

Localised intraspecific variation in the swimming phenotype of a coral reef fish across different wave exposures

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Abstract Wave-driven water flow is a major force structuring marine communities. Species distributions are partly determined by the ability to cope with variation in water flow, such as differences in the assemblage of fish species found in a given water flow environment being linked to swimming ability (based on fin shape and mode of locomotion). It remains unclear, however, whether similar assembly rules apply within a species. Here we show phenotypic variation among sites in traits functionally linked to swimming ability in the damselfish *Acanthochromis polyacanthus*. These sites differ in wave energy and the observed patterns of phenotypic differences within *A. polyacanthus* closely mirrored those seen at the interspecific level. Fish from high-exposure sites had more tapered fins and higher maximum metabolic rates than conspecifics from sheltered sites. This translates to a 36 % larger aerobic scope and 33 % faster critical swimming speed for fish from exposed sites. Our results suggest that functional relationships among swimming phenotypes and water flow not only structure species assemblages, but can also shape patterns of phenotypic divergence within species. Close links between locomotor phenotype and local water flow conditions appear to be important for species distributions as well as phenotypic divergence across environmental gradients.

Keywords Aerobic capacity · Aspect ratio · Critical swimming speed · Metabolic rate · Respirometry

Introduction

Organisms frequently appear to be adapted to their local environment. As environments are often highly variable, organisms must (1) have evolved locally due to selection for fitter genotypes, (2) have environmentally induced means of adjusting their phenotype to match the prevailing conditions (i.e. show adaptive phenotypic plasticity; West-Eberhard 1989), or (3) have moved to more suitable habitats for their phenotype. In both terrestrial and aquatic ecosystems, variation in the physical environment is a major force influencing patterns of phenotypic distribution through time and space (e.g. Leonard et al. 1998; Fulton et al. 2005; Desrochers 2010).

In aquatic habitats, numerous physical factors structure communities across a range of spatial scales (e.g. Bertness et al. 1999; Kaandorp 1999; Bellwood et al. 2002; Chapman et al. 2002). In particular, water motion, caused by waves and currents, influences species distributions, and selects for various functional traits that are needed to exploit these environments (e.g. Kaandorp 1999; Denny and Gaylord 2002; Fulton et al. 2005; Langerhans 2008; Mims and Olden 2012). For example, in fish, functional traits that affect swimming performance predict interspecific patterns of habitat use. Over 60 % of coral reef fishes primarily use their pectoral fins for swimming [labriform swimming (Webb 1994; Fulton and Bellwood 2005)]. In this group, pectoral fin shape affects swimming performance likely due to biomechanical constraints: species with tapered, high-aspect ratio (AR) fins are faster steady swimmers (i.e. straight-line swimming at a constant

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velocity) than those with rounded, low-AR fins, which are better at manoeuvring in low-flow environments (Vogel 1994; Fulton et al. 2005). Since reef fish often need to swim at speeds dictated by the ambient water velocity, fishes with high-AR fins tend to dominate high-flow wave-swept habitats whereas low-AR-finned species are abundant on sheltered, low-flow reefs (Webb 1994; Bellwood et al. 2002). Living in high-flow habitats may also require a higher aerobic capacity to support a wider range of swimming speeds (U). Aerobic scope (AS) is a measure of the metabolic range within which an animal can sustain aerobic activities (Claireaux and Lefrancois 2007). A large AS may enable fishes to sustain energetically demanding activities across a wider range of water flow conditions. As such, AS could be a key trait driving the exploitation of wave-exposed habitats by coral reef fishes.

The functional relationship between swimming phenotype and wave-driven flow has been well explored in freshwater and marine fishes by looking at variation in habitat use among species (e.g. Bellwood et al. 2002; Fulton et al. 2005; Langerhans 2008). However, we have yet to fully resolve whether similar processes are responsible for structuring the distribution of individuals of the same species in marine environments (Fulton et al. 2013). Evidence for local adaptation and/or plastic responses to water flow conditions would suggest important, currently overlooked mechanisms that influence species distributions and the potential for expansion into new environments.

The Pomacentridae are a large family of pectoral-fin-swimming fishes, ideal for functional studies due to their diversity and abundance in coastal systems worldwide (Cooper et al. 2009). On the Great Barrier Reef, *Acanthochromis polyacanthus* is one of the few cosmopolitan species able to thrive in a range of reef habitats including shallow reef crests and lagoons (Williams 1982). Unlike other pomacentrid fishes, *A. polyacanthus* lacks a pelagic larval stage (Doherty et al. 1994; Kavanagh 2000). This has important implications for gene flow. Population divergence occurs over spatial scales as little as 3 km when sites are separated by deep-water (>10 m) channels providing a foundation for exploring variation in functional traits at small spatial scales (Doherty et al. 1994; Kavanagh 2000; Planes et al. 2001; Bay 2005; Bay et al. 2008; Miller-Sims et al. 2008).

We tested the hypothesis that populations of the widespread coral reef damselfish, *A. polyacanthus*, at sites with high versus low exposure to waves differ in their swimming phenotypes. More specifically, we predicted that fish at high-exposure sites will: (1) display higher AR pectoral fins, (2) have faster steady U , and (3) have a greater AS. These predictions are based on patterns seen when comparing these traits among species that vary in their preference for habitats with high and low water flow.

Materials and methods

Study system and abundance surveys

Fish were collected between February and March 2011 at six sites around Lizard Island, northern Great Barrier Reef, Australia ($14^{\circ}40'S$, $145^{\circ}28'E$). Three sites were chosen on the windward (wave-exposed) and three on the leeward (sheltered) side of the island (Fig. 1). Patterns of water motion at these sites have been previously measured, with wave height and water flow velocity differing more than sixfold between sites of different exposure during windy conditions (Fulton and Bellwood 2005): wave-exposed sites experience average water flows of approximately 38 cm s^{-1} , whereas sheltered sites experience flows of about 6 cm s^{-1} . Windward and leeward sites around Lizard Island are relatively similar in terms of coral canopy cover, structural complexity, fish habitat use, and other abiotic variables (Crossland and Barnes 1983; Goatley and Bellwood 2011; Heatwole and Fulton 2013).

The abundance of adult *A. polyacanthus* was recorded at all study sites by divers using underwater visual censuses. Censuses were conducted on calm weather days (winds <5 knots) on reef crests (1.5–4 m depth). All individuals >5 cm total length (TL) were counted within four replicate 50-m \times 4-m belt transects at each site. We surveyed each site extensively, covering approximately 800 m² of habitat

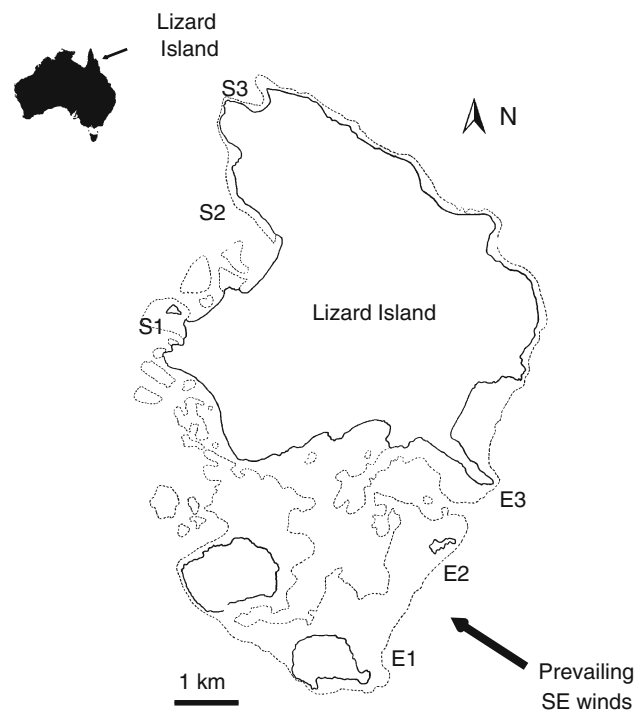


Fig. 1 Map of Lizard Island with the location of the three sheltered (S1, S2, S3) and three exposed (E1, E2, E3) sites. Experimental swimming and respirometry trials were conducted on specimens collected from sites E1, E2, S1 and S2

per site. The sites surveyed encompassed a range of habitat types typical of mid-shelf reefs. The average fish density (no. individuals m^{-2}) was calculated for each transect.

Fin morphology

Ten to 12 fish per site were collected at all six sites using microspears or barrier nets, sedated with 10 % Aquai-S solution and euthanised in an ice slurry so that we could measure their pectoral fin morphology. Pectoral fins were dissected at the base of the fin, spread out and pinned onto a foam sheet, fixed into position using a concentrated formalin solution (39 % formaldehyde), and digitally photographed (Panasonic Lumix DX3) on gridded paper (Binning and Fulton 2011). The length of the leading edge and total fin surface area were measured using ImageJ software (version 1.43). Fin AR was then calculated as the length of the leading edge squared divided by the total fin area. In total, we measured fins from 63 adult individuals [TL (L_T) = 120.5 ± 2.5 mm; mass = 31.5 ± 1.6 g; mean \pm SEM].

Experimental swimming and respirometry trials

We measured experimental U and estimated aerobic metabolic rates ($\sim O_2$ consumption rate, $\dot{M}O_2$ in $mg\ O_2\ kg^{-1}\ h^{-1}$) in adults from two wave-exposed and two sheltered sites (Fig. 1). Five fish of similar size from each site (20 fish in total, $L_T = 129.4 \pm 1.1$ mm; mass = 41.5 ± 0.9 g; no significant differences in wet fish mass among sites; $F_{1,3} = 0.293$, $P = 0.83$) were collected with ultra-fine barrier nets and transported to the aquarium facilities at the Lizard Island Research Station within 2 h of capture. Fish were held in individual holding aquaria (40.0 width \times 29.0 length \times 18.0 height; cm) with a flow-through water system directly from the reef. Fish were fasted for 24 h prior to the swimming trials to ensure a post-absorptive state that maximizes energy availability for swimming (Niimi and Beamish 1974; Johansen and Jones 2011). Length measures were obtained by gently holding each fish on a wet surface and measuring TL, body width and body depth with handheld calipers. Mass was measured by placing the fish into a tared container of water on a scale, which minimized air exposure and stress prior to each trial. For this species, this method is as accurate as weighing the individual directly on the scale. These measures were used to calibrate the respirometer and calculate the flow rate of water in total body lengths (BL) per second. Swimming trials were carried out in an 11.9-L Loligo swimming respirometer (swim chamber dimensions 40.0 length \times 10.0 width \times 10.0 height; cm) filled with aerated, filtered and UV sterilized seawater at a constant temperature of 28 ± 0.1 °C. We used intermittent-flow

respirometry (Steffensen 1989) and O_2 levels in the respirometer were recorded using a fiber optic oxygen meter (Presens Fibox 3) online feed into the AutoResp 1 software (Loligo Systems, Denmark). The flow in the working section of the respirometer was calibrated using a digital TAD W30 flow meter (Höntzsch, Germany). The flow profile varied less than 3 % across the full cross-section of the swim chamber, with the lowest flow occurring in the central part of the chamber. We did not observe individuals favouring one corner or particular side of the working section during the swim trials. Solid blocking effects of the fish in the working section were corrected by the respirometry software (AutoResp, Loligo Systems) following the equations of Bell and Terhune (1970).

We measured $\dot{M}O_2$ as a function of U following a standard critical U (U_{crit}) protocol (Brett 1964; Steffensen et al. 1984; Rouleau et al. 2010; Binning et al. 2013; Roche et al. 2013). We used 10-min cycles with a 240-s flush, 60-s wait and 300-s measure cycle. During the flush phase, oxygenated water from the surrounding water bath is pushed into the chamber to replenish the O_2 depleted by the swimming fish. The flush period ensured that the O_2 concentration throughout the trial did not decrease below 80 % air saturation, and avoided CO_2 build up. The short wait period ensured that water in the chamber was sufficiently well mixed before measurements of $\dot{M}O_2$ commenced. Once an individual's length and mass measures were inputted into the respirometry software, three cycles were run without a fish to measure initial background rates of respiration due to the bacterial load in the test chamber. Fish were then placed in the test chamber of the respirometer and left to acclimate for 5–8 h at a U corresponding to 1 BL s^{-1} until their O_2 consumption rate stabilized. This speed ensured constant swimming while minimizing spontaneous activity in this species. We measured O_2 consumption rate at 1.0 BL s^{-1} by averaging the three $\dot{M}O_2$ measurements immediately prior to the onset of the first trial (Roche et al. 2013). To start the trial, the flow speed was then slowly increased to 1.5 BL s^{-1} for three 10-min $\dot{M}O_2$ measurement cycles. Flow speed was then incrementally increased by 0.5 BL s^{-1} every three cycles (i.e. every 30 min) for the duration of the experiment. Fish were continually monitored for a gait change from pectoral-fin swimming to pectoral-caudal-fin swimming (Drucker and Jensen 1996) for more than 5 s continuously, at which point the flow speed and time into the interval was recorded (Johansen and Jones 2011). The trial stopped when the fish could no longer swim unassisted or was forced to rest on the back of the flow chamber for five or more seconds (Johansen and Jones 2011). The time and flow speed was recorded and the water flow was

then reduced to 1.0 BL s^{-1} to ensure the fish's recovery from O_2 debt. We determined that a fish had recovered when its O_2 consumption rate fell back to near its rate at the start of the experiment at 1.0 BL s^{-1} . The fish was then returned to its holding tank. Three additional cycles were run to measure final background rates of respiration in the chamber (Clark et al. 2013). Background O_2 consumption rates at the end of each cycle were determined from the slope of the linear regression between initial and final background rates, and were subtracted from each $\dot{M}\text{O}_2$ cycle. To reduce bacterial growth and respiration in the chamber, the respirometer was drained and rinsed in freshwater when the background O_2 consumption rates exceeded 20 % of the resting metabolic rate of the fish.

Swimming speed calculations

We calculated a fish's gait transition speed (U_{p-c}) and U_{crit} following the equation in Brett (1964):

$$U_{p-c} \text{ and } U_{crit} = U + U_i x (t/t_i)$$

where U is the penultimate U before the fish changed gait (U_{p-c}) or fatigued and stopped swimming (U_{crit}); U_i is the U at which the fish changed swimming gait or was unable to continue swimming (i.e. U at increment i); t is the length of time the fish swam at the final U where fatigue or gait change occurred; t_i is the amount of time fish were swam at each speed interval in the trial (i.e. 30 min).

O_2 consumption rate curves and aerobic scope

We used a hydrodynamics-based power function with three parameters to describe the relationship between U and $\dot{M}\text{O}_2$ for each site (Roche et al. 2013):

$$\dot{M}\text{O}_2 = a + bU^c$$

where a is the estimated $\dot{M}\text{O}_2$ at zero speed (standard metabolic rate; SMR). In another species of coral reef fish, fitting a three-parameter power function to the O_2 consumption curve obtained in a swimming respirometer was shown to provide accurate estimates of SMR which did not differ significantly from estimates obtained in a resting respirometer (Roche et al. 2013). Maximum metabolic rate (MMR) was measured at the maximum U where fish completed at least one 10-min $\dot{M}\text{O}_2$ determination; we averaged $\dot{M}\text{O}_2$ values when fish completed more than one determination (up to three determinations; Roche et al. 2013). We calculated the AS as MMR minus SMR (Clark et al. 2013). We also calculated factorial AS as $(\text{MMR} - \text{SMR})/\text{SMR}$. We obtained similar results using both calculations; therefore, we only present AS.

Statistical analyses

We used two-way mixed-effect ANOVAs to test for differences in fish density, fin morphology (AR), swimming performance (U_{p-c} , U_{crit}) and metabolic performance (SMR, MMR, AS) among sites (random factor) and wave exposures (fixed factor) using SPSS version 19. Fish body mass did not differ among sites ($P = 0.83$) and including this predictor in the metabolic performance analyses did not qualitatively change the results. O_2 consumption rates and swimming performance data were normally distributed (Shapiro-Wilk's test, $P > 0.18$ in all cases). Fish density was \log_{10} transformed to meet the assumptions of the model. We used a general linear mixed effects model (LMM; lme function in R version 3.0.1) to test for differences in the $\dot{M}\text{O}_2$ - U relationship across wave exposures. We specified the relationship between U and $\dot{M}\text{O}_2$ as a second-degree polynomial; site and fish identity were included as random factors.

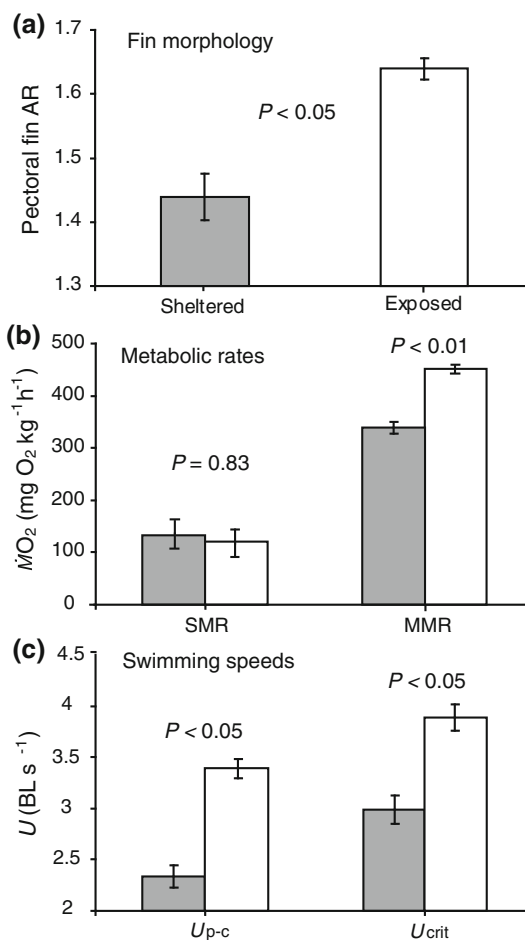


Fig. 2 Average (\pm SE) **a** pectoral fin aspect ratio (AR), **b** metabolic rates (SMR standard metabolic rate; MMR maximum metabolic rate), and **c** experimental (U_{p-c} , U_{crit}) swimming speeds (U) for *A. polyacanthus* from sheltered (grey) and wave exposed (white) sites

Table 1 Mean fish total length (*TL*), mass (*M*), pectoral fin aspect ratio (*AR*), gait transition speed (U_{p-c} ; where *U* is swimming speed), critical *U* (U_{crit}), maximum metabolic rate (*MMR*) and aerobic scope (*AS*) for *Acanthochromis polyacanthus* collected from sites around Lizard Island (\pm SE)

Site	Exposure	TL (mm)	M (g)	AR	U_{p-c} (BL s ⁻¹)	U_{crit} (BL s ⁻¹)	MMR (mg O ₂ kg ⁻¹ h ⁻¹)	AS (mg O ₂ kg ⁻¹ h ⁻¹)
E1	Exposed	127.8 ± 2.1	42.5 ± 2.2	1.63 ± 0.03	3.34 ± 0.11	3.72 ± 0.18	430.0 ± 37.1	307 ± 32
E2	Exposed	127.8 ± 2.0	41.2 ± 1.9	1.61 ± 0.03	3.45 ± 0.16	4.06 ± 0.17	473.9 ± 42.7	336 ± 37
E3	Exposed	–	–	1.66 ± 0.02	–	–	–	–
S1	Sheltered	128.6 ± 2.4	40.0 ± 1.3	1.47 ± 0.05	2.25 ± 0.10	3.09 ± 0.16	344.8 ± 31.8	222 ± 42
S2	Sheltered	131.4 ± 1.8	42.3 ± 2.1	1.51 ± 0.07	2.42 ± 0.20	2.89 ± 0.23	341.9 ± 45.7	215 ± 94
S3	Sheltered	–	–	1.33 ± 0.06	–	–	–	–

BL Body length

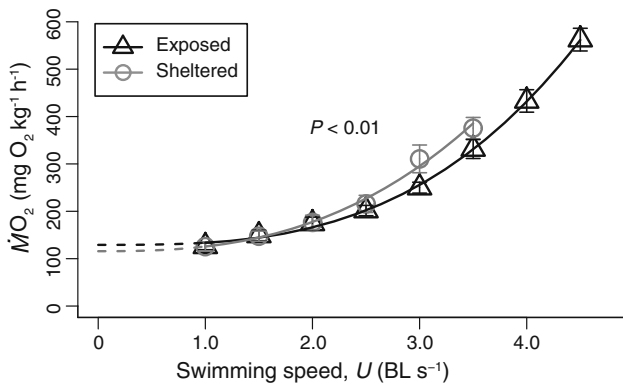


Fig. 3 Oxygen consumption rate ($\dot{M}O_2 \pm$ SE) as a function of swimming speed (*U*, body lengths second⁻¹) for exposed and sheltered fish from each of four sites sampled ($n = 10$ fish per exposure, black triangles = exposed; grey circles = sheltered). Oxygen consumption curves are as follows: $\dot{M}O_2 = 4.5U^{3.0} + 129.1$ for wave exposed fish; $\dot{M}O_2 = 9.93U^{2.63} + 115.8$ for sheltered fish

Results

Acanthochromis polyacanthus were equally abundant at high and low wave exposures ($F_{1,22} = 0.07, P = 0.80$) with an average density of 0.1 individuals m⁻². Pectoral fin shape differed between wave exposures with fish from exposed sites having higher AR pectoral fins (mean \pm SE; 1.63 \pm 0.02) than fish from sheltered sites (mean \pm SE; 1.44 \pm 0.04; $F_{1,4} = 12.85, P < 0.05$; Fig. 2a). Fish from sheltered sites exhibited more variation in pectoral fin AR between individuals than fish from exposed sites (Table 1).

There was a significant difference in the shape of the $\dot{M}O_2$ -*U* relationship between exposures (LMM interaction term; $F_{2,97} = 7.82, P < 0.01$), with sheltered fish consuming more O₂ than exposed fish at higher *U* (Fig. 3). In addition, fish from wave-exposed sites out swam those from sheltered sites during the trials: wave-exposed fish had a significantly higher MMR ($F_{1,18} = 8.87, P < 0.01$), greater AS ($F_{1,18} = 6.43, P < 0.05$), higher U_{p-c} ($F_{1,2} = 21.29, P < 0.05$) and faster U_{crit} ($F_{1,2} = 21.29, P < 0.05$) than

those from sheltered sites (Table 1; Fig. 2b, c). SMR did not differ between fish from high- and low-wave-exposure sites ($F_{1,18} = 0.05, P = 0.83$). Differences in AS are therefore due to a higher MMR in fish from exposed sites, consistent with the higher U_{crit} observed in these individuals.

Discussion

Water motion is a critical force structuring coral reef communities and leading to predictable effects of wave exposure on the presence or absence of species (e.g. Kaandorp 1999; Bellwood et al. 2002; Fulton et al. 2005). This predictable influence of water flow on community structure is widely attributed to the functional relationship between phenotypic traits that affect swimming performance and the ability to swim efficiently at different water flow rates. Here, we show that this functional relationship might also explain the spatial distribution of phenotypic variation within a single species. Differences in wave-driven flows experienced by *Acanthochromis polyacanthus* at exposed and sheltered sites are a plausible factor responsible for differences among sites in several traits that are known to be related to swimming ability. Across populations of *A. polyacanthus* separated by <10 km along a mid-shelf island, we found significant differences in fin shape, swimming performance and AS that mirror patterns observed in interspecific studies. That is, fish from sites exposed to higher wave energy possessed traits that are thought to enhance swimming capabilities under fast water-flow conditions.

Although *A. polyacanthus* displays relatively high levels of genetic diversity across our study sites (Bay 2005; Bay et al. 2008), our ability to assert large-scale trends is limited since we only examined four to six sites on a single mid-shelf island. While we observed a strong relationship between water flow and the morpho-physiological traits we measured, this evidence is correlational. Nonetheless, our results likely apply to other reef locations where similar differences in wave energy occur. Two additional studies support this view. First, Fulton et al. (2013) found similar

patterns in fin shape and U across flow gradients in *A. polyacanthus* distributed across a 40-km cline in wave-driven water motion. Second, another study at similar sites around Lizard Island found that many fishes, including *A. polyacanthus*, respond to varying wave conditions by changing their patterns of fin use and their body orientation relative to the flow in exposed sites during rough weather conditions (Heatwole and Fulton 2013). These results were not attributable to differences in habitat use. Specifically, *A. polyacanthus* occupies a similar mean water column height (approximately 50 cm above the substrate) on both the leeward and windward sides of the island in all weather conditions (Heatwole and Fulton 2013). In combination, both these studies suggest that water motion is a primary driver of phenotypic differences between exposed and sheltered sites in *A. polyacanthus*.

A. polyacanthus use their fins to produce lift-based thrust similar to the wing flapping pattern of swimming penguins (Vogel 1994). With this form of locomotion, high-AR fins can increase the lift-to-drag ratio on the fin surface and enhance the ability to generate forward thrust, especially in the presence of water flow (Vogel 1994). Conversely, high-AR fins are less useful in low-flow habitats since generating thrust through lift is less effective in these conditions (Vogel 1994). In addition to morphological adaptations, *A. polyacanthus* from wave-exposed sites presumably require a greater range of U performances. They likely achieve this through various modifications to their cardiovascular system leading to a higher AS than their sheltered conspecifics. Our swimming trials found that fish from wave-exposed sites swam up to 1.1 BL s^{-1} or 33 % faster than fish from sheltered sites. This difference appears to be fuelled by a 36 % increase in AS. A large AS presumably allows these fish to carry out several different activities simultaneously without incurring an O_2 debt (Claireaux and Lefrancois 2007). Rates of plankton delivery and detritus deposition are often greatest in high-flow habitats (Wilson et al. 2003; Clarke et al. 2005), so the increased supply of food at these sites may offset any costs of increased energy requirements for swimming faster in wave-exposed habitats. Interestingly, our census indicated that *A. polyacanthus* was equally abundant across the six study sites, suggesting no clear preference for wave exposure. Fully understanding these results requires additional studies exploring the costs of maintaining a large AS, as well as bioenergetic models exploring relative rates of energy gain and expenditure across different habitats.

Adaptive radiations in coral reef fishes have generally been attributed to divergence in trophic structures to exploit different food niches (e.g. Wainwright 1991). Our results suggest that distinct flow habitats created by reef locations (windward vs. leeward) might also promote additional phenotypic divergence among populations based

on swimming ability. Changes in locomotor traits facilitate range expansions into novel environments in a range of taxa. For instance, the recent adaptive radiation of *Anolis* lizards into habitats of varying complexity in the Caribbean has been linked to divergence in hind limb length affecting sprint speed, jumping and perching ability (Losos 1990a, b). Similarly, the morphological and physiological adaptations displayed by *A. polyacanthus* might partly explain its widespread distribution throughout the Great Barrier Reef and Coral Sea. Patterns of fin shape and U across flow gradients similar to those observed here also occur at larger spatial scales (gradient from inner to outer reef sites) in *A. polyacanthus* (Fulton et al. 2013). One interpretation is that selection for genes expressing phenotypes suited to the local wave environments has occurred (Langerhans 2008; Fulton et al. 2013). However, *A. polyacanthus* also shows relatively quick physiological adaptation (i.e. adaptive phenotypic plasticity) in response to changing thermal conditions in the laboratory (Donelson et al. 2011, 2012). Consequently, a role for environmentally induced plasticity in driving population variation in traits that affect swimming ability cannot be ruled out. This is an intriguing possibility. If true, it would represent some of the first empirical evidence of adaptive plasticity to natural environmental gradients in a coral reef fish. The degree to which phenotypic plasticity and natural selection on genetic variation drive intraspecific variation in the swimming ability of *A. polyacanthus* (and of other labriform swimmers) should be further explored through comparisons across multiple islands to test the extent to which the pattern observed on Lizard Island can be generalised. In addition, split brood and/or common garden experiments are needed to determine the relative contribution of genetic and environmental factors to phenotypic variation in *A. polyacanthus*. Ultimately, the strong functional relationship among swimming morphology, physiology, performance, and flow habitat that we have observed within a single species closely mirrors the well-documented pattern seen when looking across species of coral reef fishes. Given the known effect of this functional relationship on community assemblages globally, it is a remarkable pattern that warrants further investigation. We need to determine whether it can also explain spatial variation in phenotypes within a wide range of individual species.

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References

- Bay LK (2005) The population genetic structure of coral reef fishes on the Great Barrier Reef. PhD dissertation, School of Marine and Tropical Biology, James Cook University, Townsville, Queensland, Australia
- Bay LK, Caley MJM, Crozier RH (2008) Meta-population structure in a coral reef fish demonstrated by genetic data on patterns of migration, extinction and re-colonisation. *BMC Evol Biol* 8:248. doi:10.1186/1471-2148-8-248
- Bell WH, Terhune LDB (1970) Water tunnel design for fisheries research. *J Fish Res Bd Can* 195:1–69
- Bellwood DR, Wainwright PC, Fulton CJ, Hoey A (2002) Assembly rules and functional groups at global biogeographical scales. *Funct Ecol* 16:557–562. doi:10.1046/j.1365-2435.2002.00655.x
- Bertness MD, Leonard GH, Levine JM, Bruno JF (1999) Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. *Oecologia* 120:446–450. doi:10.1007/s004420050877
- Binning SA, Fulton CJ (2011) Non-lethal measurement of pectoral fin aspect ratio in coral reef fishes. *J Fish Biol* 79:812–818. doi:10.1111/j.1095-8649.2011.03070.x
- Binning SA, Roche DG, Layton C (2013) Ectoparasites increase swimming costs in a coral reef fish. *Biol Lett* 9:20120927. doi:10.1098/rsbl.2012.0927
- Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *J Fish Res Bd Can* 21:1183–1226
- Chapman LJ, Chapman CA, Nordlie FG, Rosenberger AE (2002) Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. *Comp Biochem Physiol A-Mol Integr Physiol* 133:421–437
- Claireaux G, Lefrancois C (2007) Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philos Trans R Soc B-Biol Sci* 362:2031–2041. doi:10.1098/rstb.2007.2099
- Clark TD, Sandblom E, Jutfelt F (2013) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *J Exp Biol* 216:2771–2782. doi:10.1242/jeb.084251
- Clarke RD, Buskey EJ, Marsden KC (2005) Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. *Mar Biol* 146:1145–1155. doi:10.1007/s00227-004-1528-y
- Cooper WJ, Smith LL, Westneat MW (2009) Exploring the radiation of a diverse reef fish family: phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. *Mol Phylogeny Evol* 52:1–16. doi:10.1016/j.ympev.2008.12.010
- Crossland CJ, Barnes DJ (1983) Dissolved nutrients and organic particulates in water flowing over coral reefs at Lizard Island. *Aust J Mar Freshwater Res* 34:835–844
- Denny M, Gaylord B (2002) The mechanics of wave-swept algae. *J Exp Biol* 205:1355–1362
- Desrochers A (2010) Morphological response of songbirds to 100 years of landscape change in North America. *Ecology* 91:1577–1582. doi:10.1890/09-2202.1
- Doherty PJ, Mather P, Planes S (1994) *Acanthochromis polyacanthus*, a fish lacking larval dispersal, has genetically differentiated populations at local and regional scales on the Great Barrier Reef. *Mar Biol* 121:11–21. doi:10.1007/BF00349469
- Donelson JM, Munday PL, McCormick MI, Nilsson GE (2011) Acclimation to predicted ocean warming through developmental plasticity in a tropical reef fish. *Glob Change Biol* 17:1712–1719. doi:10.1111/j.1365-2486.2010.02339.x
- Donelson JM, Munday PL, McCormick MI, Pitcher CR (2012) Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nature Clim Change* 2:30–32. doi:10.1038/nclimate1323
- Drucker EG, Jensen JS (1996) Pectoral fin locomotion in the striped surfperch. 1. Kinematic effects of swimming speed and body size. *J Exp Biol* 199:2235–2242
- Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol Oceanogr* 50:255–264. doi:10.4319/lo.2005.50.1.0255
- Fulton CJ, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. *Proc R Soc B* 272:827–832. doi:10.1098/rspb.2004.3029
- Fulton CJ, Binning SA, Wainwright PC, Bellwood DR (2013) Wave-induced abiotic stress shapes phenotypic diversity in a coral reef fish across a geographical cline. *Coral Reefs* 32:685–689. doi:10.1007/s00338-013-1039-8
- Goatley CHR, Bellwood DR (2011) The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE* 6:e27307. doi:10.1371/journal.pone.0027307
- Heatwole SJ, Fulton CJ (2013) Behavioural flexibility in reef fishes responding to a rapidly changing wave environment. *Mar Biol* 160:677–689. doi:10.1007/s00227-012-2123-2
- Johansen JL, Jones GP (2011) Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Glob Change Biol* 17:2971–2979. doi:10.1111/j.1365-2486.2011.02436.x
- Kaandorp JA (1999) Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. *Mar Biol* 134:295–306. doi:10.1007/s002270050547
- Kavanagh KD (2000) Larval brooding in the marine damselfish *Acanthochromis polyacanthus* (Pomacentridae) is correlated with highly divergent morphology, ontogeny and lift-history traits. *Bul Mar Sci* 66:321–337
- Langerhans RB (2008) Predictability of phenotypic differentiation across flow regimes in fishes. *Integr Comp Biol* 48:750–768. doi:10.1093/icb/icn092
- Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395–1411. doi:10.1890/0012-9658(1998)079[1395:FDVHC]2.0.CO;2
- Losos JB (1990a) Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr* 60:369–388. doi:10.2307/1943062
- Losos JB (1990b) The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44:1189–1203. doi:10.2307/2409282
- Miller-Sims VC, Gerlach G, Kingsford MJ, Atema J (2008) Dispersal in the spiny damselfish, *Acanthochromis polyacanthus*, a coral reef fish species without a larval pelagic stage. *Mol Ecol* 17:5036–5048. doi:10.1111/j.1365-294X.2008.03986.x
- Mims MC, Olden JD (2012) Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology* 93:35–45. doi:10.1890/11-0370.1
- Niimi AJ, Beamish FWH (1974) Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body-weight and temperature. *Can J Zool* 52:447–456
- Planes S, Doherty PJ, Bernardi G (2001) Strong genetic divergence among populations of a marine fish with limited dispersal, *Acanthochromis polyacanthus*, within the Great Barrier Reef and the Coral Sea. *Evolution* 55:2263–2273. doi:10.1111/j.0014-3820.2001.tb00741.x

- Roche DG, Binning SA, Bosiger Y, Johansen JL, Rummer JL (2013) Finding the best estimate of metabolic rates in a coral reef fish. *J Exp Biol* 216:2103–2110. doi:[10.1242/jeb.082925](https://doi.org/10.1242/jeb.082925)
- Rouleau S, Glemet H, Magnan P (2010) Effects of morphology on swimming performance in wild and laboratory crosses of brook trout ecotypes. *Funct Ecol* 24:310–321. doi:[10.1111/j.1365-2435.2009.01636.x](https://doi.org/10.1111/j.1365-2435.2009.01636.x)
- Steffensen JF (1989) Some errors in respirometry of aquatic breathers: how to avoid and correct them. *Fish Physiol Biochem* 6:49–59
- Steffensen JF, Johansen K, Bushnell PG (1984) An automated swimming respirometer. *Comp Biochem Physiol A* 79:437–440. doi:[10.1016/0300-9629\(84\)90541-3](https://doi.org/10.1016/0300-9629(84)90541-3)
- Vogel S (1994) *Life in moving fluids: the physical biology of flow*, 2nd edn. Princeton University Press, Princeton
- Wainwright PC (1991) Ecomorphology: experimental functional anatomy for ecological problems. *Am Zool* 31:680–693
- Webb PW (1994) The biology of fish swimming. In: Maddock L, Bone Q, Rayner JMV (eds) *Mechanics and physiology of animal swimming*. Cambridge University Press, Cambridge, pp 45–62
- West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. *Annu Rev Ecol Syst* 20:249–278. doi:[10.1146/annurev.es.20.110189.001341](https://doi.org/10.1146/annurev.es.20.110189.001341)
- Williams DM (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1:35–43. doi:[10.1007/BF00286538](https://doi.org/10.1007/BF00286538)
- Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanogr Mar Biol* 41:279–309