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Wave energy and swimming performance shape coral reef fish assemblages

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Physical factors often have an overriding influence on the distribution patterns of organisms, and can ultimately shape the long-term structure of communities. Although distribution patterns in sessile marine organisms have frequently been attributed to functional characteristics interacting with wave-induced water motion, similar evidence for mobile organisms is lacking. Links between fin morphology and swimming performance were examined in three diverse coral reef fish families from two major evolutionary lineages. Among-habitat variation in morphology and performance was directly compared with quantitative values of wave-induced water motion from seven coral reef habitats of different depth and wave exposure on the Great Barrier Reef. Fin morphology was strongly correlated with both field and experimental swimming speeds in all three families. The range of observed swimming speeds coincided closely with the magnitude of water velocities commonly found on coral reefs. Distribution patterns in all three families displayed highly congruent relationships between fin morphology and wave-induced water motion. Our findings indicate a general functional relationship between fin morphology and swimming performance in labriform-swimming fishes, and provide quantitative evidence that wave energy may directly influence the assemblage structure of coral reef fishes through interactions with morphology and swimming performance.

Keywords: aspect ratio; exposure; flow speed; pectoral fin; ecomorphology

1. INTRODUCTION

Physical factors can play a major role in structuring communities, with the distribution patterns of species often being determined by interactions between their physiology and physical attributes of the environment. In marine systems, factors, such as temperature, salinity and water motion, have been linked to the distribution of species from local to regional biogeographical scales (Beaugrand *et al.* 2002; Bellwood *et al.* 2002; Gray 2002; Chevaldonne & Lejeusne 2003). Physical factors can even override biological interactions such as competition and predation, where physical disturbances from extremes in water temperature or wave energy can cause mass mortality and major shifts in community structure (Dayton 1971; Lassig 1983; Booth & Beretta 2002). Given that physical factors can be potent influences on community structure, it is critically important to determine the underlying functional mechanisms in order to understand the potential ramifications of changes in these physical conditions.

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. Denny 1994). 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 species distributions. Previous examinations of hydrodynamic forces and the functional morphology of sessile organisms have indicated a strong link between wave energy and the functional attributes of algae (Gaylord *et al.* 1994), corals (Dennison & Barnes 1988), echinoderms (Denny & Gaylord 1996) and gastropods (Denny & Blanchette 2000). Although there are strong indications that wave energy may also have a considerable influence on the functional attributes of mobile taxa (Martinez 2001; Fulton & Bellwood 2004), quantitative examinations have generally been limited by the paucity of appropriate information on wave-induced water motion at the relevant spatial scales. In this study we provide a direct comparison between the functional attributes of coral reef fishes, a group of highly mobile organisms, and their distribution patterns across a quantified gradient of wave-induced water motion.

Swimming using solely the pectoral fins for the production of thrust (labriform swimming; Webb 1994) is the dominant swimming mode in coral reef fishes, with up to 65% of taxa using this mode during daily activities (Fulton & Bellwood 2005). Biomechanical analyses have suggested 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 using tapered fins (Blake 1981; Vogel 1994; Walker & Westneat 2002). This morphological diversity has been linked to differences in swimming performance among taxa. 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 (Drucker & Lauder 2000; Walker & Westneat 2000; Wainwright *et al.* 2002).

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Table 1. Range of field and experimental speeds observed in each of three reef fish families, with the number of species, average total length (TL), and correlations (*r*) between pectoral fin morphology (aspect ratio) and each of the swimming speed measures indicated.
(All correlations were highly significant ($p < 0.01$).)

	species *n*	mean TL (cm)	minimum–maximum (cm s^{-1})	minimum–maximum (TL s^{-1})	*r*
(*a*) 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
(*b*) 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
(*c*) 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

Consequently, swimming performance appears to be closely linked with the pectoral fin morphology of labriform-swimming fishes (Wainwright *et al.* 2002; Walker & Westneat 2002).

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 in both tropical and temperate systems (Bellwood & Wainwright 2001; Fulton & Bellwood 2004). These studies hypothesized that such patterns may be due to higher water velocities in wave-swept habitats requiring resident species to sustain higher swimming speeds to achieve daily activities. While this seems promising, such a hypothesis has yet to be examined for the majority of reef fishes which use labriform propulsion, and tested against a quantitative gradient of wave-induced water motion. Therefore, we explore the relationship between fin shape and swimming performance, both in the field and laboratory, for three diverse families of labriform-swimming fishes: the Acanthuridae, Labridae and Pomacentridae. These three families 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). We compare these functional attributes with recently published information on wave-induced water motion in coral reef habitats (Fulton & Bellwood 2005) to directly evaluate the extent to which wave energy and swimming performance shape the functional structure of coral reef fish assemblages.

2. MATERIAL AND METHODS

(a) *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) tend to use a labriform gait during locomotion (Fulton & Bellwood 2005). 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 1 h 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 v.4.0.2 (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 three adult individuals for each species recorded 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 fishes as they swam undisturbed on the reef in an approximately linear path; if during an observation an individual was seen to deviate markedly from a constant velocity or straight swimming path, the trial was discontinued. The beginning and end of each trial was marked by a stopwatch as the fishes travelled past noted landmarks on the reef. Immediately after each trial the distance between these landmarks 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 minimize the effects of water motion on swimming speeds. A minimum of 10 individual observations was taken for each species, with the average travel distance and duration of each trial being 248 cm and 7.2 s, respectively.

Experimental speeds were measured in a 194 l re-circulating flow tank of a design following Vogel & LaBarbera (1978). Each incremental velocity trial measured the maximum prolonged swimming speed reached using solely the pectoral fins for locomotion (U_{pc}), following the protocols of Walker & Westneat (2002). This was repeated for a minimum of three individuals per species, with the average trial duration being 138 min. Of the total number of species censused in each family, over 75% were included in these field and experimental performance trials, with an overall total of 1293 field and 194 experimental trials (table 1). 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 experimental speed residuals were compared by Pearson's correlation and least-squares linear regression using the 44 species for which both measures were taken.

Relationships between swimming speed residual and pectoral AR were then examined for each family using Pearson's correlations and linear regressions.

(b) *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. Censuses were made at 3 m depth within each of two sites at four reef locations of different exposure to prevailing South East winds and incident wave energy (exposed, oblique, lagoon and sheltered). Within exposed sites, censuses were also conducted within several habitat zones of different depth: base (15 m), slope (9 m), crest (3 m) and flat (2 m). All fishes within the three families were identified to species and counted within $50\times5\ \mathrm{m}^2$ belt-transects, repeated three times within each habitat at each site. These habitats and sites were chosen to maximize the range of wave-induced water motion encountered in coral reef habitats of both similar and different depths (Fulton & Bellwood 2005). Differences in the mean fin ARs among habitats were examined for each family by calculating the average AR for all individuals of that family within each habitat at each site (based on three transects from each site). Relationships between mean AR and water motion values for the exact same habitats and sites were examined for each family using Pearson's correlation and linear least-squares regressions. Water motion values were based on previously published estimates taken from the calibrated dissolution of plaster forms in these locations during a 24 h period of neap tidal conditions (Fulton & Bellwood 2005); while relatively coarse in resolution, this method provides a time-averaged estimate of net flow speeds experienced under the low to moderately turbulent conditions in these locations (Dennison & Barnes 1988; Kawamata 2001).

3. RESULTS

(a) *Fin morphology and swimming performance*

Pectoral fin shape varied considerably among species in all three families, with average ARs 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 1). Field and experimental speeds were strongly correlated and exhibited an almost isometric linear relationship (figure 1); direct comparisons between absolute field and experimental speeds (in units of $\mathrm{cm\ s^{-1}}$) revealed that each species displayed a field speed which was 83±4% (average ±1 s.e.) of the speed attained under experimental conditions. Strong correlations were also found between fin AR and swimming speed (table 1), with all three families displaying a similar linear relationship between pectoral fin AR and swimming speed (figure 2). Under both field and experimental conditions, species with higher AR fins attained faster swimming speeds (figure 2).

(b) *Spatial variation in fish assemblages and water motion*

The distribution of these functional characteristics among habitats of different water motion was highly congruent among families (figure 3). Strong positive relationships between the mean fin AR of individuals and the water velocity of habitats were displayed in all three families (figure 3). In particular, crest habitats from different wave exposures with varying flow velocities displayed a corresponding variation in mean fin ARs (figure 3). Notably, the range of actual swimming speeds ($\mathrm{cm\ s^{-1}}$) observed in the swimming performance trials appeared to span the range of flow velocities in the habitats examined (table 1, figure 3).

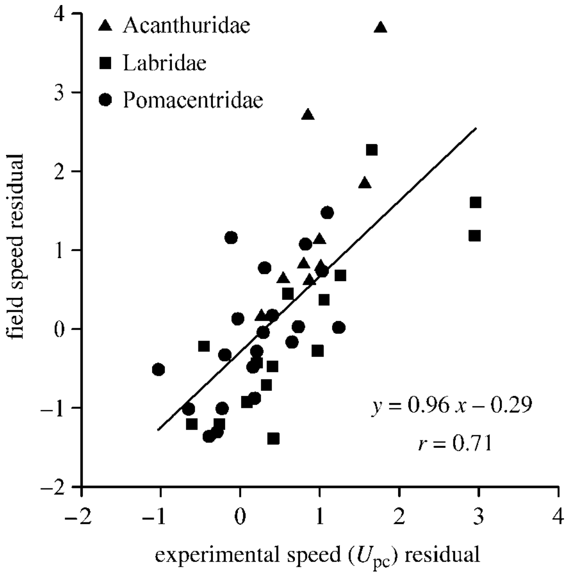

Figure 1. Relationship between field and experimental swimming speed in 44 species of labriform-swimming fishes. Both axes have been corrected for body size; high positive residuals represent high speeds for a given size. Note that the linear regression is close to isometric (slope = 1.0).

4. DISCUSSION

Relationships between incident wave energy and the structure of reef fish assemblages are well documented (e.g. Talbot 1965; Williams 1991; Friedlander *et al.* 2003). Recent studies on wrasses have indicated that swimming morphology and performance may play a major role in shaping distribution patterns across a range of wave exposures (Bellwood *et al.* 2002; Fulton & Bellwood 2004). We expand on these findings considerably, demonstrating that the functional relationship between fin morphology and swimming performance is a general phenomenon among labriform-swimming fishes. Furthermore, for the first time, we make a direct comparison between the distribution of these swimming abilities and quantitative values of water movement across a range of coral reef habitats and exposures. Our quantitative evidence suggests that wave energy may directly influence the structure of coral reef fish assemblages through interactions between wave-induced water motion and differences in swimming performance.

Fin morphology appears to be a powerful predictor of at least one aspect of locomotor performance in labriform-swimming fishes. We found that all three families 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,

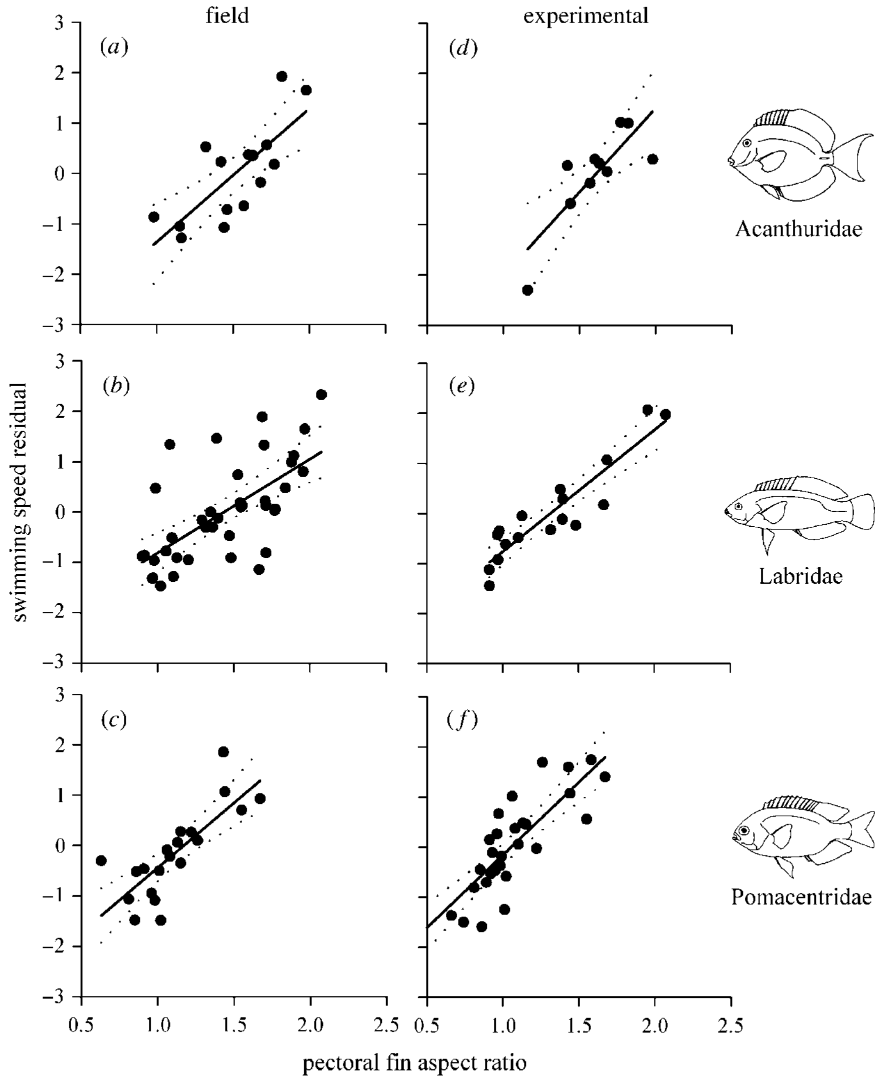

Figure 2. Pectoral fin morphology and swimming performance in the field (*a*, *b*, *c*) and under experimental conditions (*d*, *e*, *f*) for three reef fish families (the Acanthuridae, Labridae and Pomacentridae, respectively). Experimental speeds are the maximum speeds reached using pectoral fins only (U_{pc}). Vertical axes have been corrected for body size; high positive values represent high speeds for a given size. The range of actual speeds and correlations are given in table 1. Dotted lines indicate 95% confidence limits.

labriform-swimming fishes with tapered fins (high AR) attained faster swimming speeds for their size. Notably, the average field speeds displayed by each species were around 83% of their prolonged swimming speed attained under experimental conditions, indicating that labriform-swimming fishes are swimming close to their maximal speed during daily swimming activities. Biomechanical analyses suggest that the critical mechanism underlying the relationship between fin shape and performance is the differential use of thrust; fishes with tapered pectoral fins predominantly use lift-based flapping, which 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). 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-swimming fishes owing to fundamental biomechanical constraints and trade-offs, regardless of taxonomy or trophic biology.

Ecological arrangement of these functional characteristics along a gradient of water motion was also highly congruent among families. Positive relationships between wave-induced water motion and pectoral fin AR 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 2005) displayed marked differences in the mean fin AR of individuals.

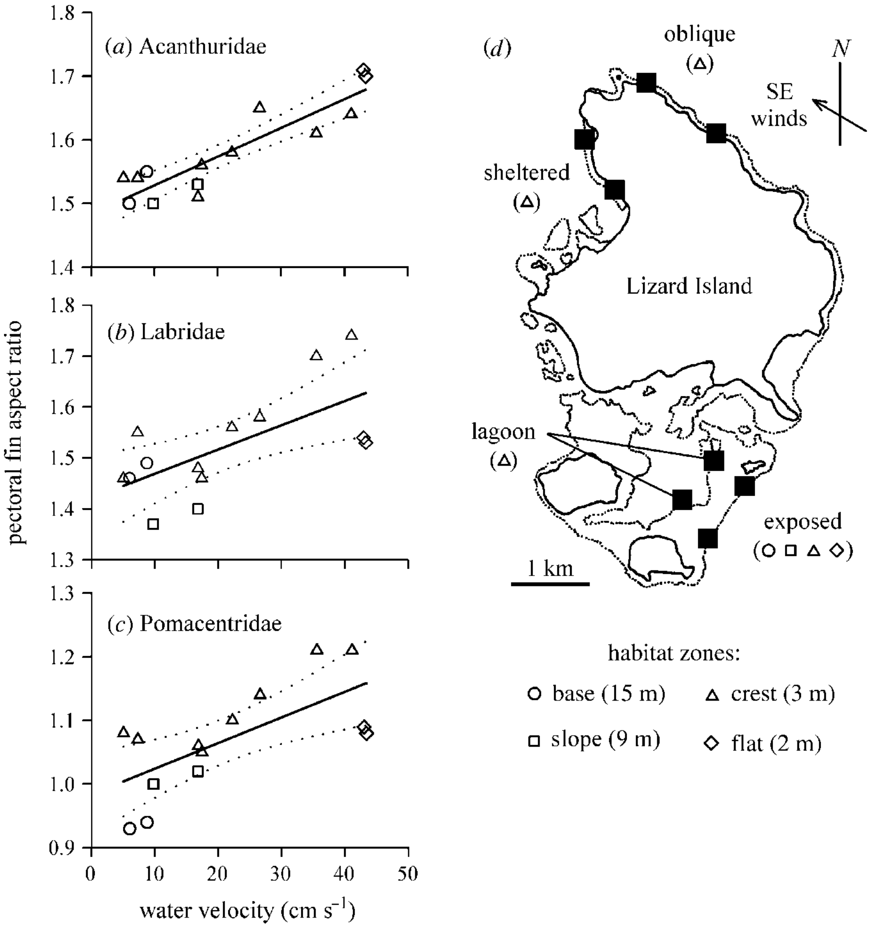

Figure 3. Relationship between pectoral fin aspect ratio and net water velocity (after Fulton & Bellwood 2005) for each of the families (*a*) Acanthuridae ($r=0.901$, $p<0.01$), (*b*) Labridae ($r=0.656$, $p<0.05$) and (*c*) Pomacentridae ($r=0.689$, $p<0.01$). Fin aspect ratio values were calculated as the average of all individuals of that family within each habitat. Dotted lines indicate 95% confidence limits. (*d*) Location of censused habitats among four different exposures around Lizard Island (filled squares), with the different habitat zones indicated for each in parentheses.

Such congruence in these relationships 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 & Bellwood 2005). Indeed, average ARs of all individuals in each habitat indicated that taxa with a fin morphology that may facilitate efficient maintenance of high sustained speeds (tapered fins of high AR; Walker & Westneat 2002) were the dominant occupants of locations with high water flow velocities. Moreover, the range of actual swimming speeds displayed in each of the three families appeared to span the range of water velocity 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}; Fulton & Bellwood 2005). 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.

5. CONCLUSIONS

Overall, fin morphology provides a powerful tool for understanding ecomorphological relationships between diverse reef fish assemblages and the physical characteristics of reefs. Given the applicability of this relationship 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 fishes found on coral reefs. Ultimately, wave-induced water motion appears to have interacted in both ecological and evolutionary terms with the locomotor abilities of fishes to provide an underlying theme in coral reef ecosystems: wave energy and swimming performance shape coral reef fish assemblages.

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