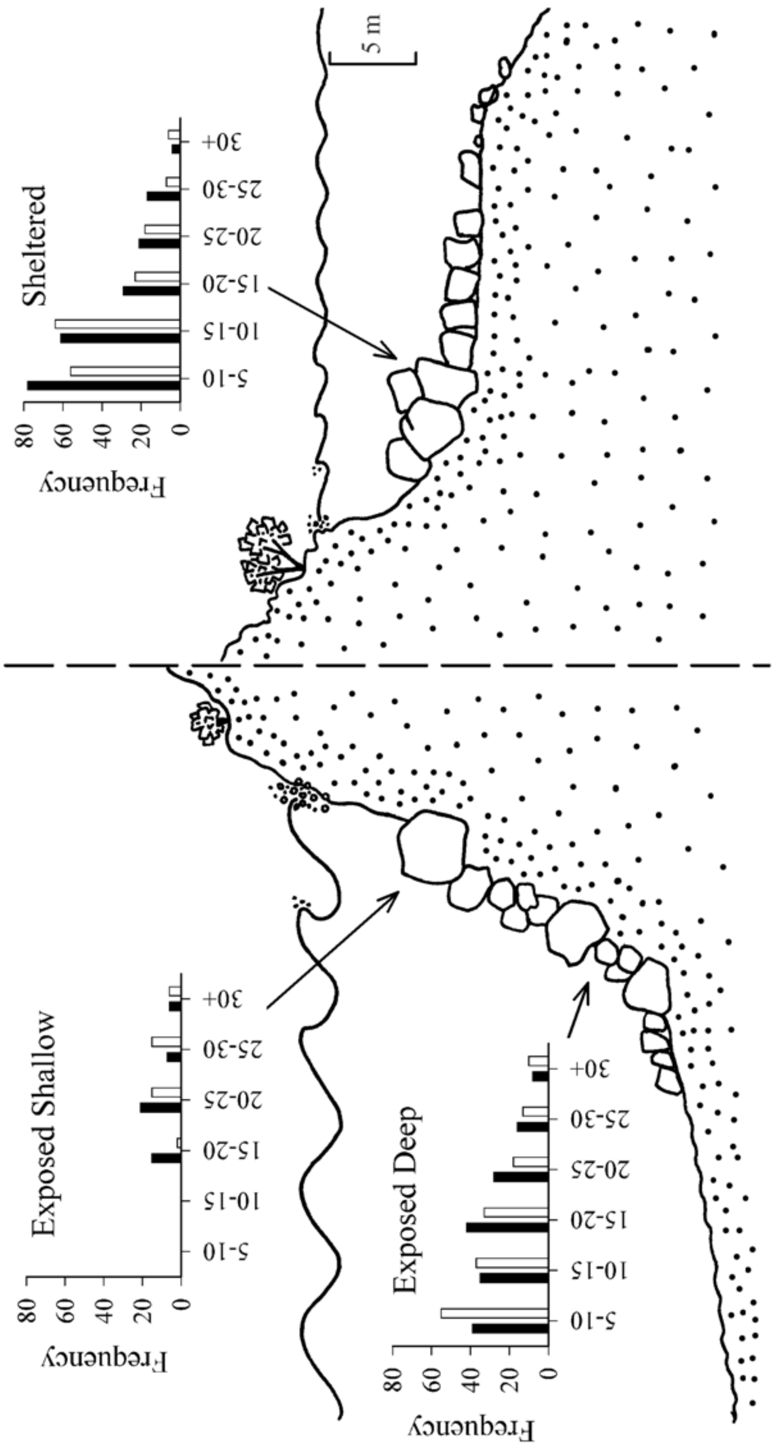


Fig. 5.4. Size-frequency distributions of labrid fishes across three habitats at each of the two rocky reef sites of Broughton Island (closed bars) and Cabbage Tree Island (open bars). Individuals within each total length size class (cm) are pooled from all species observed in each habitat.

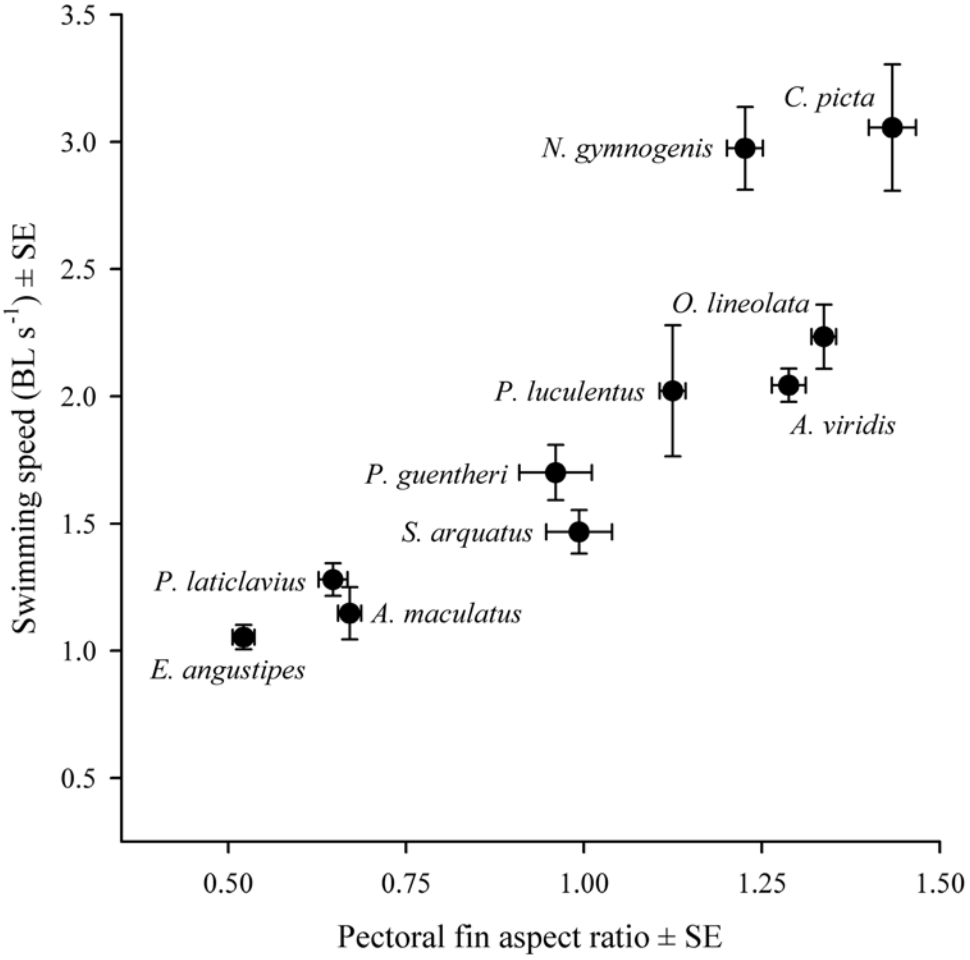


Fig. 5.5. Mean field swimming speed against mean pectoral fin aspect ratio for ten species of temperate labrid fishes. Means are based on measurements taken from adult individuals only (n > 3 for aspect ratio means, n > 5 for swimming speed means).

Table 5.2. One-way ANOVA comparing the mean pectoral fin aspect ratios from adult individuals of ten temperate labrid species, with species as a fixed factor.

Source of Variation	df	SS	MS	*F*	*p* value
Species	9	0.36	0.04	143.59	<0.01
Error	74	0.02	2.79×10^{-4}		
Total	83	0.38			

Swimming speeds differed significantly among species (Table 5.3), with average speeds ranging from a low of 1.05 BLs^{-1} in *Eupetrichthys angustipes* to a high of 3.06 BLs^{-1} in *Coris picta*. These differences in swimming performance appeared to be related to pectoral fin shape in the species examined (Fig. 5.5), which was supported by a strong significant correlation between the two variables (Pearson's Correlation 0.884, n = 10, p < 0.001). Size also appeared to be related to swimming performance, with absolute swimming speed displaying a positive relationship with size in all of the species examined, with the only exception being *Achoerodus viridis* (Table 5.4, Fig. 5.6). This trend of increasing speed with increasing size, combined with differences in the maximum observed size of each species, resulted in a broad range of maximum speeds observed (Table 5.4).

Table 5.3. One-way ANOVA comparing mean field swimming speeds (BLs^{-1}) from adult individuals of ten temperate labrid species, with species as a fixed factor.

Source of Variation	df	SS	MS	*F*	*p* value
Species	9	1.33	0.15	35.60	<0.01
Error	106	0.44	4.16×10^{-3}		
Total	115	1.77			

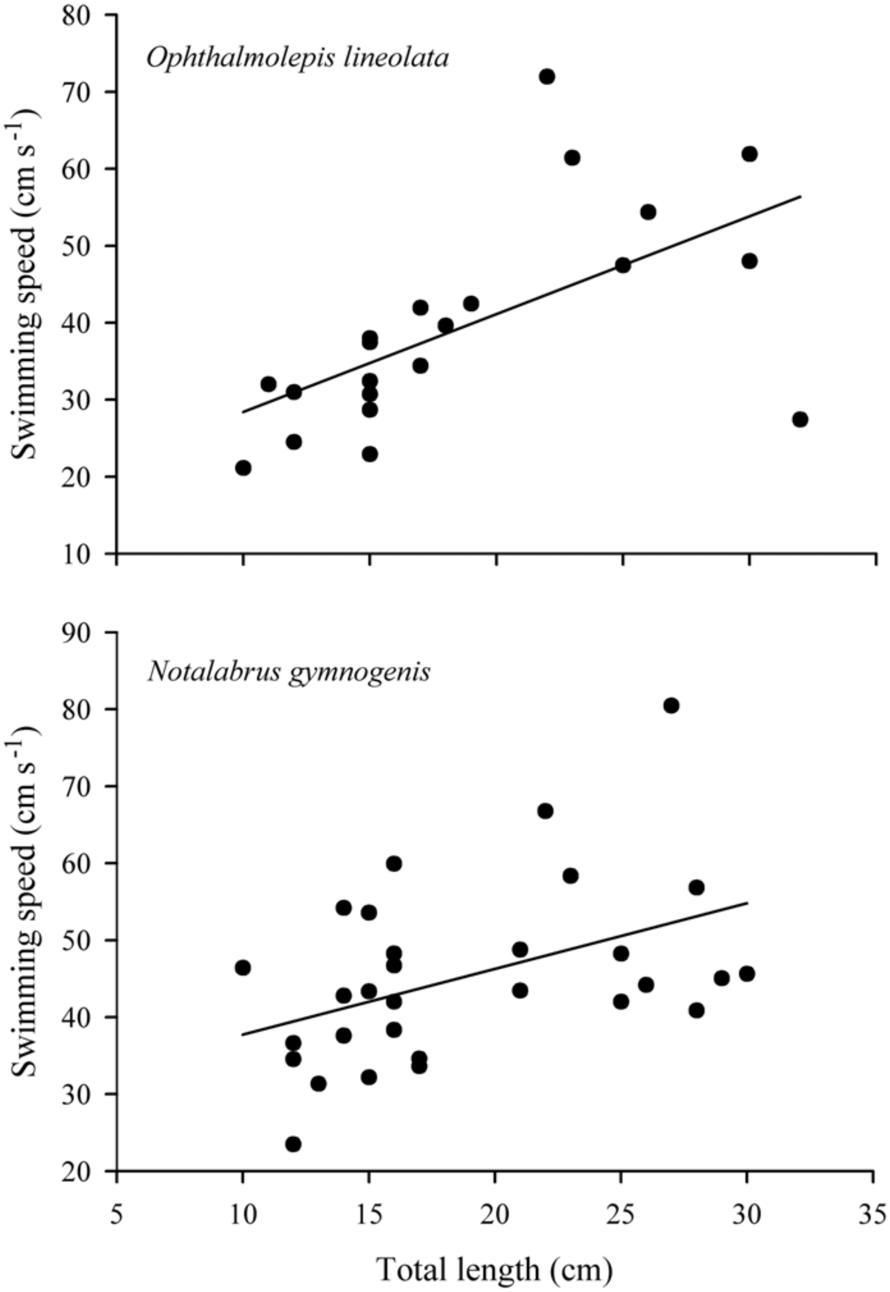


Fig. 5.6. Relationship between size and field swimming speed in two of the ten labrid species examined. Details of the least squares linear regressions for these species are given in Table 5.4.

Table 5.4. Least squares linear regressions of swimming speed against size for ten species of temperate labrids, ranked by maximum speed. Max size and max speed refers to the maximum total length and field swimming speed observed for that species, respectively.

Species	Slope	r^2	max size (cm)	max speed (cm s^{-1})	n
Coris picta	2.35	0.31	27	81.7	22
Notolabrus gymnogenis	0.85	0.20	32	80.5	31
Ophthalmolepis lineolata	1.27	0.37	32	72.0	21
Achoerodus viridis	0.03	0.02	90	54.9	7
Pseudolabrus luculentus	1.51	0.03	15	38.5	6
Pseudolabrus guentheri	1.13	0.18	17	31.5	17
Austrolabrus maculatus	1.38	0.59	17	28.2	16
Eupetrichthys angustipes	1.51	0.68	18	24.8	21
Pictilabrus laticlavius	1.12	0.26	16	23.3	9
Suezichthys arquatus	2.63	0.56	12	20.5	13

5.4. Discussion

Temperate wrasses displayed distinct patterns in their distribution and abundance among rocky reef habitats of different wave exposure. Several species were restricted to sheltered habitats (e.g. *Pictilabrus laticlavius*, *Eupetrichthys angustipes*), and very few species were found to be abundant in the shallow exposed habitats (primarily *Ophthalmolepis lineolata* and *Notolabrus gymnogenis*); the latter habitat being characterised by a 79% reduction in species richness when compared to each of the other habitats censused. These trends were similar, albeit on a reduced scale of diversity, to those reported for labrid fishes in tropical localities, where species were generally found in abundance in either deep exposed or sheltered habitats, and shallow, high wave energy habitats were characterised by relatively few abundant species (Green 1996, Bellwood & Wainwright 2001, Fulton et al. 2001, Gust et al. 2001). Differences in fin morphology and swimming performance were suggested to be important determinants of these patterns on coral reefs (Fulton et al. 2001, Bellwood et al. 2002, Chapter 4), and this study demonstrates a comparable link between swimming performance and labrid distributions in a temperate reef ecosystem.

Relationship between fin shape, performance and habitat-use

Temperate labrids displayed a range of pectoral fin morphologies that were strongly correlated to their swimming speeds on the reef, where species with a low fin aspect-ratio (AR) were found to display slower swimming speeds for their size than species with a higher fin AR. These trends in performance closely resembled the functional relationship seen in tropical labrids, where species with a high fin AR tended to use a lift-based flapping of the fins to produce and maintain higher swimming speeds than could be attained by their drag-based, low fin AR counterparts (see Wainwright et al. 2002, Walker & Westneat 2002). When compared to the locomotor diversity of labrids on coral reefs, however, temperate labrids represent a relatively small subset of the total diversity in the family, in terms of both morphology and performance. Spanning much of the same range of body sizes seen in tropical assemblages, temperate labrids displayed a reduced range of pectoral fin morphologies (Fig 5.7). Although the lowest AR displayed in the temperate assemblage (0.52 in *Eupetrichthys angustipes*) was comparable to that reported for a tropical labrid (0.56 in *Pseudocheilinus evanidus*, Wainwright et al. 2002), the highest AR reported for a temperate labrid (1.43 in *Coris picta*) was markedly lower than the highest found on the Great Barrier Reef (2.08 in *Stethojulis bandanensis*, Chapter 4). Similarly, the highest average swimming speed displayed by a temperate labrid (3.0 BL s^{-1}) was less than half the highest seen in labrids from the Great Barrier Reef (6.8 BL s^{-1}, Chapter 4). While this evidence indicates that temperate labrid assemblages do encompass a range of locomotor morphologies and

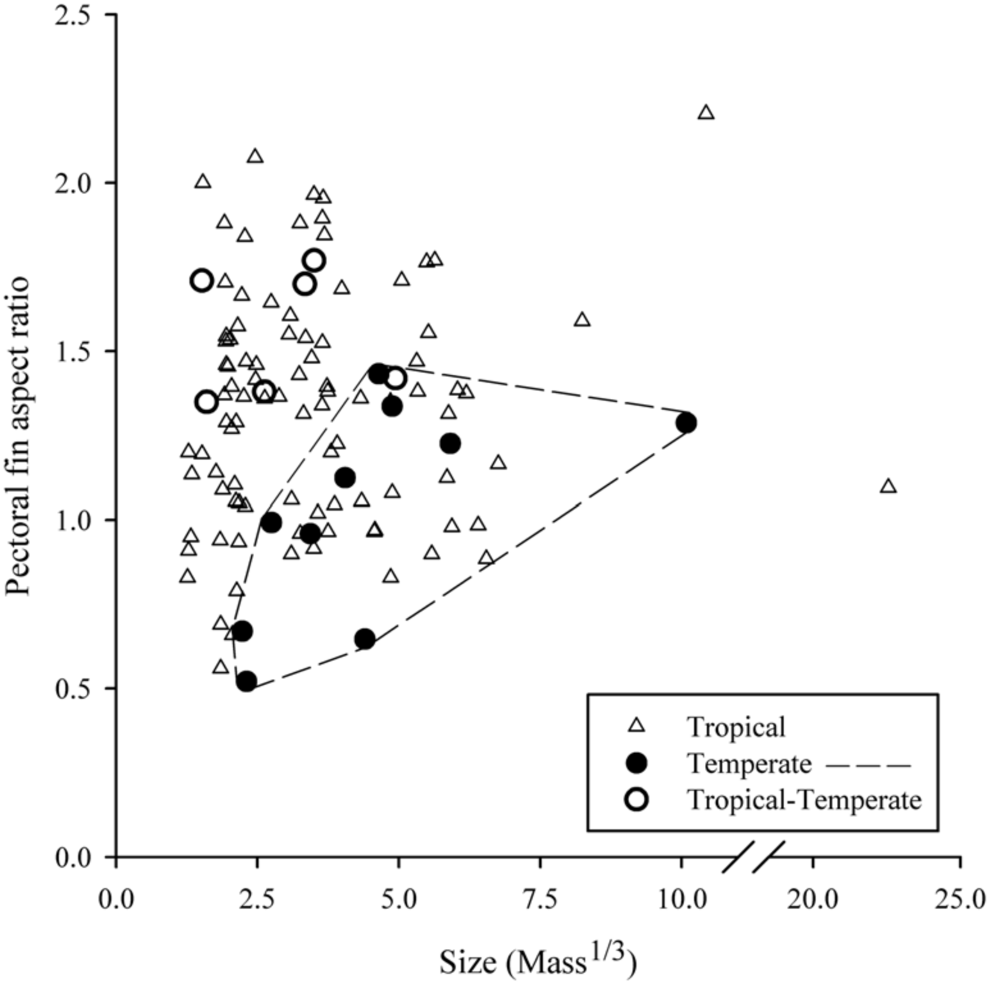


Fig. 5.7. Plot of pectoral fin shape against size for species of labrid found on tropical coral reefs (Tropical) and temperate rocky reefs (Temperate), with species overlapping between the two assemblages indicated (Tropical-Temperate). Morphospace for the temperate labrid species is bounded by the dotted line. Morphometric data for the tropical and tropical-temperate species from the Great Barrier Reef were modified after Wainwright et al. (2002) and Chapter 4.

performances, when compared with tropical labrids there appears to be an under-representation of high fin AR species that predominantly use lift-based locomotion.

Despite this reduced locomotor diversity in the temperate assemblage, differences in fin morphology and swimming performance provided some explanation for their observed distribution patterns in relation to wave exposure. In particular, species that were restricted to the most sheltered habitats (*Eupetrichthys angustipes*, *Austrolabrus maculatus* and *Pictilabrus laticlavius*) displayed much lower fin ARs and relative swimming speeds than species which were more widespread. Under conditions of high water movement in exposed reef habitats, the ability to undertake daily tasks may be strongly dependent on locomotor ability, specifically requiring an ability to efficiently maintain high sustained swimming speeds on a daily basis. Given that the above species displayed fin morphologies and swimming speeds which indicate that they are almost exclusively drag-based locomotors (Blake 1981, Wainwright et al. 2002, Walker & Westneat 2002), these species might be unable to maintain the required speeds, or at the very least, be at a disadvantage to their faster-swimming counterparts, and must therefore avoid habitats of high water movement. A similar mechanism has been proposed for the habitat-use patterns of some stream fishes, where differences in morphometrics and swimming capacity between species have been suggested for their differential use of habitats of fast and slow water flow (Sagnes et al. 1997, 2000, Bhat 2005, Kodric-Brown & Nicoletto 2005).

For more widely distributed species, however, among-habitat differences in distribution and abundance did not appear to be linked with differences in pectoral fin morphology. One of the most striking trends in the distribution patterns of labrids on these offshore rocky reefs was the presence of very few species in the most wave-affected, shallow habitats on the exposed reef fronts (*Ophthalmolepis lineolata*, *Notolabrus gymnogenis* and *Achoerodus viridis*), with these same species being the dominant taxa in most of the habitats censused. However, they displayed fin morphologies (1.23 - 1.34 mean fin AR) that were similar to several other species in the assemblage that were absent from the shallow exposed habitats. This suggests that swimming performances based on differences in fin morphology are relatively uninformative for examining the distribution patterns of these widespread temperate species, particularly for those occurring in the most wave-affected habitats.

Body size effects

Size effects on swimming performance, however, may provide an explanation. Whilst various advantages are associated with fin shape and the use of different modes of thrust, these relate to relative differences in the swimming performance of individuals of a given size (Vogel 1994, Walker & Westneat 2002). Absolute swimming speeds, however, are often influenced to a greater extent by the overall size of an individual. Larger individuals of a given species, whilst producing relatively slower speeds in terms of their size, are capable of higher absolute swimming speeds than smaller individuals, both within and among taxa (Wardle 1977, Beamish 1978, Bellwood & Fisher 2001, Blake 2004) – a trend that was strongly evident in the majority of temperate taxa examined in this study. Essentially this means that in the absence of mechanical advantages associated with changes in fin morphology and stroke kinematics, substantial increases in performance may be gained through attaining a greater size and muscle mass to produce faster overall swimming speeds. On temperate reefs, it appears that this strategy is being utilised by labrid fishes to access a greater range of habitats, particularly the most wave exposed habitats. Temperate labrids displayed distinct differences in their size distribution amongst habitats, with fishes in the exposed shallow habitats being strongly biased towards larger sizes (>25cm total length). Notably, with only one exception (*Coris picta*), the only three species that were abundant in the exposed shallow habitats were the only taxa that attained a maximum size of greater than 20 cm total length, and displayed a maximum absolute swimming speed of greater than 50 cm s^{-1}. There may be some threshold of size and swimming speed required to access these most wave-affected rocky reef habitats, and the aforementioned three taxa are able to do so by attaining sizes and maximum sustained swimming speeds that exceeded most of the other observed species.

Size versus fin shape: alternative strategies for wave-swept habitats

In contrast to this temperate rocky reef assemblage, size appears to be relatively unimportant in tropical assemblages. Whilst tropical labrids were found to have a rather uniform average size amongst habitats, temperate individuals displayed marked differences in size distribution across habitats equivalent (in terms of depth and aspect) to coral reef zones (Fig. 5.8). Rather than a shift in size between habitats, tropical labrids displayed distinct differences in their fin morphologies. In particular, coral reef labrids that were abundant in high wave energy habitats displayed an extremely tapered fin shape, indicating a predominant use of lift-based thrust (Bellwood & Wainwright 2001, Fulton et al. 2001, Bellwood et al. 2002). These fishes were often so numerically dominant in these habitats, that population sizes were often an order of magnitude larger than their drag-based counterparts (Bellwood et al. 2002).

If high fin AR, lift-based taxa are so successful in occupying wave-swept habitats on tropical reefs, why are these fishes, or at least a functional equivalent, lacking in the temperate assemblage? Phylogeny may play a major role in the lack of lift-based species on temperate reefs. Fishes which are the characteristic, numerically

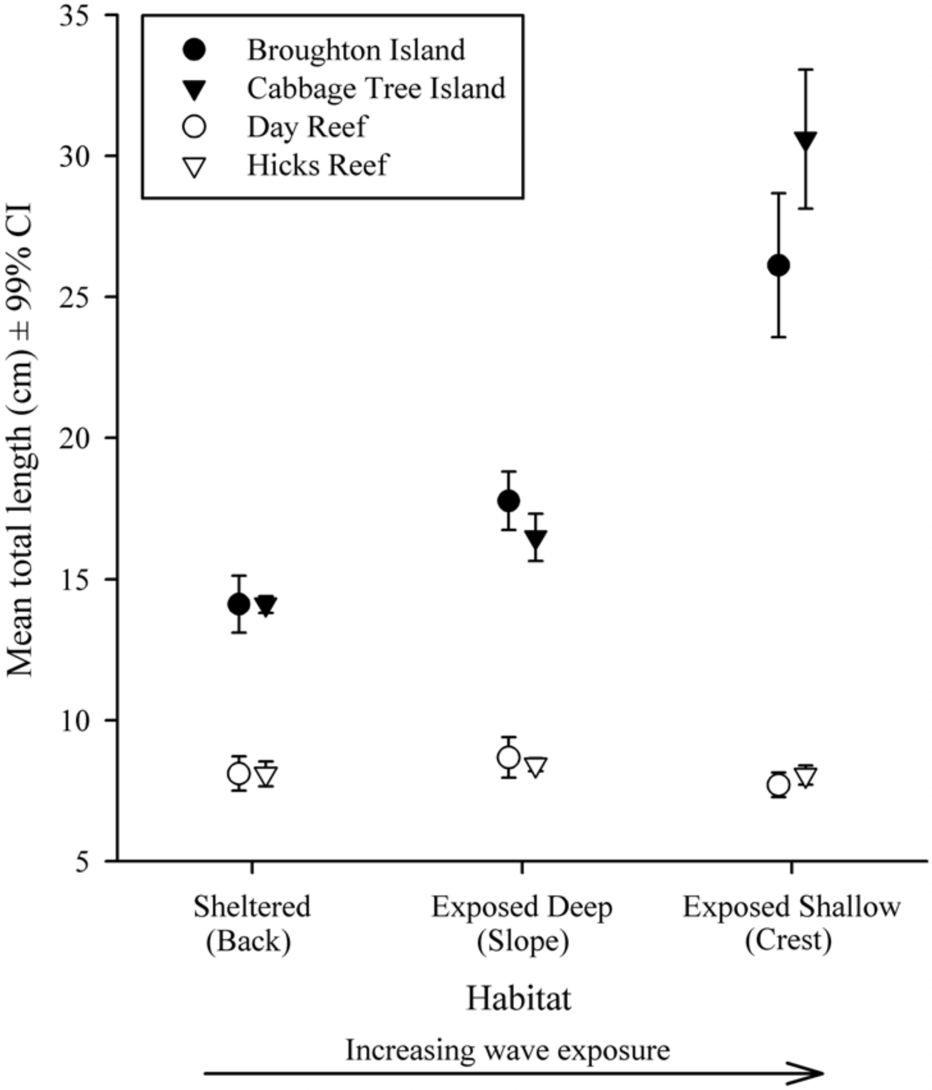


Fig. 5.8. Average total length of labrid individuals in three tropical and three temperate reef habitats, based on three censuses (10 minute swim, 5 metre wide transect) in each habitat at each of two reef sites. Tropical census data is from two outer-shelf reefs of the Great Barrier Reef, modified after Bellwood & Wainwright (2001).

dominant taxa in high wave energy habitats at several coral reef locations (*Thalassoma* and *Gomphosus*, Bellwood et al. 2002) were either rare or entirely lacking in this temperate assemblage, and no equivalent lift-based species were evident in the corresponding high wave energy rocky reef habitats. It appears that a lineage of lift-based taxa, which probably evolved within the tropics (Wainwright et al. 2002, Westneat et al. 2005), has not expanded to temperate locations, and a functionally analogous lineage has not evolved within this temperate assemblage. Furthermore, temperate labrids appeared to display a generally larger average size than their tropical counterparts (Fig. 5.8). The use of their inherently larger size may represent the most readily available mechanism for these temperate fishes to exploit wave exposed locations, and thus preclude the need for (or selective advantages of) other mechanisms. Alternatively, the advantages of lift-based swimming may not apply within a temperate reef ecosystem. For example, differences in temperature may ultimately affect the energetic advantage that is thought to be associated with the long-term use of lift-based thrust (Walker & Westneat 2000, Wainwright et al. 2002). Lower ambient sea temperatures in temperate latitudes would essentially mean lower average metabolic rates in these poikilothermic animals (Schmidt-Nielsen 1997). If efficiency in locomotion and conservation of energy are the primary advantages of using lift-based thrust for sustained locomotion in high wave energy habitats, a lower metabolic rate may proportionally reduce this advantage. An examination of the functional characteristics of a mid-latitude reef fish assemblage, with a considerable overlap in the presence of tropical and temperate taxa in the one locality, may help to clarify the relative importance of these issues.

Conclusions

Regardless of the differences in locomotor strategy to occupy wave-swept habitats, there appears to be underlying trend in both tropical and temperate reef systems: wave energy exerts a direct influence on the distribution and abundance of reef fishes. Furthermore, the evidence presented herein indicates that swimming performance may play a major role in this relationship in both reef ecosystems. Whilst it was found that fishes which occupy the most wave-swept habitats in both localities exhibited greater swimming performance than taxa which reside in more sheltered locations, the means by which this increased swimming performance was achieved differed in each locality. On coral reefs, labrids appeared to use morphologically-associated mechanical efficiencies and different modes of thrust, whereas increased speed through increased overall size appears to be the dominant strategy on temperate reefs. The relative importance of phylogeny and abiotic conditions in underscoring these differences in strategy are yet to be determined, however, the results highlight the utility of functional characteristics in examining the ecological patterns of two taxonomically distinct assemblages.

Concluding Discussion

Swimming mode classifications based on the different body and fin structures used by fishes are central to our understanding of fish locomotion. Field observations in the present study identified the swimming modes being used in an entire assemblage of coral reef fishes, and confirmed previous predictions that most demersal fish taxa use a labriform mode (Lindsay 1978, Webb 1984, 1994). Furthermore, these swimming modes were found to have an overriding influence on the swimming speed performance of reef fishes, which had been anticipated by previous biomechanical analyses of fish locomotion (Alexander 1967, Lindsay 1978, Webb 1988, Videler 1993). While differences in swimming speed performance amongst modes were most apparent under field conditions, strong correlations between laboratory and field measures of performance supported the suggestion that critical swimming speed provides an ecologically relevant measure of swimming performance (Hammer 1995, Plaut 2001, Fisher et al. in press). In the three swimming modes examined, field speeds could be reliably estimated from either a 20% reduction of critical swimming speed in labriform taxa, or a 50 - 55% reduction of critical swimming speed in chaetodontiform and subcarangiform taxa (Chapter 2). Collectively, these findings reinforce the utility of laboratory studies for examining the swimming capabilities of fishes (Webb 1994, Blake 2004), and highlight the overriding importance of swimming mode in shaping patterns of fish locomotion.

Differences in swimming mode and performance can play a crucial role in the ecology of fishes by shaping their ability to access habitats, acquire food and avoid predation (Videler 1993, Webb 1994, Blake 2004). Using swimming performance information in conjunction with assessments of wave-induced water motion, this study provided the first quantitative evidence that swimming speed performance is linked to patterns of habitat-use in demersal reef fishes (Chapter 3). Previous comparisons of swimming mode and lifestyle in marine fishes have indicated that pectoral-swimming provides an effective means of interacting with structurally complex demersal habitats, whereas body and caudal fin propulsion may be more appropriate for locating widely-spaced prey items in a relatively unstructured pelagic habitat (Videler 1993, Webb 1994, Blake 2004). Accordingly, this study found that labriform fishes were the most abundant in all of the demersal reef habitats surveyed and displayed almost complete dominance of the most wave-swept habitats, while fishes using a caudal-swimming mode were relatively rare and largely restricted to more sheltered habitats and locations. This differential distribution of swimming modes among reef habitats was a direct reflection of the comparative swimming speed performance of modes. Labriform fishes displayed average field speeds of up to 70 cm s^{-1}, which exceed the average wave-induced flows found in the wave-swept crest and flat habitats (40 - 60 cm s^{-1}), whereas chaetodontiform and subcarangiform fishes averaged speeds of less than 40 cm s^{-1} in the field. As highlighted by previous functional analyses of coral reef wrasses (Bellwood & Wainwright 2001, Bellwood et al. 2002), direct links between swimming performance and water motion were most apparent at the level of individuals, with the swimming speed performance of fishes in each habitat being positively correlated with increasing levels of water motion, regardless of mode or taxonomic affiliation. Previous functional analyses have found analogous links between wave energy and the distribution of coral and algal functional groups (Sebens & Done 1992, Sebens 1997, Steneck & Dethier 1994). Ultimately, it appears that wave energy has a profound effect on coral reef communities by shaping the distribution and abundance of both mobile and sessile taxa according to their functional characteristics.

Mechanical and energetic efficiency may underpin these differences in reef fish swimming performance and ecology. While the present study did not directly examine swimming energetics, available evidence suggests that the broad range of swimming speeds and generally higher field speeds found in labriform fishes are a consequence of low costs of transport (Korsmeyer et al. 2002, Walker & Westneat 2002, Chapter 2). Moreover, labriform fishes that dominated the most wave-swept habitats were identified as those which use the highly efficient lift-based form of propulsion (Wainwright et al. 2002, Walker & Westneat 2002, Chapter 4). Conversely, caudal-swimming fishes of similar size may incur higher costs of transport with increasing speed, which would prohibit the long-term maintenance of high swimming speeds during daily activities on the reef (Boisclair & Tang 1993, Blake 2004). Equivalent links between swimming ability and habitat-use patterns have been found in freshwater fishes, where bioenergetic analyses have shown that many species may avoid high-flow habitats during foraging and migrations due to excessive costs of locomotion (Hughes & Dill 1990, Nislow et al. 2000, Rosenfeld & Boss 2001). While similar bioenergetic analyses of reef fish assemblages may provide further insights into the implications of locomotion for reef fish ecology, further work is needed on the comparative energetics of swimming modes.

Manoeuvrability may also play an important role in these patterns, as wave-induced water movements may require the ability to brake, turn and remain in a stable posture to interact with a complex substratum under changing flow conditions (Gerstner 1999, Webb & Fairchild 2001, Weihs 2002, Blake 2004). While the present study identified strong biophysical links between flow velocity and swimming speed performance, there appeared to be little or no correlation with flow periodicity (rate of flow direction change). However, comparisons between flow periodicity and measures of manoeuvrability may reveal an additional biophysical interaction between wave energy and fish swimming performance, analogous to the speed-velocity relationship established in this study. Given that labriform-swimming fishes are generally thought to exhibit high levels of manoeuvrability (reviews Webb 1994, Blake 2004), such comparisons between manoeuvrability and wave-induced water motion may provide a more complete picture of why labriform fishes are so successful in wave-swept habitats.

Caudal locomotion has historically been the dominant mode of swimming in fishes (Webb 1982, Lauder 2000, Drucker & Lauder 2002), with a dramatic increase in the prevalence of purely pectoral forms of locomotion following the extensive radiation of teleost fishes in demersal, reef-associated habitats during the Cenozoic (Bellwood & Wainwright 2002, Wainwright et al. 2002). Extensive variations in pectoral fin morphology and swimming speed performance within labriform fishes suggests that pectoral locomotion may be a major axis of diversification in reef fish assemblages, comparable to the diversity seen in trophic morphology and diet (Wainwright et al. 2004, Westneat et al. 2005). Consistent functional relationships between pectoral fin shape and performance were found in coral reef fishes from three diverse families, which were linked to their distribution patterns in relation to wave energy (Chapter 4). In particular, the use of tapered pectoral fins for lift-based propulsion appears to have played an important role in the ecology of labriform fishes. Labriform taxa possessing tapered pectoral fins display an almost complete dominance of shallow, wave-swept reef habitats, a pattern which has been repeatedly found in wrasse assemblages located on both tropical and temperate reefs around the globe (Bellwood et al. 2002, Denny 2004, Chapters 4 & 5).

Preliminary evidence indicates that the lift-based mechanism of labriform propulsion may have arisen independently in several divergent perciform lineages (Wainwright et al. 2002, Thorsen & Westneat 2005, Chapter 4). Could this lift-based mechanism have facilitated the expansion of reef fish communities into shallow wave-swept habitats? Indeed, the congruent distribution patterns of labriform species according to pectoral fin shape suggest that the physical demands imposed by wave energy may have shaped labriform fishes from several independent lineages into a convergent ecomorphological form. While such evolutionary hypothesis may provide invaluable insights into the mechanisms shaping patterns of locomotion in reef fishes, they must wait until a fully resolved phylogenetic framework becomes available (Thorsen & Westneat 2005). Nonetheless, evidence presented herein suggests that pectoral swimming is a particularly successful swimming mode on reefs, with a diversity of fin morphologies, kinematics and speed performances translating to the successful exploitation of a wide range of demersal habitats.

Overall, this study has provided a renewed understanding of fish locomotion in demersal reef systems by providing direct comparisons of fin use, swimming speed performance and ecology within tropical and temperate reef fish assemblages. While the distribution patterns of reef fishes may be influenced by a suite of physical and biological factors, this study found evidence of a direct, overriding influence of wave energy on the distribution patterns of reef fishes. Swimming speed performance appears to be a major factor in shaping the distribution patterns of reef fishes in relation to wave energy, although further research into the comparative manoeuvrability and energetics of swimming modes may provide additional insight. Ultimately, wave-induced water motion appears to have interacted in both ecological and evolutionary terms with the locomotor characteristics of fishes to provide an underlying theme in reef ecosystems: wave energy and swimming performance shape reef fish assemblages.

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Appendix 1

Publications arising from thesis:

Publications derived from each of the thesis chapters are listed below. Reprints of the three published articles are enclosed at the end of this thesis.

1. **Fulton CJ**, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol. & Oceanogr.* **50,** 255-264.
2. **Fulton CJ** (in prep) Swimming speed performance in coral reef fishes: field validations reveal distinct functional groups. To be submitted to *J. Exp. Biol.*
3. **Fulton CJ** (in prep) Environmental constraints on habitat-use in coral reef fishes through variations in locomotor performance. To be submitted to *Ecology*.
4. **Fulton CJ**, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. *Proc. R. Soc. B* **272,** 827-832.
5. **Fulton CJ**, Bellwood DR (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Mar. Biol.* **144,** 429-437.

Appendix 2

Flow tank calibration:

Calibration of flow speeds in the 194 L recirculating flow tank was performed by high speed video tracking (200 frames s^{-1}) of passive particles (unexpanded Styrofoam balls) using a JVC JRDVL9800 digital video camera. Flow velocity was measured at each of 3 Hz increments of motor shaft rotation speed by tracking particles travelling within 3, 5, 8 & 11 cm of the acrylic wall of the working section, for a minimum of three particles at each distance and motor rotation setting (Table A2.1).

Table A2.1. Mean flow velocities at four distances from the wall of the flow tank working section, taken at a range of motor rotation speeds. Percent variation in flow was calculated from the difference between the fastest and lowest values recorded at that motor speed.

Motor speed (Hz)	Distance from flow tank wall (cm)				% variation flow speed
	3	5	8	11	
3	4.43	4.55	4.84	4.88	9.19
6	9.99	10.00	10.61	10.97	8.93
9	14.36	15.06	15.85	15.52	7.43
12	22.69	22.92	23.08	25.00	9.25
15	26.08	27.57	28.95	28.41	8.22
18	34.33	35.29	37.50	37.66	8.84
21	36.97	37.89	38.89	40.67	9.08
24	41.75	44.75	45.44	45.00	7.22
27	51.40	53.55	55.00	55.56	7.47
30	58.55	60.00	63.09	64.29	8.93
33	63.33	64.29	64.29	70.00	9.52
36	65.58	67.61	68.99	70.35	6.78
39	70.33	71.43	72.43	74.82	6.00
42	73.43	74.93	80.57	81.38	9.77
45	79.92	84.13	86.28	87.33	8.49
48	86.54	91.09	93.43	94.28	8.21
				Overall:	**8.33**

An average flow velocity was taken from all measured particles at each motor speed to construct a calibration curve relating motor shaft rotation speed (Hz) with flow speed (cm s^{-1}) in the working section of the flow tank (Fig. A2.1).

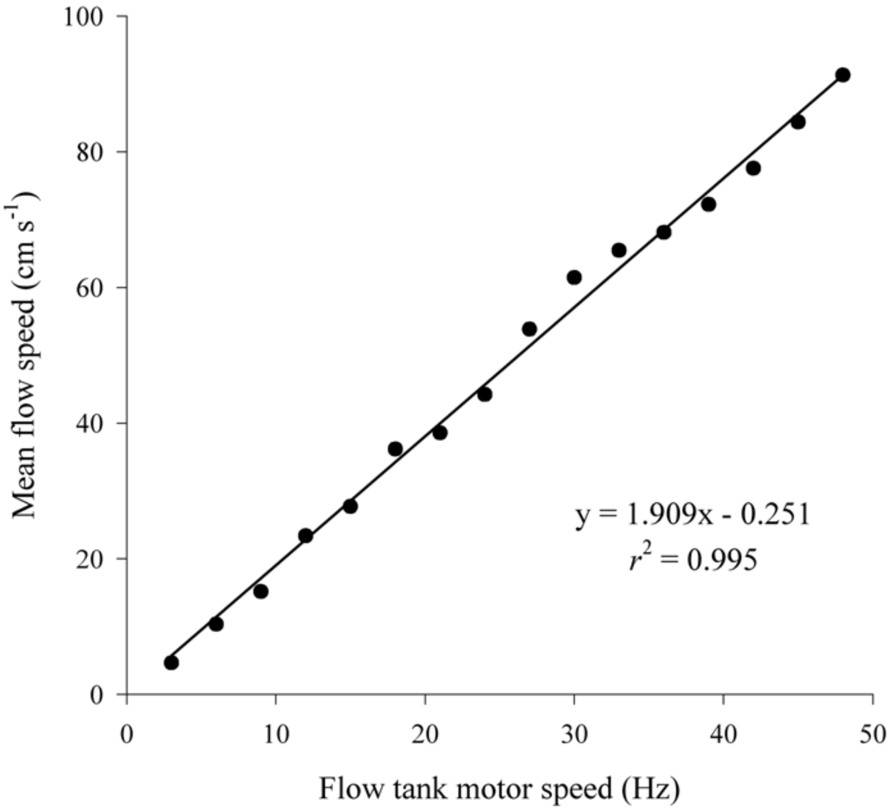

Fig. A2.1. Mean flow speed in working section of the 194 L recirculating flow tank against shaft rotation speed of the 0.75 kW electric motor. Flow speeds are means taken from high speed video tracking of 12 replicate passive particles at each motor speed.

Wave-induced water motion and the functional implications for coral reef fish assemblages

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Wave energy and swimming performance shape coral reef fish assemblages

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Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages