

SEA URCHIN BIOMECHANICS: MORPHOLOGICAL AND BEHAVIORAL ADAPTATIONS TO HEAVY FLOW CONDITIONS IN MO'OREA, FRENCH POLYNESIA

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Abstract. This study investigates the biomechanics, behavior, and distribution of urchin species in Mo'orea, French Polynesia to understand how they withstand hydrodynamic forces. Field surveys examined the flow distribution of four species: *E. mathaei*, *Tripneustes gratilla*, *Diadema savignyi* and *Echinotrix calamaris*. Flow tests were conducted on two *Echinometra mathaei* subspecies to measure spine angle under no flow and heavy flow conditions. Short spine urchin species were found in significantly higher flows than were long spine urchin species. Experimental findings revealed that *E. mathaei* type B temporarily adopts a more streamlined shape in response to increasing flow velocity, while *E. mathaei* type A does not. Understanding the streamlining behavior and other strategies for surviving hydrodynamic conditions is necessary in order to examine these organisms' role in their environment.

Key words: *biomechanics; Echinometra; streamlining; Mo'orea, French Polynesia*

INTRODUCTION

Hydrodynamic fluctuation often favors morphological tradeoffs and can dictate organism behavior (Denny 1987). Organisms that live in highly variable aquatic environments frequently depend on the flow of water to provide them with food or oxygen, yet at the same time are vulnerable to powerful hydrodynamic forces. Hydrodynamic forces manifest, in part, as drag. Drag is created by a decrease in pressure on the downstream side of an organism and an increase on the upstream side (Koehl 1984). This threatens to dislodge benthic organisms, which makes them more vulnerable to predation (Stewart and Britton-Simmons 2011). The amount of drag experienced by an organism depends on characteristics of the fluid flow and on that organism's morphology, meaning taxa exposed to identical hydrodynamic force may experience unique drag (Koehl 1984).

Benthic organisms employ a variety of strategies to remain sedentary despite highly variable hydrodynamic forces. Some taxa aggregate into groups to reduce the hydraulic stress experienced by each individual (Koehl 1984, Engel 1992). Another tactic exhibited by some organisms is having a "flow-dependent shape" (Vogel 1984). This is when an organism adjusts its structure to become more or less streamlined depending on the environmental conditions. By preserving the ability to become less streamlined when

conditions are calm, organisms can benefit from multiple morphologies. An example of this is the red sea urchin *Strongylocentrotus franciscanus*, which moves its spines into a streamlined position during periods of heavy flow (Stewart and Britton-Simmons 2011). Alternatively, evidence suggests that the presence of constant, heavy flow has influenced another urchin species to adapt a more permanent morphology. In Hawaii, the truncation and loss of spines in *Colobocentrotus atratus* has been linked to a life history in turbulent, wave swept environments (Denny 1996).

In the absence of hydrodynamic stress, urchins' ability to obtain food and deter predators is maximized by having long spines dispersed evenly at all angles. This is because spines protect against predators and entangle drifting algae, their food source. However, in quickly moving water spines can be a liability because they increase the surface area of the organism that is perpendicular to the flow direction. This causes the animal to experience a greater drag force. Therefore there is a tradeoff between ease of obtaining food and deterring predators, and an urchin's susceptibility to dislodgement.

This study investigated the biomechanics, behavior, and distribution of urchin species in Mo'orea, French Polynesia, to understand how morphology and behavior affect the ability to withstand hydrodynamic forces. *E. mathaei* was exposed to increasing current velocity in a laboratory flume to test two hypotheses: first,

that individuals streamline their shape by reducing spine angles when exposed to heavy flow conditions, and second, that a decrease in the ratio of spine length to central body size will increase the velocity threshold necessary to dislodge the organism.

METHODS

Study organisms

Laboratory experiments were conducted on *E. mathaei*. This relatively small species, weighing approximately 10-20g, is easy to handle and abundant in French Polynesia. Two subspecies of *E. mathaei* are recognized on Mo'orea, type A and type B (Collisson 1995). Past studies have revealed zonation between these subspecies, but have been unable to identify a cause (Collisson 1995, Zizka 2011). Type A, which is identified by distinct white tips on its spines, is found primarily in the lagoon and fringing reef, while type B, which solid in color, is confined to the barrier reef (Collisson 1995, Zizka 2011).

Considering Koehl's (1977) explanation that tall, thin structures experience more stress than do short, wide shapes, a representative species from four genera were selected that represent a variety of spine morphologies. *E. mathaei* has short, thick spines; *Diadema savignyi* has long, thin spines; *Echinotrix calamaris* has both short, thin and long, thick spines; and *Tripneustes gratilla* has short, thin spines.

Study sites

Research was conducted from the Gump Field Station in Mo'orea, French Polynesia, during October and November of 2012 (Fig. 1). Field surveys were conducted at two sites: Temae Public Beach and the Gump Field Station. These were the only two locations around Mo'orea where this study found that all four species were present. These sites represented two extremes with regard to flow regimes found around the island's shallow lagoon habitats. At the Temae Public Beach, the narrow lagoon generates strong tidal currents. The Gump station is located on the interior of Cook's Bay. Protected from the open ocean, this site is calm and experiences weaker average flows.

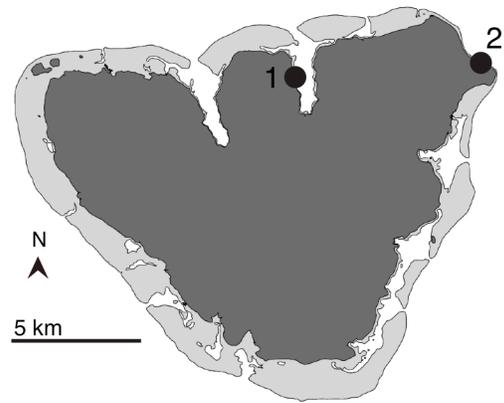


FIG. 1. Study sites on Mo'orea, French Polynesia. 1) Gump Station: 17°29'28.20"S, 149°49'33.15"W. 2) Temae Public Beach: 17°29.839"S, 149°45.251"W.

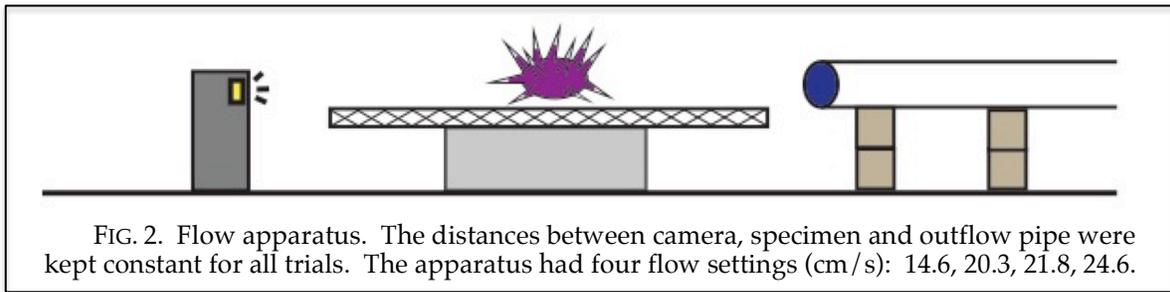
Flow distribution

Surveys were conducted at the Temae Public Beach and outside the Gump station to determine the range of flow conditions generally experienced by *E. mathaei*, *T. gratilla*, *D. savignyi* and *E. calamaris*. Plaster of Paris clod cards were used to measure relative flow velocity in the field (Jokiel and Morrissey 1993). These dissolve in water at a constant rate, so measuring the weight loss of multiple clod cards provides relative values for average flow velocity at each card location. Clod cards were positioned adjacent to 10-15 individuals of each species at each site and left for three days. Student's t-tests were conducted to reveal differences in the average flow experienced by each species within a site. All data were analyzed using the statistical program JMP.10 SAS Institute Inc.2012.

Spine angle

Controlled laboratory experiments were conducted using a gravity-fed flow apparatus (Fig. 2). Urchins were placed on a plexiglass test plate covered in wire mesh and allowed time to acclimate before experiments. Organisms were considered acclimated once they had flattened their basal spines and began moving around on the test plate.

The flow apparatus was used to determine if *E. mathaei* individuals change their spine angle when exposed to flow. Each test subject was observed first under zero flow conditions. Flow was then introduced, and tests ran for two minutes or until the organism moved to the edge of the test plate.



Analyses were conducted on photographs extracted from video taken of flow trials. Angle measurements were taken of the thirteen longest spines with respect to horizontal (Fig. 3).

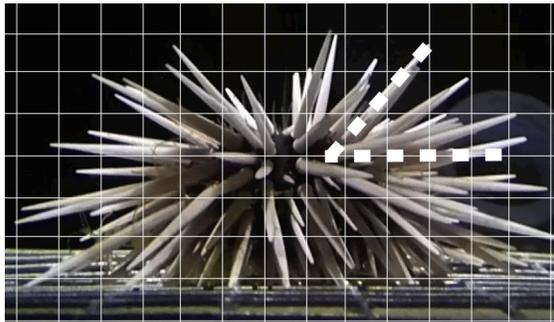


FIG. 3. Photograph of *E. mathaei* during no flow conditions. A sample angle measurement is highlighted in white.

A matched pairs analysis was conducted to determine if introduction of flow prompted a significant change in spine angle.

Trim tests

Experiments were conducted to determine if the ratio of spine length to body size affects an organism's ability to withstand flow. 26 *E. mathaei* individuals were exposed to increasing flow, and the velocity at which they began to slip and get dislodged from the substrate was recorded as the dislodgement threshold for that organism. A high dislodgement threshold corresponded to an individual's ability to withstand heavy flow.

Test subjects were then divided into two groups: control and trim. Individuals in the trim group then had their spines trimmed 7-12mm. To replicate this stress in the control group, the tips of their spines were clipped without impacting length. Following treatment, all organisms were given one hour to rest before the dislodgement flow test was repeated. Data were analyzed using a matched pairs analysis.

RESULTS

Flow distribution

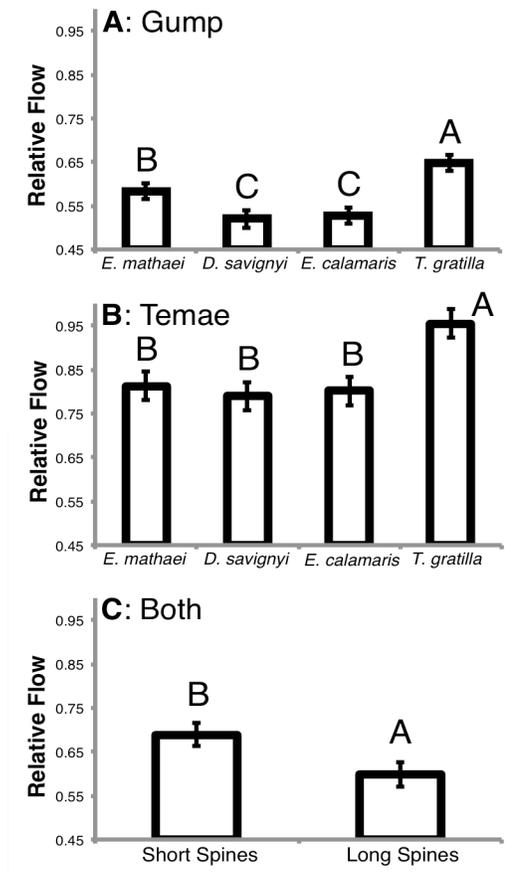


FIG. 4. A) Relative Flow Distribution: Gump (N=21). *T. gratilla* was found in highest flows, *E. mathaei* in intermediate flows, and *D. savignyi* and *E. calamaris* in the lowest flows. B) Relative Flow Distribution: Temae (N=8). *T. gratilla* was consistently found in the highest flows at Temae. C) Spine Length Flow Distribution: averaged between sites. Combining flow distribution data into short and long spine categories revealed that short spine urchins experience higher average flow. Within each graph, columns connected by different letters are statistically different from one another, and error bars reflect one standard error. For statistical parameters, see Table 1; Appendix A.

Flow distribution surveys conducted at Gump and Temae tested the relationship between species' spine morphology and distribution with respect to flow. At the Gump field site, surveys revealed that *T. gratilla* experienced the highest flow and *E. mathaei*, the second highest. *D. savignyi* and *E. calamaris* were found in the lowest flow microhabitats. No patterns for flow distribution were observed at Temae. Grouping species into two categories by spine length revealed short spine urchins experience significantly higher flows (chart of statistical parameters is included in Appendix A).

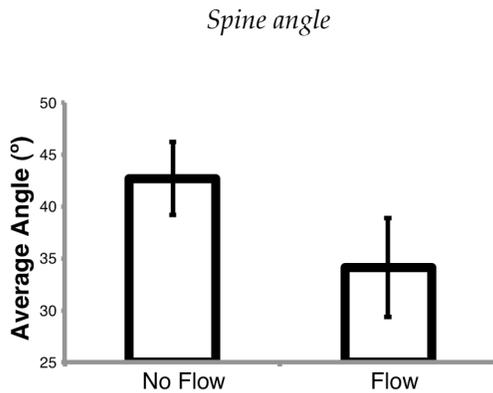


FIG. 5. Effects of flow on *E. mathaei* average spine angle (N=10). Error bars reflect one standard error.

E. mathaei's average spine angle was measured under flow and no flow conditions to determine if individuals streamline their shape. Average *E. mathaei* spine angle

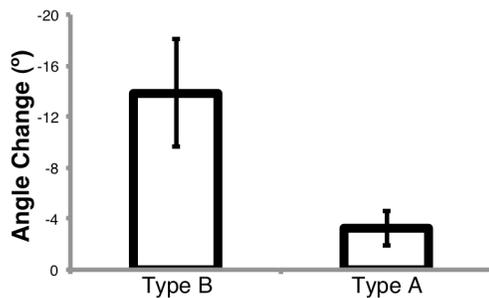


FIG. 6. Streamlining response in *E. mathaei* subspecies type A and type B (N=5). Error bars reflect one standard error.

decreased 8.6 degrees when organisms were exposed to flowing water. A matched pairs analysis determined that spine angle was significantly lower under flow conditions ($T=-3.131$, $DF=9$, $P=0.0121$).

When exposed to flow, type B significantly decreased spine angle ($T=-3.28$, $DF=4$, $p=0.0304$), while type A exhibited no significant response.

Trim tests

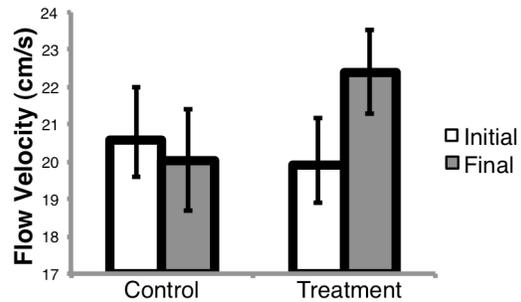


FIG. 7. Effect of spine length on *E. mathaei* dislodgement threshold (N=13). White columns indicate initial dislodgement threshold, and grey columns reflect dislodgement threshold following spine trimming or clipping. There were no statistically significant results. Error bars reflect one standard error.

Trim experiments tested whether decreasing spine length allowed *E. mathaei* individuals to withstand stronger flows, also known as increasing their dislodgement threshold. Average dislodgement threshold for the control group decreased by 0.6cm/s following the control treatment ($T=-3.88$, $DF=12$, $P=0.648$). Dislodgement threshold for the treatment group increased from an average of 19.9cm/s before the treatment to 22.4cm/s after. This difference was nearly significant ($T=1.70$, $DF=12$, $P=0.057$).

DISCUSSION

Flow distribution

Field surveys revealed that zonation of spine morphology with respect to average flow varies among sites. Zonation at the low flow site coincided with expectations based on Koehl's (1977) explanation that tall, thin shapes experience more stress than do short, wide shapes. *E. mathaei*, whose spines are short and thick, was found in stronger average

flows at Gump than did *D. savignyi*, whose spines are long and thin. At Temae, however, there was no such pattern. The overall flow at this site is much higher than at Gump, and even causes even seemingly protected microhabitats to experience turbulence. In this stronger flow regime, individuals that are particularly vulnerable may have already been selected against.

To understand and predict morphology distribution, ecological factors must also be taken into account. These principles were unable to explain spine thickness, but across both survey sites, the short spines were distributed in significantly higher flows than long spines.

Zonation revealed in the field surveys of spine morphologies by flow strength warrants further investigation. Until differences in life history have been accounted for, the observed patterns cannot be attributed to spine morphology alone.

Spine angle

Flow experiments confirmed that *E. mathaei* adopts a more streamlined shape in response to increasing flow velocity. Like the streamlining behavior in *S. franciscanus* demonstrated by Stewart and Britton-Simmons (2011), small variation in flow velocity did prompt *E. mathaei* to significantly alter the angle of its spines.

Further examination of test subjects revealed that equal numbers of *E. mathaei* subspecies A and subspecies B were tested, and only type B exhibited a streamlining response.

Within *E. mathaei*, streamlining in response to flow explains zonation between two subspecies. *E.m.* type B responded to flow with a dramatic angle change, whereas *E.m.* type A did not respond at all. Past researchers have quantified the zonation between types A and B, with B found primarily on the barrier reef and A found in the lagoon and fringing reef (Zizka 2011, Collisson 1995). Researchers have struggled to explain this pattern on Mo'orea, and while they have often mentioned the drastically different flow regimes between these regions, no study has thoroughly investigated flow as the factor responsible for the zonation (Zizka 2011, Collisson 1995). Given the dramatic streamlining response exhibited by *E.m.* type B, and the absence of any response by *E.m.* type A, I propose that their observed zonation around Mo'orea is maintained by

differential ability to withstand hydrodynamic conditions.

Future research should investigate the differences between organisms found on both the barrier and fringing reef. Such different disturbance regimes between these sites have likely prompted the development of habitat-specific behaviors in other organisms as well.

Trim tests

Data from the *E. mathaei* spine length manipulation suggest that decreased spine length enables individuals to withstand stronger flows. Although the results were not significant, analysis was conducted using conservative dislodgement threshold values that likely do not accurately depict the full effect from the trim treatment. In some cases, urchins' dislodgement thresholds exceeded the maximum flow that could be generated in the laboratory setup (0.25L/s), so those exact values remain unknown. This occurred most commonly when urchins were retested after their spines had been trimmed. Excluding these data would have selectively eliminated the most dramatic treatment effects, thereby biasing results. To be included in statistical analyses, they were therefore assigned a dislodgement threshold of 0.26L/s, the most conservative possible value. This yielded a compelling trend and results that were nearly significant. The true dislodgement thresholds were probably greater, and if measured precisely would likely have generated significant results.

Future studies should examine the relationship between spine length and dislodgement threshold across species.

Conclusions

E. mathaei type B's ability to inhabit a more physically stressful environment than its type A counterpart is explained by type B's response to sudden increases in flow. Streamlining is an effective strategy that has allowed organisms to thrive in challenging hydrodynamic conditions. *E. mathaei*'s abundance across flow regimes provides excellent opportunities to examine relationships between morphology and behavioral response to strong physical strain. Echinoidea is a morphologically diverse class and serves as an excellent model for studying multiple strategies employed by benthic organisms to remain sedentary despite variable hydrodynamic forces.

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APPENDIX A

A: Gump	B: Temae	C: Both
T=1.990, DF=80 <i>T. gratilla</i> - <i>D. savignyi</i> : P<0.0001 <i>T. gratilla</i> - <i>E. calamaris</i> : P<0.0001 <i>T. gratilla</i> - <i>E.mathaei</i> : P=0.0161 <i>E. mathaei</i> - <i>D. savignyi</i> : P=0.0195 <i>E. mathaei</i> - <i>E. calamaris</i> : P=0.0376	T=2.048, DF=28 <i>T. gratilla</i> - <i>D. savignyi</i> : P=0.0011 <i>T. gratilla</i> - <i>E. calamaris</i> : P=0.0022 <i>T. gratilla</i> - <i>E.mathaei</i> : P=0.0041	T=1.981, DF=114 P=0.0016

TABLE 1. Significant T-test values for FIG. 4.