

Mechanisms, performance and ecological implications of the body and fin use in herbivorous fish feeding

Tal Perevolotsky, under supervision of Prof. Roi Holzman, Tel Aviv University

Herbivorous fish play a crucial ecological role in maintaining coral reef ecosystems, and exemplify how species-specific feeding behaviors can have an immense environmental impact. In the reef, corals compete with fast-growing algae for space, light, and nutrients. Through grazing, herbivores protect the reef from algal overgrowth and facilitate coral settlement, growth, and reproduction, thus boosting reef resilience and resistance to environmental disturbances (1,2). Exclusion of herbivores from the reef may result in rapid coral degradation, potentially leading to a phase shift, where the reef becomes dominantly covered by algae rather than corals (3,4,5). Owing to their ecological importance, many studies have focused on herbivorous fish feeding in the hopes to better understand, quantify, and predict its environmental effects. And yet, the functional mechanisms governing herbivorous feeding remain largely unresolved. Specifically, the functional morphology of the teeth and jaws is considered the only mechanisms underlying feeding success (6,7).

During my M.Sc. studies, I have discovered that the feeding process of herbivorous fish is far more complex than previously conceived, involving precise body control and fin movements. I demonstrated how browsing herbivores, feeding on protruding macroalgae, use the movement of their body, head and pectoral fins to generate a pull force that tears the algae, and revealed that it is in fact this force that determines the biomass of algae removed during feeding (8 [Perevolotsky et al 2020](#)). Hence, it is **body movements, rather than those of the mouth, that determine feeding success in herbivorous browsing fish.** This newly discovered functional axis has raised many questions regarding the functional morphology, biomechanics, and evolution of herbivorous reef fish, and has made evident that the mechanisms underlying herbivorous feeding are far from being resolved.

My research presents a new approach to studying herbivorous fish biting, arguing that the force exerted on the substrate stands at the base of herbivory, determining both performance and function, and that body kinematics could shed much light on herbivorous function in coral reefs.

I am currently focusing on the following questions:

Developing a biomechanical approach to functional classification of fish herbivory - Coral reef herbivores are an extremely heterogenous guild, and as such are usually categorized into functional groups, defined as a group of species performing a similar function and retaining the same role in ecosystem processes (2,9). The main drawback of the prevailing classification is that it relies greatly on the fish's realized niche, and accounts only for functional morphology of the feeding apparatus. In my research I use a novel *in-situ* underwater system (Fig 1) to provide a new perspective to herbivore classification. Based on previous analyses (Fig 2) and current observations I suggest that herbivore functional diversity is driven by two

biomechanical axes: **1) The direction of the force fish exert on the substrate and prey during feeding and 2) Gape cycle restriction during feeding.** Different forces, in different magnitudes and direction, are required in order to break, tear, or scrape food from the substrate. Producing such force, regardless of the direction (push or pull), cannot be achieved via mouth kinematics and requires movements of the body and fins in order to accelerate towards or away from the substrate, or to maintain constant contact with it. Fish relying on different forces during feeding therefore require a different set of kinematics (and thus morphologies), executed differently through the biting cycle. Examining the timing, magnitude, and direction of feeding kinematics provides insights to current and potential diets and functions and therefore provides a much more informative classification for herbivory. Observations and analyses of feeding events of a range species show two distinct modes of biting (Fig 3). **Single-bite** species exhibit one complete bite cycle that includes opening and closing their mouth and performing a set of relevant body kinematics. In this mode fish break contact with the substrate in every cycle, before returning for the sequential bite (see [video](#)). Single-biters usually display reduced cranial mobility, and exert a strong perpendicular force (either push or pull). **Multi-bite** species perform multiple mouth opening and closing cycles during feeding, remain in constant contact with the substrate, and display body kinematics that facilitate this contact. This mode generates a weak push on the substrate but the continuous contact enables highly efficient scraping of algal material. A rigorous examination of body kinematics, gape cycle, and force exerted while feeding will provide a better understanding and more accurate assessment of herbivore ecological affiliation and functional roles in coral reefs.

Examining the relationship between functional flexibility and trophic niche – Herbivore functional diversity is one of the major contributors to coral reef resilience (10), and fish with different functional roles are many

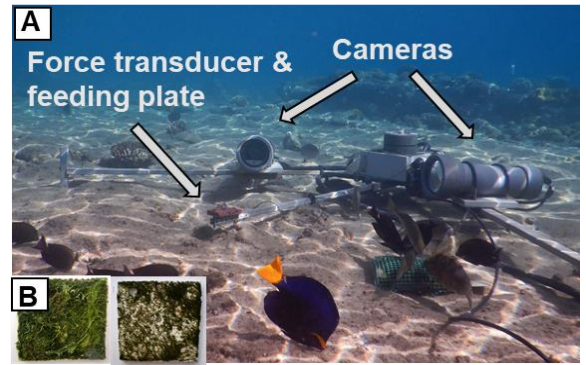


Figure 1: A new system to examine in-situ herbivore feeding performance. (A) Two high-speed cameras provide 3D kinematics and a force transducer records forces exerted by fish feeding under natural conditions. (B) Specially grown feeding plates provide biomass removed during feeding, quantifying feeding success

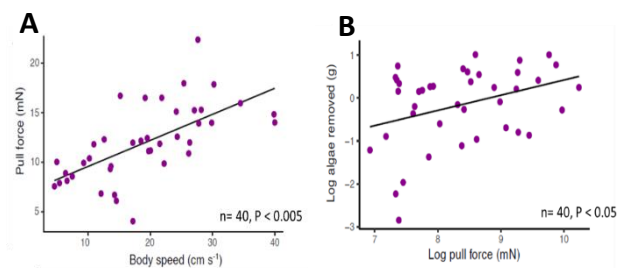


Figure 2: Fin and body kinematics determine feeding success in browsing herbivorous fish: (A) during feeding, *Zebrasoma xanthurum* and *Z. desjardinii* display a forward motion of the pectoral fins and a fast lateral movement of the head (head-flick), increasing the speed at which fish back away from the substrate, at the end of the bite. This speed is significantly and positively correlated with the pull force exerted on the substrate during feeding. (B) The pull force exerted on the substrate, in turn, is positively and significantly correlated with the amount of algae removed (Perevolotsky et al. 2020).



Figure 3: Herbivore functional diversity quantified in the system. Acanthurids (left to right: *Z. xanthurum*, *Z. desjardinii*, *A. nigrofuscus*) tear algae using a pull force and perform a single cycle of gape opening and body kinematics in a feeding event. These fish are therefore categorized as **Single-bite pullers**. Other species (left to right: *S. rivulatus*, *K. vaigiensis*) use a push force to scrape the substrate and perform multiple gape cycles and kinematics that retain their contact with the substrate. They would be categorized as **Multi-bite pushers**.

times considered to have a complementary effect, where each group removes algae in their relevant niche and form, and thus maintaining the algae-coral balance under control (11). I suggest that the variation in feeding kinematics, and associated force exerted on the substrate, can be used as a way of assessing functional niche breadth and potential redundancy. Functional flexibility is the extent to which fish feeding behavior and kinematics changes in response to change in external condition such as the substrate or algae they feed upon. In my research I showed that acanthurids display highly stereotypic feeding kinematics that showed low variation regardless of the properties of the substrate (8, Fig 4A). This means that the trophic niche of acanthurids is restricted to only algae that can be attained by pulling. Siganids on the other hand were observed to have very high feeding flexibility, corresponding to prey demands. When feeding on turf algae or gel, fish display a multi-bite feeding mode, pushing against the substrate and effectively scraping algae. When presented with large macroalgae fish changed their feeding repertoire to that of single-bite pullers, displaying body kinematics that generate a pull force, facilitating algal tear. This kinematic flexibility may be required in generalist herbivores, for it provides access to a large variety of prey types. In my research I examine the relationship between feeding flexibility, which indicates potential trophic niche, and dietary preferences, which indicate the current trophic niche. I use the integrative system (Fig 1) to quantify kinematic flexibility and perform visual surveys of herbivorous parrotfish (Scaridae) feeding in the reef, documenting the micro-habitat they feed upon, in order to quantify their current dietary characteristics (Fig 4B). This integration will enable detection of both current and potential functional overlaps in the herbivore community, along with an examination of how different species behaviour coincide with their currently ascribed functional roles.

This research is the first rigorous examination of a new axis of fish functional diversification, providing insights to ecological function, morphology, and performance of herbivorous reef fish. Results from this work will elucidate not only the evolutionary bases of herbivory, but also enable a more informed and accurate ecological assessment of the functional roles performed by herbivores on coral reefs, aiding in both present and future reef management and conservation.

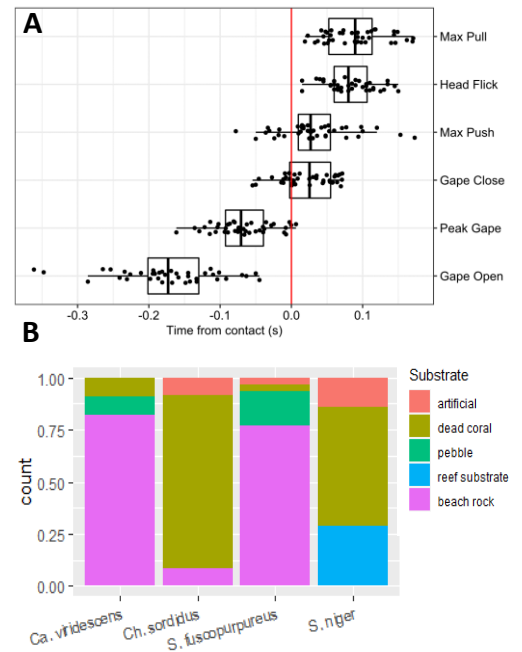


Figure 4: kinematic repertoire and dietary niche. (A) low variation in kinematic profiles of 40 feeding events demonstrate the highly stereotypic feeding of acanthurids, displaying a single-bite pull feeding mode (Perevolotsky et al. 2020). (B) micro-habitat feeding preferences of four parrotfish representing different functional groups demonstrate unexpected similarities in trophic niche which can be elucidated by examining their kinematic repertoire

References: 1- Ogden & Lobel. 1978, 2- Bellwood et al. 2004, 3- Hughes 1994, 4 - Hughes et al. 2007, 5 - Edwards et al. 2013, 6 - Bellwood & Choat 1990, 7 - Nanami 2016, 8 - Perevolotsky et al. 2020, 9 - Green & Bellwood 2009, 10 - Adam et al. 2015, 11 - Burkepile and Hay 2008