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

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Abstract

Using a functional approach, we quantified water motion and the distribution of fish swimming modes across five habitat zones and four exposure regimes commonly found on coral reefs. There were major spatial variations in net flow velocity (7.4–43.2 cm s^{-1}) and rates of flow direction change (0.06–0.66 Hz) among habitats of different depth. Water motion within the shallow crest and flat habitats appeared to be largely wave driven, with rates of flow direction change (0.63–0.66 Hz) corresponding with approximately double the wave periodicity (0.31–0.36 Hz) and relatively little contribution (14–16%) from drift flow velocities. A similar variation in water motion was found among reefs of different exposure, with the highest and lowest velocities recorded in the exposed and sheltered locations, respectively. Exposed and oblique reef crests displayed greater temporal variation in wave height and water motion (24.4–59.5 cm s^{-1} net velocities) when compared with the relatively static conditions in sheltered (6.2–12.6 cm s^{-1}) and lagoonal sites (17.1–25.3 cm s^{-1}). We examined the distribution and functional structure of seven coral reef fish families (156 species) across the full range of water motion variation on these reefs. Pectoral-swimming fishes were the most abundant group, predominating in areas with high levels of water motion; pectoral-caudal– and caudal-swimming fishes displayed the opposite trend. We suggest that these differences are the result of an interaction between water motion and the biomechanical and energetic attributes associated with each swimming mode.

Wave energy is an important physical determinant of community structure in intertidal and subtidal aquatic ecosystems. In sessile organisms, water movements produced by the crash and surge of waves have been found to affect rates of fertilization (Denny and Shibata 1989), dispersal (Gaylord et al. 2002), growth (Dennison and Barnes 1988), and mortality (McQuaid and Lindsay 2000). Community-level effects have also been documented, where the removal of sessile individuals from habitats by wave-induced water movements have produced shifts in competitive interactions and predation rates in rocky intertidal communities (Paine and Levin 1981; Ebeling et al. 1985; Kawamata 1998). Accordingly, 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; Gaylord 1999).

Although extreme levels of wave energy can also displace mobile individuals from habitats (Lassig 1983), many mobile taxa either endure short-term extremes in wave energy or subsequently return after such events have passed (Cheal et al. 2002). Despite this apparent tolerance to extremes, extensive evidence links the long-term community structure of mobile taxa to relative levels of wave exposure in both tropical and temperate systems (Denny 1988; Williams 1991), and it is these long-term relationships that are yet to be adequately explained for the majority of mobile taxa. Available evidence suggests that average levels of wave-induced water motion can affect pedestrian locomotion in mobile invertebrates such as crabs and echinoids (Kawamata 1998; Martinez 2001) and swimming performance in fishes (Webb 2004). Such impediments to locomotion can have significant ecological consequences for mobile organisms by influencing foraging activities and patterns of habitat use (Menge 1978; Kawamata 1998; Fulton et al. 2001). Ultimately, daily levels of wave-induced water motion could shape the long-term distribution patterns of mobile aquatic taxa through interactions with their locomotor performance.

Swimming in fishes can be characterized by several different modes depending on the fins used to produce thrust (Lindsey 1978; Webb 1994). Biomechanical considerations suggest that these swimming modes are often associated with specific aspects of locomotor performance, such as maneuverability, stability, or energetic efficiency (Lindsey 1978; Webb 1994; Weihs 2002). Consequently, the distribution of fishes among different hydrodynamic environments could be shaped by locomotor performance according to the swimming mode employed (Webb 1994). Recent studies on a family of coral reef fishes have provided some support for this hypothesis, revealing 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). Although maximum sustained swimming speeds were relatively important for this relationship, these studies identified a major separation according to the type of thrust used by taxa (Wainwright et al. 2002). Specifically, species that predominantly use lift-based thrust were highly abun-

dant in wave-swept habitats, whereas drag-based taxa were restricted almost entirely to sheltered habitats (Fulton et al. 2001; Bellwood et al. 2002; Wainwright et al. 2002). Although promising, this concept is yet to be adequately tested through a direct comparison between quantitative measures of water motion and the distribution of reef fishes spanning several different families and swimming modes.

Previous evaluations of wave energy effects on coral reefs have generally relied on categorical differences in wave exposure ("exposed" and "sheltered"), largely because of the paucity of detailed information on wave-induced water motion. Although uncommon, studies that include 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 (Thomas and Atkinson 1997), deposition of sediments and detrital matter (Crossman et al. 2001), primary production and calcification rates in corals (Dennison and Barnes 1988; Patterson et al. 1991), and productivity in algal turfs (Carpenter and Williams 1993). These and other estimates of wave-induced water motion have identified flow velocities in the range of 3–140 cm s^{-1} (Young 1989; Kench 1998). Although these studies have indicated the potential for substantial variations in water motion on coral reefs, the general focus on sessile organisms and benthic processes has meant that these water motion observations were often made very close to the substratum. Consequently, water motion estimates that are directly applicable to major spatial variations in the distribution patterns of mobile taxa are yet to be quantified for coral reefs.

In this study, therefore, we combine five complementary measures to characterize water motion at scales relevant to the distribution of mobile organisms over a range of exposures and habitats found on coral reefs. For the first time, these quantitative gradients of wave-induced water motion are directly compared with the distribution and functional composition of a highly mobile group of organisms—coral reef fishes. We examine a possible causal link between water motion and the functional structure of coral reef fish assemblages through functional groupings based on swimming modes. Specifically, we aim 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, (2) examine the effect of temporal changes in sea conditions on these patterns of water movement, and (3) determine the distribution of swimming modes in coral reef fish assemblages in relation to wave-induced water motion.

Materials and methods

Water motion—We used five measures that encompassed both surface (wave height, wave period) and subsurface conditions (net flow velocity, drift flow velocity, and rate of flow direction change) 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 by an enhanced plaster dissolution technique that previously had been successfully applied to subtidal ecosystems (Dennison and

Barnes 1988; Jokiel and Morrissey 1993; Kawamata 2001). In addition to the usual measure of plaster mass loss, we also examined multidimensional changes in the size of gypsum balls, 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). Gypsum balls were constructed from calcium sulfate 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 molds made from rubber tennis balls. A piece of galvanized wire (210 mm long, 2.5 mm thick) embedded in each ball provided an attachment point. Gypsum balls were left to set in the mold 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 the 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) were recorded for each individually tagged ball. Predeployment 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 sizes and material 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 and 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 (cm s^{-1}; Dennison and Barnes 1988). Because gypsum dissolution is strongly related to water temperature (Jokiel and 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-liter recirculating flow tank (water replacement rate of 15 L min^{-1}) of a design following Vogel and LaBarbera (1978). Each trial was conducted for 24 h and repeated three times at each flow velocity 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).

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. 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 southeast 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) during the different southeasterly wind strengths of "calm" and "rough" (6.0 ± 0.3 and 11.9 ±

0.5 m s^{-1}, respectively, 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 rigidly mounted 60 cm above the substratum on a metal frame, with the *x*-axis orientated perpendicular to the incident wave fronts. A minimum of 50 m separated adjacent balls within each site. Balls were deployed for a 24-h period (± 20 min) during neap tidal conditions (maximum tidal range 0.98 m) to minimize 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 by 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 by placing a wave staff against the substratum and recording the distance between the highest crest and the lowest trough after 1 min, and wave period (*T*), for which 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-min period, and drift velocity (v_d), which was measured as the horizontal distance traveled by the passive particle after a 5-min period.

Distribution of fish swimming modes—Fish distribution patterns were quantified for seven reef fish families (the Acanthuridae, Chaetodontidae, Labridae, Pomacanthidae, Pomacentridae, Serranidae, and Siganidae) using a visual census technique following Fulton et al. (2001). All fish individuals were identified to species and counted within three belt transects (50 × 5 m) within each of the habitats and sites for which water motion was assessed. Functional attributes of these fishes in the form of swimming mode was then evaluated by recording the fins being used during the 3-s period following identification of each individual. Each species was assigned to a functional group (swimming mode) according to the fins used in 50% or more of the individuals observed.

Statistical analyses—After initial data exploration, all violations of normality and homoscedasticity were corrected by log($x + 1$) 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 with two-way analysis of variance, with either habitat and site or exposure and site as fixed factors. Net flow velocities during rough and calm deployments were compared by a three-way analysis of variance, with sea condition, exposure, and site as fixed factors. The relationship between net velocity and

wave height was examined by Pearson's correlation and least-squares linear regression. Distributions of species per swimming mode were examined, with habitat and site as fixed factors and the three swimming modes as variables in a two-way multivariate analysis of variance, with relationships between species per swimming mode and flow velocity of the habitat being explored through least-squares linear regressions. 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.

Results

Water motion—Weight loss (WL) of gypsum balls was found to display a strong linear relationship with experimental flow velocity (*v*) at both water temperatures (Fig. 1A), 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 their orientation to the direction of experimental flow. Specifically, a greater reduction in diameter was displayed across the *x*-axis (parallel to flow direction) compared with the *y*-axis and *z*-axis (perpendicular to the flow direction; Fig. 1B).

Field deployments revealed statistically significant differences in net flow velocity among habitats ($F_{4,20} = 115.58$, $p < 0.001$), with no significant site effect ($F_{1,20} = 0.24$, $p = 0.630$) or interaction ($F_{4,20} = 2.45$, $p = 0.080$). Crest and flat habitats displayed the highest estimated net flow velocities (38.3 and 43.2 cm s^{-1}, respectively), with the drift velocities (5.3 and 6.9 cm s^{-1}) appearing to be a relatively minor contribution (14% and 16%) to the total velocities in these habitats (Fig. 2A). Notably, the reduction in wave height on the shallow back reef (81%) corresponded to a marked reduction in net velocity (65%) compared with the exposed reef crest of the same depth (Fig. 2A,D). 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 ($F_{4,20} = 1.08$, $p = 0.391$). Although 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. 2B). Diameter losses on balls deployed in the reef crest and flat differed among the three measured axes, with a markedly greater loss found across the *x*-axis in these shallow habitats (Fig. 2C). In contrast, diameter loss was relatively uniform among the three axes in the deeper habitats of slope and base (Fig. 2C).

Significant differences in net 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
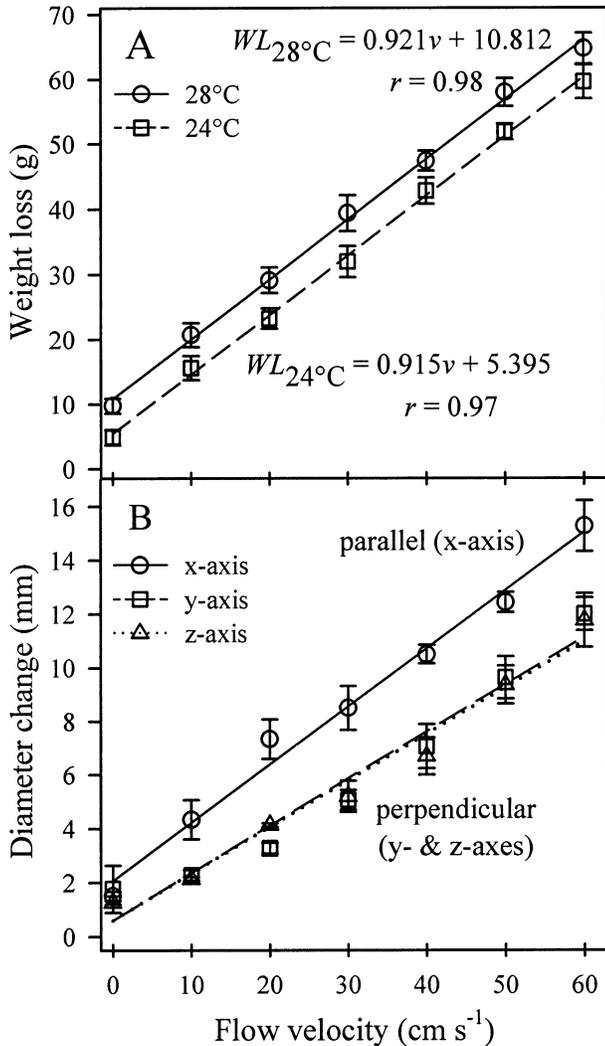
Fig. 1.   Gypsum dissolution calibration. (A) Weight loss (WL) from gypsum balls after 24-h exposure to seven flow velocities (v) at two water temperatures. (B) Diameter change after 24-h exposure to seven flow velocities at 24°C. Error bars are standard errors of the mean.

correlation (Pearson's correlation 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. 4).

Distribution of fish swimming modes—Visual censuses recorded a total of 66,027 individuals and 156 species (49 genera) from the seven fish families. Three major modes of fin use were recorded—pectoral, pectoral-caudal, and caudal—with 100, 41, and 15 species being recorded in each mode, respectively. Significant differences were found in the distribution of species per swimming mode among habitats (Pillai's trace 1.67, $F_{12,60} = 6.27$, $p < 0.001$) and exposures (Pillai's trace 1.86, $F_{9,48} = 8.68$, $p < 0.001$), with no significant site (Pillai's trace 0.04, $F_{3,18} = 0.24$, $p = 0.867$ and Pillai's trace 0.08, $F_{3,14} = 0.42$, $p = 0.739$, respectively) or interaction effects (Pillai's trace 0.37, $F_{12,60} = 0.37$, $p = 0.741$ and Pillai's trace 0.28, $F_{9,48} = 0.55$, $p = 0.830$, respectively). Although there was no significant correlation between mean species richness and net velocity across all of the sites examined (Pearson's correlation -0.14, $n = 14$, $p = 0.64$), divergent linear relationships were evident between the incidence of species using each swimming mode and average net flow velocity (Fig. 5). Pectoral-swimming fishes were the most prevalent overall, this prevalence increasing in locations of high water velocity, whereas caudal-swimming species decreased with increased water velocity (Fig. 5).

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 on the basis of depth and aspect to prevailing winds (e.g., Geister 1977; Bradbury and Young 1981; Done 1983). Furthermore, variations in the structure of reef fish assemblages across these predicted differences in wave energy have also been well reported (e.g., Talbot 1965; Williams 1991; Friedlander et al. 2003), with recent studies demonstrating that such patterns might be linked to swimming abilities in one family of pectoral-swimming fishes, the wrasses (Fulton et al. 2001; Bellwood et al. 2002). Using a combination of several hydrodynamic measures, we quantified marked variations in water motion across spatial gradients of depth and exposure that largely support previous predictions. These gradients in water motion provide direct evidence in support of the hypothesis that wave energy can shape assemblages of mobile organisms revealing a clear relationship between water motion and the distribution of swimming modes in seven families of coral reef fishes.

Spatial and temporal variations in water motion—Exposed shallow habitats (reef crest and flat) displayed the highest overall flow velocities and rates of flow direction change, with these values decreasing with increasing depth of the habitat. Using comparisons of surface and subsurface 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

recorded in the 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. 3). Comparison across a temporal change in sea condition (calm vs. 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. 3B,C; Table 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 velocity (Fig. 3B,C). Average wave periodicities across exposures were similar under calm and rough conditions for all habitats (0.31 and 0.33 Hz, respectively), as were rates of flow direction change (0.61 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
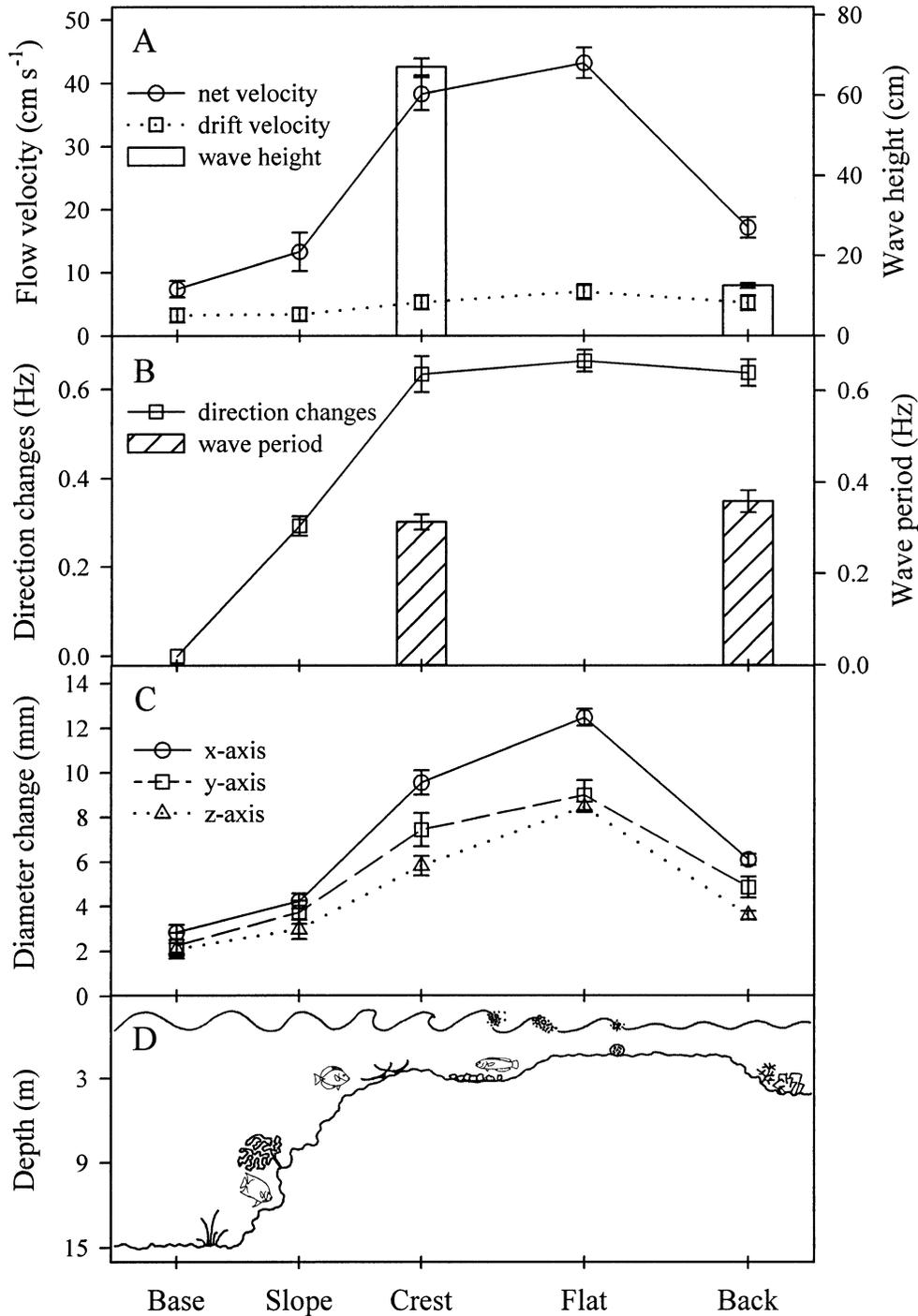
Fig. 2. Water motion assessments among five habitats on an exposed reef at Lizard Island. (A) Net flow velocities from gypsum dissolution, with drift velocities recorded for each habitat and incident wave heights for this exposed location. (B) Wave period and rates of flow direction change recorded in 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.

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 in the direction of wave travel. Although 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 hab-
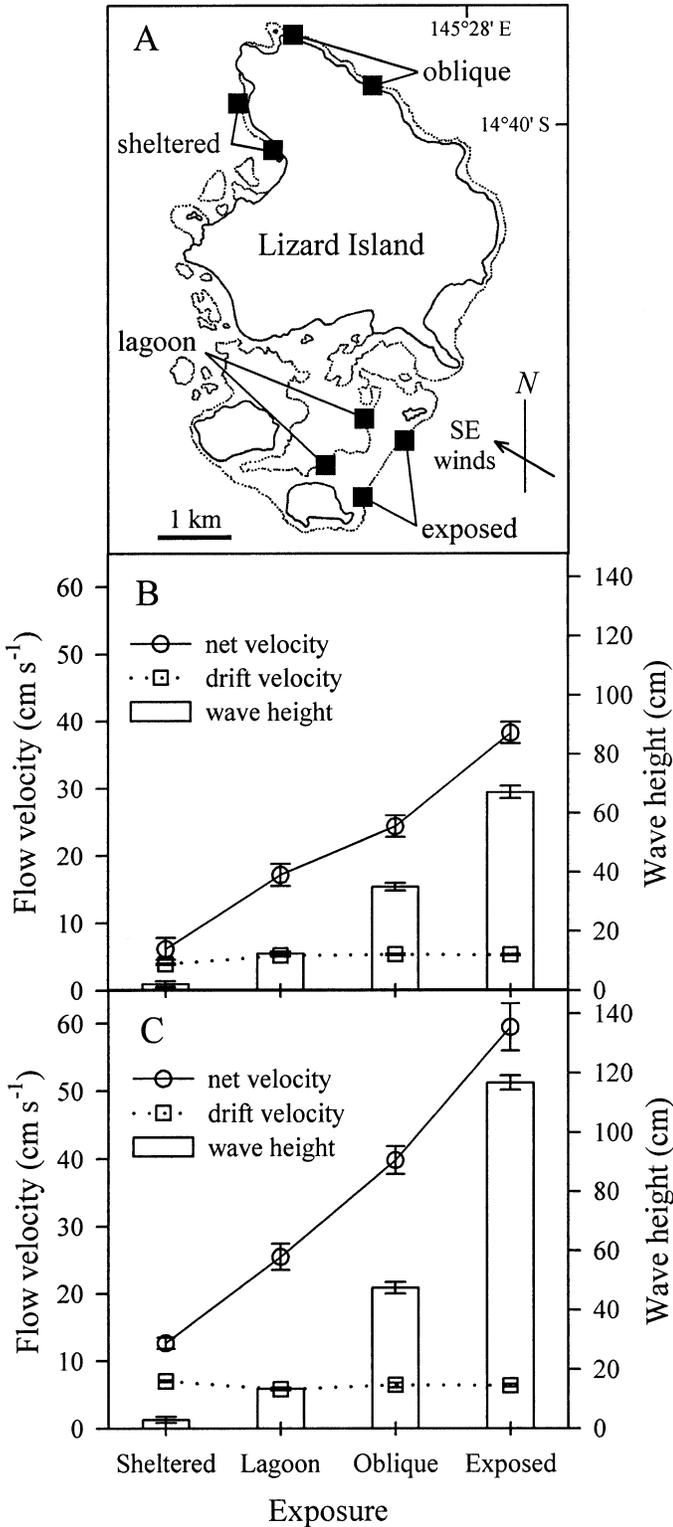
Fig. 3. Water motion assessments among four exposures around Lizard Island, with mean wave heights, net flow, and drift velocities indicated. (A) Location of sites. (B) Calm sea conditions. (C) Rough sea conditions. Error bars are standard errors of the mean.

itats 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 among reefs of different exposure were of a similar magnitude to those found among 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. Although the relative differences between exposures in our study largely correspond with previous categorical appraisals (Geister 1977; Bradbury and Young 1981; 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 favorably to previous estimates of 75–90% that varied according to depth and incident wave height (Young 1989; Hardy and 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; Kench 1998). Although 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 this study agree with average values for a midshelf location on the GBR (Young 1989; Hardy and Young 1996; Crossman et al. 2001). A temporal change from calm to rough sea conditions in this 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}), which ran parallel to the reef face, correspond to the lower end of spring tidal flow values (0–20 cm s^{-1}) taken on a midshelf reef of the GBR (Leonard et al. 1988). In

Table 1. Summary of 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	1,978.59	1,978.59	81.02	<0.001
Exposure	3	10,126.55	3,375.52	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	13,467.57			

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 and 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 m) comparable to this study (Kawamata 2001). Furthermore, the strong relationship between wave height and flow speed found in this study suggests that our methodology was appropriate for the range of wave conditions encountered. Overall, these estimates of water motion provide the opportunity to directly evaluate the role of wave-induced water motion in shaping the distribution of mobile coral reef organisms.

Distribution of swimming modes and water motion— Functional groups are a useful tool to investigate distribution patterns without the constraint of taxonomic boundaries (Wainwright 1994; Bellwood et al. 2002). This has particularly been the case when examining the influence of physical variables, given that the functional attributes of individuals are often shaped by environmental challenges (Denny 1994; Wainwright 1994). In this study, we found a clear relationship between spatial variations in wave-induced water motion and the incidence of functional swimming groups. Pectoral-swimming fishes were the most prevalent functional group overall, with species that used this mode increasing with greater levels of net flow velocity, whereas caudal-swimming fishes displayed the opposite trend. Although fishes that utilized pectoral-caudal swimming were intermediate between these two groups, they also decreased in prevalence with increased levels of water motion.

Our results considerably extend the findings of previous studies that identified a relationship between wave energy and swimming abilities within a single family of pectoral-swimming fishes, the wrasses (Fulton et al. 2001; Bellwood et al. 2002). These previous studies indicated that a major separation in the use of swimming thrust between habitats of different wave energy might be driven by alternative energetic strategies. Specifically, it was hypothesized that lift-based swimming provided the most energetically efficient means of maintaining high swimming speeds in wave-swept habitats compared with drag-based locomotion (Bellwood et al. 2002; Wainwright et al. 2002). However, these studies were based on theoretical estimates of the relative levels of water motion among locations of different wave exposure. We have established similar relationships in seven families of reef fishes spanning three modes of swimming, and with
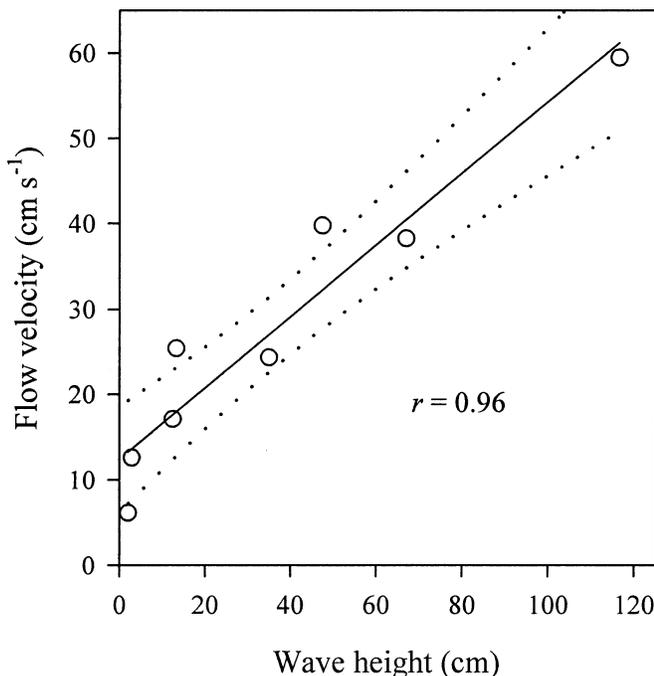

Fig. 4. Relationship between wave height and net flow velocity as measured by gypsum dissolution on reefs around Lizard Island. Values are means from each exposure for both calm and rough deployments. Dotted lines represent 95% confidence limits.
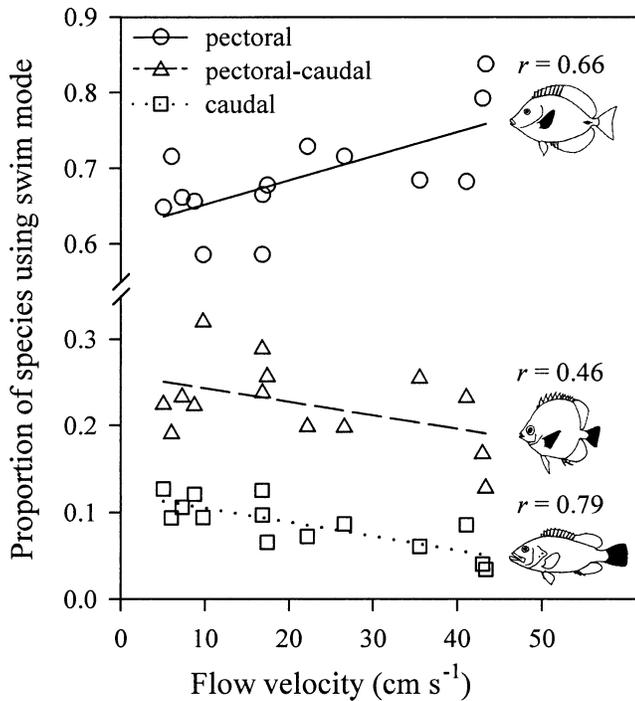
Fig. 5.   Distribution of fish species (total of 156) that use each of three swimming modes against net flow velocities in each habitat at Lizard Island. Values are presented as an average proportion of the total number of species in each habitat. Significance of regressions were $p < 0.01$ for the pectoral and caudal swimming modes and $p < 0.05$ for the pectoral-caudal mode.

our quantitative estimates of water motion, we are now in a position to directly evaluate the energetic implications of locomotion in various coral reef habitats.

Our estimates of water motion 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). Taking the two extremes in our estimates of flow velocity, inhabitants of exposed reefs could be subjected to up to 5.2 times greater flow speeds than inhabitants of sheltered locations. If an individual fish were to station-hold against average flow velocities within each of these locations, daily energy use associated with such swimming behavior on exposed reefs could be up to 45 times greater than station-holding in an equivalent sheltered reef habitat. Given that this estimate is outside the 15-fold increase in metabolic rate that has previously been seen during swimming in many fishes (Beamish 1978), such increases 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 characterized by few species (Fulton et al. 2001; Bellwood et al. 2002). Although these estimates incorporate simplifying assumptions and do not take into account behavioral modifications such as flow-refuging (Gerstner 1998), they suggest that increased energetic costs of

locomotion might be a considerable barrier to the occupation of wave-swept habitats by fishes.

Biomechanical attributes associated with different locomotor modes can often confer considerable energetic advantages through increases in locomotor efficiency (Lindsey 1978; Vogel 1994; Weihs 2002). Such biomechanical differences between modes might therefore provide some insight into the relationships between water motion and the distribution of swimming modes in this study. Pectoral swimming is generally associated with high efficiency of movement, particularly when the use of lift-based thrust is involved (Vogel 1994; Webb 1994; Walker and Westneat 2000). Such efficiency would provide a considerable competitive advantage when occupying wave-swept habitats that might be energetically costly environments. Previous work on labrids has demonstrated that taxa that dominate wave-swept habitats predominantly use lift-based thrust (Bellwood et al. 2002; Wainwright et al. 2002), a form of pectoral swimming that provides the most efficient means of maintaining high sustained speeds (Walker and Westneat 2000). A similar relationship may be expected for the other pectoral-swimming taxa in this study; however, this would require a detailed comparison of species-specific patterns of fin shape, locomotor performance, and distribution patterns in relation to water motion to provide further insight.

Maneuverability might also be important, with pectoral swimming often being associated with precise maneuverability and high stability (Lindsey 1978; Webb 1994; Weihs 2002). Given that wave-swept habitats are often associated with high rates of flow direction change, a high level of maneuverability would provide significant advantages for conducting daily activities, such as interacting with a complex substratum to obtain food and shelter. Indeed, fine-scale water movements such as turbulence and boundary layer effects could play a significant role in shaping the distribution patterns of fishes at smaller scales than those examined in this study. Conversely, caudal swimming, which was largely subcarangiform (sensu Webb 1994) in our demersal reef fishes, is often associated with a high degree of slow-speed power and acceleration, but potentially at a greater energetic cost than pectoral swimming and with a reduced capacity for fine-scale maneuverability (Lindsey 1978; Webb 1994; Korsmeyer et al. 2002; Weihs 2002). Consequently, caudal-swimming fishes might be at an energetic disadvantage to their pectoral-swimming counterparts in high-wave energy habitats and locations. The intermediate prevalence of pectoral-caudal–swimming taxa within wave-swept habitats probably reflects the incremental benefits associated with pectoral locomotion.

Given that these relationships between swimming mode and water motion are consistent over a continuous gradient, regardless of habitat type, it appears that wave-induced water motion has a strong influence on the functional structure of reef fish assemblages. Our quantitative estimates allow for a direct evaluation of the effects of wave energy on mobile coral reef inhabitants over a wide range of habitats and exposures. Using our estimates of water motion in conjunction with energetic and biomechanical evaluations of swimming modes, we suggest that wave-swept habitats pose substantial

challenges to locomotion that can shape broad-scale patterns of habitat utilization by reef fishes.

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