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NOTE

Wave-induced abiotic stress shapes phenotypic diversity in a coral reef fish across a geographical cline

C. J. Fulton · S. A. Binning · P. C. Wainwright · D. R. Bellwood

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Abstract While morphological variation across geographical clines has been well documented, it is often unclear whether such changes enhance individual performance to local environments. We examined whether the damselfish *Acanthochromis polyacanthus* display functional changes in swimming phenotype across a 40-km cline in wave-driven water motion on the Great Barrier Reef, Australia. *A. polyacanthus* populations displayed strong intraspecific variation in swimming morphology and performance that matched local levels of water motion: individuals on reefs subject to high water motion displayed higher aspect-ratio fins and faster swimming speeds than conspecifics on sheltered reefs. Remarkably, intraspecific variation within *A. polyacanthus* spanned over half the diversity seen among closely related damselfish species from the same region. We find that local selection driven by wave-induced abiotic stress is an overarching ecological mechanism shaping the inter- and intraspecific locomotor diversity of coral reef fishes.

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C. J. Fulton (✉) · S. A. Binning
ARC Centre of Excellence for Coral Reef Studies, Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia
e-mail: christopher.fulton@anu.edu.au

C. J. Fulton · D. R. Bellwood
ARC Centre of Excellence for Coral Reef Studies, School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia

P. C. Wainwright
Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

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Introduction

Abiotic stress can exert strong pressure on organisms to enhance their performance under local conditions (West-Eberhard 1989; Schluter 2000; Via 2001; Meyers and Bull 2002). When distributed across a geographical cline, therefore, we could expect individuals of a species to display different phenotypes according to local abiotic conditions. While such intraspecific variation has been documented across environmental gradients (West-Eberhard 1989; Schluter 2000; Via 2001; Meyers and Bull 2002), demonstrations of how morphological changes are directly linked to abiotic variations are rare (Koehl 1999; McGuigan et al. 2003; Hoogenboom et al. 2008; Langerhans 2008; Madin et al. 2012; Woods et al. 2012), particularly for marine vertebrates. Here, we explore whether a widespread coral reef fish responds to a cline in environmental stress via intraspecific phenotypic variation.

Wave-induced water motion is a key environmental factor in shallow marine habitats, where the distribution of species across wave gradients can be explained by their relative capacity to perform and persist under wave stress (e.g., Kawamata 1998; Koehl 1999; Siddon and Witman 2003; Madin et al. 2012). In reef fishes, interspecific variations in swimming phenotype have been linked to the distribution of species across wave gradients spanning local to global scales (Bellwood et al. 2002; Fulton et al. 2005). A recurrent theme has arisen among fishes using solely the pectoral fins for propulsion: species with tapered, high aspect-ratio pectoral fins are able to efficiently sustain high swimming speeds and dominate wave-swept shallow habitats; species with rounded, low aspect-ratio fins are better suited to slow speeds and predominate in sheltered habitats (Vogel 1994; Drucker and Lauder 2000; Bellwood et al. 2002; Walker and Westneat 2002; Fulton et al. 2005).

Given the changing nature of wave climates worldwide (Young et al. 2011), the intriguing question is whether coral reef fishes can vary their locomotor phenotype according to local wave energy conditions? We measured the pectoral fin shapes and swimming speeds of *Acanthochromis polyacanthus* distributed across the northern Great Barrier Reef (GBR) to determine the intraspecific phenotypic response of a coral reef fish to a 40-kilometre cline in abiotic stress in the form of wave-induced water motion. We then explored how intraspecific variation in *A. polyacanthus* phenotypes compares to interspecific diversity in fin shape and swimming speed within a related group of damselfish species from the GBR.

Methods

Swimming phenotypes were characterised for *A. polyacanthus* living within the wave-exposed crest habitat of six reef sites (two each at outer-, mid- and inner-shelf positions; Fig. 1a, b) where this species displays similar

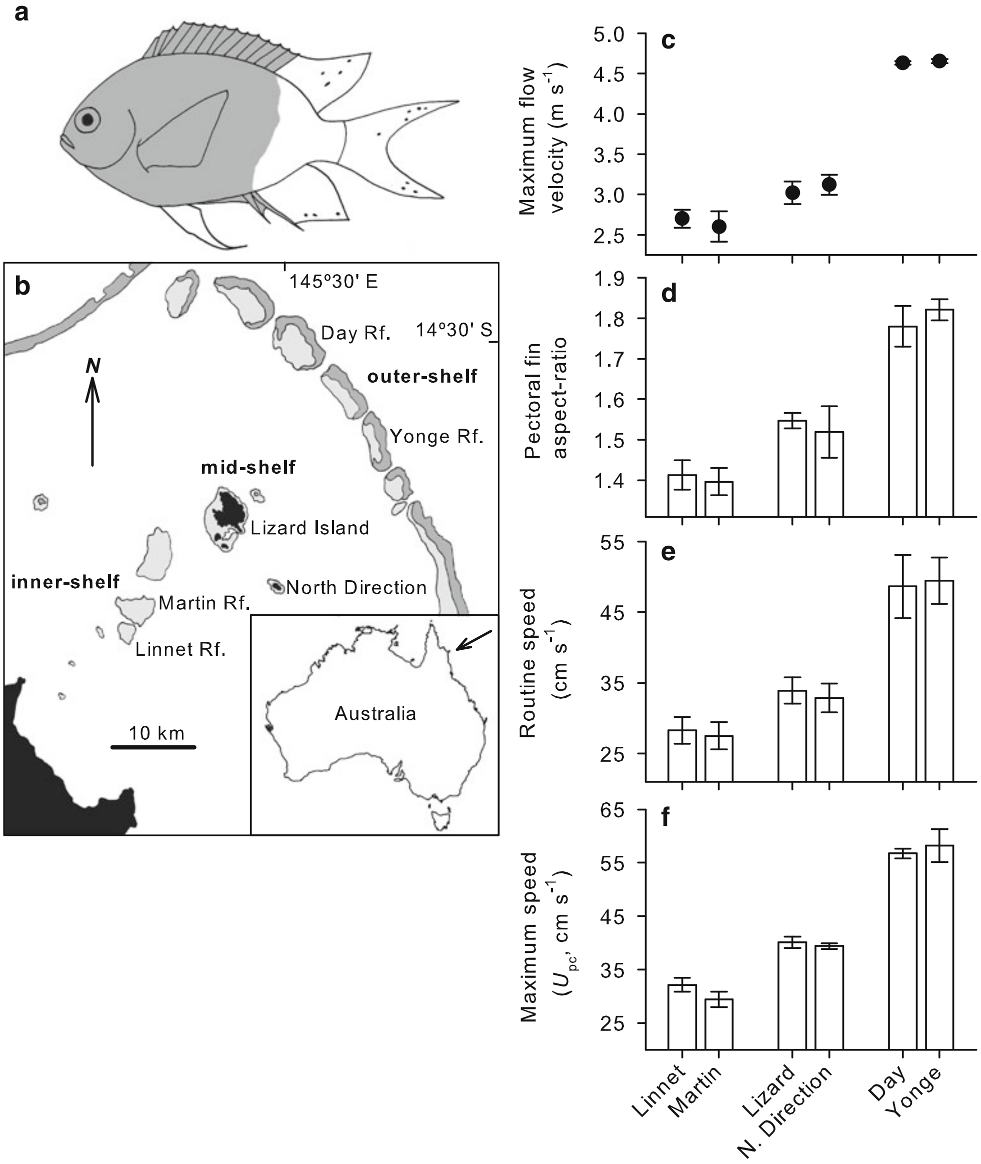

Fig. 1 Congruent variation in wave stress and swimming phenotypes of (**a**) *Acanthochromis polyacanthus* among (**b**) six reef sites distributed at three shelf positions (*inner*, *mid* and *outer*) across the continental shelf of the Great Barrier Reef, Australia. Means (±SE) of (**c**) maximum wave-induced flow velocities, (**d**) pectoral fin aspect-ratio (AR), (**e**) routine speed and (**f**) maximum speed (U_{pc}) for each reef site indicate a functional link between local wave stress and *A. polyacanthus* phenotypes

abundances across the continental shelf of the GBR (Williams 1982). We measured the swimming phenotype of adult *A. polyacanthus* from each site during January 2004 and 2007 in three ways: (1) routine speed, which we measured as the pectoral-swimming speed employed by individual fish swimming undisturbed about the reef, based upon the time (seconds) to travel a measured distance (to nearest 5 cm) between noted reef landmarks following Fulton (2007), $n = 12$ per site; (2) maximum prolonged swimming speed using pectoral-only propulsion (U_{pc}), as measured via a stepwise trial in the laboratory flow tank used by Fulton (2007), $n = 4$ per site, to calculate $U_{pc} = U + [U_i(t/t_i)]$, where U is the penultimate speed using solely the pectoral fins, t is time swum using solely the pectoral fins in the final velocity increment, t_i is the set time of each increment (15 min), and U_i is each velocity increment (0.5 total lengths s^{-1}); and (3) pectoral fin aspect-ratio (AR), calculated as AR = (fin leading edge)^2/fin area, based on measurements (to nearest mm/mm^2) taken from digitised images of an amputated pectoral fin (one per fish, $n = 4$ per site) spread to full extension on a sheet of foam (Fulton et al. 2005). Individuals were of similar total length (cm, mean ± SE) across inner- (12.2 ± 0.2), mid- (12.1 ± 0.2) and outer-shelf (12.7 ± 0.2) sites. Mean U_{pc} was plotted against mean fin AR for the six *A. polyacanthus* populations alongside means for seventeen damselfish species (Pomacentridae) from Lizard Island (Fulton et al. 2005). Swimming phenotypes of *A. polyacanthus* were then mapped against maximum flow speed at each site measured during January 2007 using three dynamometers (Bell and Denny 1994) deployed simultaneously upon the reef within the crest habitat (5 m depth) where *A. polyacanthus* reside at each site across the continental shelf, over an 8-day period during south-easterly winds that gusted above 20 knots daily. A single value of maximum water flow speed was obtained from each dynamometer, which were averaged for each site ($n = 3$) to quantify relative levels of water motion across this geographical cline within the lower part of the water column that *A. polyacanthus* tends to occupy (51 ± 3 cm above the substratum, Heatwole and Fulton 2013). Linear mixed-effect models using the lme function in R (v2.15.0, R Development Core team 2010) were used to compare differences in fin AR, routine speed and U_{pc} among *A. polyacanthus* from different shelf positions (fixed factor) while controlling for site (random factor nested within shelf), after checking for normality and homoscedasticity. Least-squares linear regressions were fitted separately to the relationship between swimming speed and fin AR for *A. polyacanthus* from each site and related damselfish species from Lizard Island using Sigmaplot (version 9, StatSoft Pty Ltd).

Results and discussion

Fin morphology ($F_{2,3} = 67.09$, $p = 0.003$), routine speed ($F_{2,3} = 33.08$, $p = 0.009$) and U_{pc} ($F_{2,3} = 150.62$, $p = 0.001$) differed significantly among *A. polyacanthus* across the continental shelf (Fig. 1, Table 1). Phenotypic variation within *A. polyacanthus* closely mirrored the spatial gradient of wave-induced water motion across the shelf (Fig. 1). We found mid- and outer-shelf sites were subject to 16 and 75 % higher water motion than inner-shelf sites, respectively (Fig. 1c), which matches previously modelled changes in mean wave energy and significant wave height along the same cross-shelf transect (Crossman et al. 2001). Similar increases in the routine swimming speeds (20 and 76 %) and U_{pc} (29 and 87 %) of *A. polyacanthus* were apparent across mid- and outer-shelf reef sites, respectively, relative to inner-shelf conspecifics, with congruent increases in fin AR (Fig. 1). Fin AR was significantly related to swimming speed within *A. polyacanthus* ($F_{1,23} = 108.2$, $p < 0.01$), but markedly steeper than the interspecific relationship for other damselfishes (Fig. 2). Notably, fin shape variation within *A. polyacanthus* (1.33–1.88) spanned over half the interspecific AR range of related species and extended beyond the upper species-level limit (0.81–1.67, Fig. 2).

Marked phenotypic variation among *A. polyacanthus* distributed across this 40 km geographical cline appears to enhance the local performance of individuals on reefs subject to different levels of water motion, mediated by the functional link between changes in fin shape and swimming speed performance (Drucker and Lauder 2000; Bellwood et al. 2002; Walker and Westneat 2002; McGuigan et al. 2003; Fulton et al. 2005; Langerhans 2008). In a general

Table 1 Pairwise contrasts of (**a**) pectoral fin aspect-ratio (AR), (**b**) routine swimming speed and (**c**) maximum prolonged speed among *Acanthochromis polyacanthus* occupying different continental shelf positions (inner-, mid- and outer-shelf) on the northern Great Barrier Reef

Comparison	*t*	*p* value	*R*	Cohen's *d*
(a) Pectoral fin AR				
Inner/mid	3.64	0.0365	0.639	1.66
Mid/outer	7.70	0.0046	0.880	3.71
Outer/inner	11.34	0.0015	0.958	6.67
(b) Routine speed				
Inner/mid	2.04	0.1339	0.386	0.84
Mid/outer	5.83	0.0100	0.708	1.47
Outer/inner	7.81	0.0044	0.593	2.01
(c) Maximum speed				
Inner/mid	5.74	0.0105	0.886	3.82
Mid/outer	11.32	0.0015	0.940	5.49
Outer/inner	17.06	0.0004	0.964	7.28

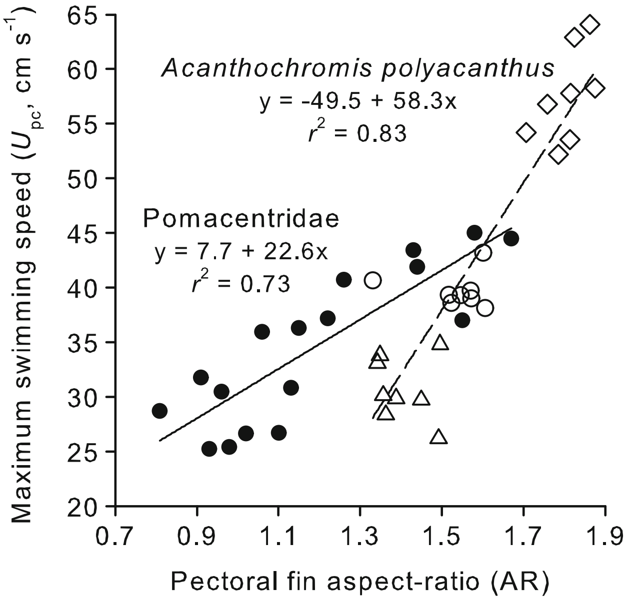

Fig. 2 Relationship between pectoral fin shape (aspect-ratio, AR) and maximum pectoral-powered (U_{pc}) swimming speed performance of *A. polyacanthus* (*dashed line*) from inner- (*triangles*), mid- (*open circles*) and outer-shelf (*diamonds*) reef sites, as compared to related damselfish species (*closed circles*, *solid line*) from the mid-shelf Lizard Island site

phenomenon now seen both among and within species, wave-swept habitats have promoted fishes that use high aspect-ratio pectoral fins and lift-based propulsion to efficiently maintain high swimming speeds (Bellwood et al. 2002; Fulton et al. 2005; Fulton 2010). Fish adopting drag-based propulsion using rounded fins with large surface areas seem better suited to sites of slower flow, because high AR fins are relatively less effective at producing thrust at slow speeds (Vogel 1994; Drucker and Lauder 2000; Bellwood et al. 2002; Walker and Westneat 2002; Fulton et al. 2005).

Intraspecific responses to environmental stress can arise via developmental plasticity, local selection upon successive generations, or a combination of these mechanisms (West-Eberhard 1989; Schluter 2000; Via 2001; Meyers and Bull 2002; Price et al. 2003). With a non-planktonic larval phase and tendency for direct dispersal within natal reefs (Kavanagh 2000), present evidence suggests *A. polyacanthus* exhibits a meta-population structure with strong genetic isolation, following a history of repeated local extinctions and asymmetrical recolonisation of adjacent reefs (Planes et al. 2001; Bay et al. 2008). With strong genetic differentiation among *A. polyacanthus* across all of our reef sites (both among and within shelf positions across the cline; Bay et al. 2008), we find *A. polyacanthus* living on the outer-shelf sites display the same phenotype suited to local levels of high wave stress, but markedly different phenotypes at other shelf positions. As such, this suggests phenotypes suited to the local wave environment may have become established in *A. polyacanthus* through local selection to ambient water motion (McGuigan et al. 2003; Langerhans 2008). However, we cannot rule out the role of plasticity and suggest common-garden experiments to examine the extent plastic development within a single generation could produce this breadth of cross-shelf phenotypic diversity in *A. polyacanthus* (West-Eberhard 1989; Price et al. 2003; Langerhans 2008). Whether similar phenotypic variation exists in other reef fishes would help shed light on this issue, particularly species with a planktonic larval phase that promotes greater dispersal and genetic connectivity among reefs.

Intraspecific variation within *A. polyacanthus* could help reveal how ecological processes may shape the interspecific diversity of coral reef fishes. Phenotypic variation within *A. polyacanthus* was reflective of the interspecific diversity expressed among a sympatric group of related damselfishes. The breadth of fin shape variation exhibited by *A. polyacanthus* across the stress gradient (maximum minus minimum AR = 0.55 and U_{pc} = 37.9 cm s^{-1}) spanned more than half the interspecific variation (AR = 0.86 and U_{pc} = 18.8 cm s^{-1}) displayed by related species occupying the gradient mid-point. Indeed, the pectoral fins of *A. polyacanthus* living on outer-shelf reefs were more similar to the maximum fin ARs of pectoral-swimming fishes from the families Labridae and Acanthuridae (Bellwood et al. 2002; Fulton et al. 2005; Fulton 2010), which display analogous patterns of distribution across wave energy gradients according to their fin shape morphology (Bellwood et al. 2002; Fulton et al. 2005; Fulton 2010). As such, the ecological mechanism of wave stress shaping intraspecific diversity within *A. polyacanthus* could have given rise to the adaptive radiation of fin diversity seen among multiple reef fish families (West-Eberhard 1989; Schluter 2000; Via 2001; Langerhans 2008).

Strong intraspecific responses in *A. polyacanthus* to local wave stress raise questions about how they may respond to changing wave climates. Increasing wave heights and extreme events (Young et al. 2011) are likely to impinge strongly on shallow coral reefs. Given the suggested meta-population dynamics of *A. polyacanthus*, a likely response to increased wave energy could be a series of local extinctions and reinvasions of the most wave-exposed reefs within their range (Planes et al. 2001; Bay et al. 2008). Clarifying the exact response of this species will need further investigation into genetically based intraspecific variation, the developmental stage when different phenotypes are expressed (Fulton 2010), and their capacity for more rapid responses through developmental plasticity within a single generation (West-Eberhard 1989; Price et al. 2003; Langerhans 2008). We note *A. polyacanthus* can be sensitive and flexible in their physiological response to thermal stress (Donelson et al. 2011). Whether such flexibility occurs in other species may determine the likely consequences of predicted changes in climate impinging on shallow marine habitats. For now, we conclude that wave stress exerts strong selection pressure on coral reef fishes to shape patterns of inter- and intraspecific biodiversity across geographical clines.

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