

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

PhD thesis submitted by

Nicolai Konow

(BSc, MSc. U. Copenhagen)

In September 2005

For the degree of Doctor of Philosophy

School of Marine Biology and Aquaculture,

James Cook University, Townsville, Queensland,

Australia

STATEMENT OF ACCESS

I, the undersigned, author of this work, understand that James Cook University will make this thesis available for use within the University Library, via the Australian Theses Network, or by other means allow access to users in other approved libraries. I understand that as an unpublished work, a thesis has significant protection under the Copyright Act and;

All users consulting this thesis will have to sign the following statement:

“In consulting this thesis, I agree not to copy or closely paraphrase it partly or in whole without the written consent of the author; and to make proper public written acknowledgement for any assistance, which I have obtained from it”.

Beyond this, I do not wish to place any restriction on access to this thesis.

06.09.2005

(Signature)

(Date)

STATEMENT OF SOURCES DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been duly acknowledged in the text and a list of references is given.

06.09.2005

(Signature)

(Date)

ELECTRONIC COPY

I, the undersigned, the author of this work, declare that the electronic copy of this thesis provided to the James Cook University Library is an accurate copy of the print thesis submitted, within the limits of the technology available.

Signature

Dec. 8th. 2005

Date

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.

All parts of this project were primarily funded by the Danish Research Agency, while additional field expenses were covered by the Australian Coral Reef Society and by internal JCU funding. Additional travel expenses to attend the 10th International Coral Reef Symposium in Okinawa, and the 7th International Meeting for Vertebrate Morphologists in USA were covered by JCU DRS funding. Jimmy Robinson (Pixoft/ NAC) sponsored me with a MOVIAS motion analysis software package, and Martyn Shorten (BioMechanica) lent me his DVconvert program.

Acknowledgements

Throughout my candidature, many individuals and organisations have provided inspirational, logistical and practical input, or personal support in order to aid my research progress and completion.

I am particularly indebted to Prof. D. R. Bellwood, who has remained a tremendous source of inspiration since we first met, for providing his vast knowledge-pool to my project, for his knack of perceiving what I struggle to write, and for his invaluable personal support in times of need.

It has been a pleasure working in the extended Bellwood laboratory (*Café Salmonella*) with my past and present student-colleagues: A. Barnett, M. Depczynski, R. Fisher, C. Fulton, M. Gagliano, A. Hoey, M. Marnane, C. Read, T. Stieglitz, L. Valentine & S. Wilson. I thank all these marvellous individuals for enthusiastic idea bouncing, endless amounts of proofreading, mutual personal support through trials and tribulations, great friendship – and good coffee!

I have been lucky to have had opportunities to discuss my findings and get advice from peers, including: P. Wainwright, who was a source of great inspiration during my research visit in his lab; D. Bolnick, H. Choat, L. Ferry-Graham, A. Herrel, S. Huskey, R. Kristensen, R. Kuitert, G. Lauder, M. McCormick, P. Motta, P. Munday, R. Rowe, C. Sanford, J. Steffensen, A. Summers, R. Turingan, J. Webb & C. Wilga. I owe special thanks to A. Barnett, H. Choat, M. Marnane & J. Moore for proof reading this thesis.

Many individuals and organisations generously assisted me with specimens: J. Nielsen and P. Møller (ZMUC), O. Gon and P. Heemstra (Grahamstown) lent me specimens to examine; L. Olsen (Danish Public Aquarium), B & D. Neo (PMA, Singapore), P. Boserio & F. Walsh (Cairns) provided live or fixed material. R. Walker & J. Fargo (The Marine Centre, TX) got *Genicanthus* specimens from the GBR for my UCDAVIS research.

During travels, J. Nielsen, J. Høeg and A. Garm (U. Copenhagen) unflinchingly provided safe harbour when I was laden with specimens. M. Arvedlund and A. Takemura at Sesoko Marine Lab kindly hosted me whilst collecting in Japan. R. Jackson, made my Aliwal Shoal expedition in search of *P. rhomboides* a successful venture, let me record video in his aquarium system, and provided a fresh and energetic take on fish-capture. At H.I.M.B. Oahu, fellow graduate-residents, B. Bowen, B. Greene, R. Pyle, J. Randall, R. Steyn & T. Tricas helped me with logistics and with obtaining rare endemics.

Staff members at the Orpheus, One-Tree and Lizard Island research stations and at MARFU, JCU (in particular J. Morrison & P. Wruck) helped facilitate my aquarium experiments. A. Cole, J. Moore & O. Lee were of invaluable lab assistance.

For collegial field trips and vigilance at the barrier net I thank K. Anthony, R. Bannister, L. Bay, K. Buchler, C. Chustz, R. Fitzpatrick, C. Fulton, G. Diaz, A. Frish, P. Hansen, M. Holme, M. Marnane, J. Pitt, S. Walker, and the Undersea Explorer. A. Teitelbaum and J. Moore were particularly helpful in ensnaring the wittiest of angels in the most treacherous waters.

To my mother Reidun, my brother Tom and my father Wilhelm: each of you had profound impacts on my life and progress and my completion of this thesis bears testament to what you have instilled in me, and I dedicate this thesis to your memories.

Lastly, and most importantly, a heartfelt '*Tusind Tak*' to Pernille and Philippa for your endless love, support, encouragement, understanding...and tasty cake!

Table of Contents

Title page	i
Statement of Access	ii
Statement of Sources Declaration	iii
Statement of Contribution of Others	iv
Acknowledgements	v
Table of Contents	6
List of Tables	10
List of Figures	11
Thesis Abstract	12
Chapter 1: General Introduction	
1.1 Principles of ecomorphological research	16
1.2 Additions to ecomorphology	18
1.3 Functional studies of fish feeding	19
1.4 Functional innovations and decoupling	22
1.5 Study taxa, research aims and objectives	24
Chapter 2: The functional biology of prey-capture in <i>Pomacanthus semicirculatus</i>	
Published: <i>J. Exp. Biol.</i> 208:1421-1433.	
2.1 Introduction	27
2.2 Materials and Methods	30

Table of contents

2.2.1	<i>Study taxon and specimen collection</i>	30
2.2.2	<i>Dissections, manipulations and clear staining</i>	31
2.2.3	<i>Live specimen husbandry and experimental design</i>	32
2.2.4	<i>Sampling and analysis of kinematics</i>	33
2.3	Results	35
2.3.1	<i>Jaw protrusion</i>	37
2.3.2	<i>Jaw closure</i>	42
2.3.3	<i>Jaw retraction</i>	45
2.3.4	<i>Feeding event velocity regimes and performance</i>	46
2.4	Discussion	48
2.4.1	<i>The intramandibular joint</i>	49
2.4.2	<i>Alternative mechanisms of jaw depression and protrusion</i>	49
2.4.3	<i>Within and between-mode performance variations</i>	52
2.4.4	<i>Ecological implications of intramandibular joints</i>	55

Chapter 3: Functional disparity and ecological diversification in marine angelfishes,

f. Pomacanthidae. Submitted: *The American Naturalist*.

3.1	Introduction	58
3.2	Materials and Methods	61
3.2.1	<i>Study taxa selection and collection</i>	61
3.2.2	<i>Live specimen husbandry and experimental design</i>	64
3.2.3	<i>Feeding performance and morphological sampling</i>	67
3.2.4	<i>Morphological and kinematic data analyses</i>	68

Table of contents

3.3 Results	70
3.3.1 <i>Feeding apparatus and cranial functional morphology</i>	70
3.3.2 <i>Feeding kinematics</i>	76
3.4 Discussion	81
3.4.1 <i>Pomacanthid morphological disparity</i>	81
3.4.2 <i>Pomacanthid kinematics disparity</i>	83
3.4.3 <i>Prey-capture disparity within and amongst feeding modes</i>	86
3.4.4 <i>Implications for future studies</i>	89

Chapter 4: Intramandibular joints helps reef fishes take diverse bite

In prep: Proc. R. Soc. Lond. Ser B.

4.1 Introduction	92
4.2 Materials and Methods	94
4.2.1 <i>Analysis of mandible morphology and kinematics</i>	94
4.2.2 <i>Phylogenetic mapping and optimising</i>	96
4.3 Results	98
4.3.1 <i>Intramandibular morphology and kinematics</i>	98
4.3.2 <i>Phylogenetic mapping of intramandibular flexion</i>	102
4.4 Discussion	104
4.4.1 <i>The prevalence of IMJs in biting reef fishes</i>	104
4.4.2 <i>Divergent IMJ kinematics and differential biting strategies</i>	105
4.4.3 <i>Convergent, parallel or divergent IMJ evolution?</i>	106

Table of contents

Chapter 5: Concluding Discussion

5.1 Synthesis of thesis results	108
5.2 Grab-and-tearing feeding kinematics and novel prey utilisation	112
5.3 Functional disparity in biting teleosts	115
5.4 The biting feeding mode	117
5.5 Divergent IMJ kinematics and differential microhabitat utilisation	117
5.6 Prevalence of biters in tropical marine reef ecosystems	119
5.7 Biters with IMJs in other reefal ecosystems	120
5.8 Thesis conclusions	121
References cited	122
Appendix I: MatLab code for high-speed video formatting	134
Appendix II: High-speed video sequences of pomacanthid study-taxa (+CD)	139
Appendix III: Manuscripts arising from thesis chapters and thesis related work	140
Appendix IV: Publication arising from Chapter 2	141

List of Tables

Table 2.1 Performance characteristics of prey-capture kinematics in *Pomacanthus semicirculatus*.

Table 2.2 Prey-capture performance characteristics in *Pomacanthus* compared with previously studied acanthurid and labroid taxa.

Table 3.1 Summary of pomacanthid taxa examined in this study

Table 4.1 Taxa investigated in this study

List of Figures

- 2.1 High-speed image frames from a 200 frames per second recording illustrating the feeding event in *Pomacanthus semicirculatus*.
- 2.2 Illustrations of the *Pomacanthus semicirculatus* skull based on Camera Lucida drawings from clear-stained preparations and dissections.
- 2.3 Schematic figure of the skull kinematics in *Pomacanthus semicirculatus*.
- 2.4 Mean angular excursion kinematics profiles for three *Pomacanthus semicirculatus*.
- 2.5 Mean linear excursion kinematics profiles for *Pomacanthus semicirculatus*.
- 2.6 Camera Lucida drawings of the feeding apparatus in four biting coral reef teleosts with intramandibular joints.
- 3.1 Phylogeny of the GBR-pomacanthids.
- 3.2 The eight pomacanthid study taxa subjected to kinematics analysis.
- 3.3 Skull preparation of *Pomacanthus [Euxiphipops] sexstriatus*.
- 3.4 Morphology of the feeding apparatus and cranium in the Pomacanthidae.
- 3.5 Functional and morphological differences among pomacanthid clades.
- 3.6 Mapping and optimising of character traits to the pomacanthid phylogeny.
- 3.7 2D-kinematic functional space plots of representative kinematics in the 8 study taxa.
- 3.8 Scatter-plot of mean canonical scores for the first two canonical factors generated by the DFA analysis.
- 4.1 Sample images from high-speed video and performance profile-plots for the common gape-expanding, and the unique angelfish gape-restricting intramandibular joint.
- 4.2 Camera Lucida drawings of jaw morphologies in representative study families.
- 4.3 Intramandibular flexion clade-means based on kinematics and/or biomechanical analyses.
- 4.4 ‘Super tree’ for the squamipinnid families studied, based on available phylogenetic evidence.
- 5.1 Relationships between prey posing different biomechanical challenges and combinations of presence and absence of several functional innovations in biting and ram-suction feeding teleosts in marine reef ecosystems.

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

Thesis abstract

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.* [*Euxiphypops*] and in the derived *C.* [*Xiphypops*]; planktivory in *Genicanthus* is atavistic. Gape-restricting intramandibular flexion, suspensorial rotation augmenting lower jaw protrusion and a high-

Thesis abstract

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 $27 \pm 11.1^\circ$ 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* ($16 \pm 6.6^\circ$) and *Citharoedus* ($49 \pm 2.7^\circ$).

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.

Thesis abstract

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.