Feeding ecomorphology in angelfishes, f. Pomacanthidae: the implications of functional innovations on prey-dislodgement in biting reef fishes

PhD thesis submitted by

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STATEMENT OF CONTRIBUTION OF OTHERS

This thesis includes some collaborative work with my supervisor, Prof. David R. Bellwood (Chapter 2-4), with Prof. Peter C. Wainwright (Chapter 4) and with Dr. Wayne Mallett (Appendix 1). While undertaking these collaborations, I was responsible for conceptualising the project, execution of experiments, data analysis and synthesis of results into a publishable format. My co-authors assisted financially, with editorial advice and with technical instruction for programs and experimental equipment.

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Thesis Abstract

On coral reefs, biting teleosts form a major component of reef fish assemblages. Nevertheless, they have been largely overlooked in functional research, while their ram-suction feeding counterparts have received considerable attention over the past few decades. This thesis therefore examines the functional basis of biting in coral reef fishes, with a focus on the marine angelfishes (f. Pomacanthidae), and other deep-bodied squamipinnid fishes.

To evaluate the magnitude and role of functional specialisation associated with prey-capture in angelfishes, a basal species, *Pomacanthus semicirculatus* (Cuvier, 1931) was selected as a model taxon for comprehensive functional analysis. The feeding apparatus of *Pomacanthus* contains two biomechanical mechanisms of particular interest: an intramandibular joint, and a suspensorial linkage with two novel points of flexion. Prey-capture kinematics were quantified using motion analysis of high-speed video, generating performance profiles to illustrate timing of onset, duration and magnitude of movement in the novel mechanisms. Mandible depression and suspensorial rotation coincide during jaw protrusion, and augment mandible protrusion to increase head length typically by 30%. Jaw closure at peak jaw protrusion appears to result from contraction of the *adductor mandibulae* segment A2, the only segment with insertions facilitating rotation of the dentary by approx. 30° relative to the articular. Feeding events are concluded by a high-velocity jaw retraction typically lasting 20-50 ms, and completed in 450-750 msec. *Pomacanthus* feeding morphology and kinematics differ from other biting teleosts, and more closely resemble some long-jawed ram-suction feeders, with the novel feeding kinematics matching an unusual diet of structurally resilient and firmly attached prey.

Ten angelfish species representing all phylogenetic lineages were chosen from the GBR fauna, in order to analyse morphological and kinematic disparity in the angelfish feeding apparatus. Angelfish cranial architecture exhibits remarkable evolutionary stability with constructional changes restricted to key suspensorial specialisations governing increased jaw protrusibility, differential jaw protrusion angles and variations in alimentary tract morphology. Whilst it was previously suggested that intramandibular joints increase mechanical complexity and expand jaw-gape, in angelfishes the joint is a synapomorphy with novel gape-restricting kinematics. Individual means of the 32 most informative kinematics variables in *Pomacanthus* were extracted from high-speed video of feeding events. Concordant with phylogenetic evidence, the derived pygmy-angel subgenera, *Centropyge [Centropyge]* and *C. [Xiphypops]* differ significantly in several traits, whereas the basal *Pomacanthus* subgenera are largely indistinguishable. The monotypic *Pygoplites* exhibits the most pronounced flexion and *Genicanthus* consistently demonstrate the most restricted flexion in most variables measured.

Mapping of informative alimentary traits to a phylogeny delineated divergent angelfish feeding guilds. Grab-and-tearing omnivory on sponges and other sturdy prey is utilised by several large and robust taxa and constitutes the basal trophic guild. More gracile, biting omnivory is commonly utilised in derived pygmy-angel taxa, while dislodging herbivory arose both in the basal large-bodied *P. [Euxiphipops]* and in the derived *C. [Xiphypops]*; planktivory in *Genicanthus* is atavistic. Gape-restricting intramandibular flexion, suspensorial rotation augmenting lower jaw protrusion and a high-velocity jaw retraction are important functional innovations with major implications for angelfish feeding morphology and kinematics. Coupled with distinct size differences amongst taxa, these traits form the functional basis for a considerable ecological diversification in angelfishes.

The functional basis of biting in reef fishes was investigated in 11 deep-bodied families, to examine the relationships between novel intramandibular joints and associated trophic ecology. The results suggest convergent intramandibular joint evolution leading to biting strategies in at least five families. Restricted flexion repeatedly coincides with functional reversion to zoo-planktivory while basal ram-suction feeders generally lack flexion. In angelfishes, intramandibular joints are symplesiomorphic and evolutionarily stable, exhibiting limited kinematic divergence, averaging flexion of 27±11.1° and causing jaw occlusion at peak protrusion. Angelfish kinematics contrast with all other intramandibular joint bearers, in which gape-expanding flexion concludes prior to jaw-closure. Intramandibular flexion and transition from ram-suction to biting in butterflyfishes coincide, with flexion magnitude, culminating in the crown-group of *Corallochaetodon* (16±6.6°) and *Citharoedus* (49±2.7°).

Character mapping and optimisation revealed that up to seven intramandibular flexion transitions/reversals consistently correspond with trophic transitions from free-living to attached prey. Whilst functional patterns reflect convergence of this joint, the evolutionary origin of intramandibular flexion in the squamipinnid fishes remains ambiguous. Nevertheless, a complex evolutionary history appears to have led to widespread intramandibular joint occurrence in extant biting groups, suggesting that this is a major functional innovation, and a functional prerequisite to biting in many reef fish taxa.

In summary, the functional innovations of the angelfish feeding apparatus allow these fishes to pass ecological thresholds and exploit novel trophic strategies, using grab-and-tearing for herbivory and spongivory. Intramandibular joints appear to have been an important functional innovation, playing a similar role in driving the ecological diversification of the squamipinnes as the pharyngeal jaw apparatus in the Labroidei. However, an emerging trend of reduced feeding apparatus disparity in biters, when compared to ram-suction feeding taxa, supports the theory that novel traits can pose constraints on functional diversification. The results herein illustrate the utility of direct performance testing in quantifying disparity patterns at the organismal and assemblage-level and emphasise the potential for combining ecomorphological and biomechanical techniques in elucidating the functional basis of the biting feeding mode.