

The biogeography of damselfish skull evolution: A major radiation throughout the Indo-West Pacific produces no unique skull shapes

W. J. Cooper

Department of Biology, Syracuse University, 107 College Place, Life Sciences Complex, Syracuse, NY13244, USA

wjcooper@syr.edu

Abstract

The Indo-West Pacific (IWP) is the center of damselfish biodiversity (Perciformes, Pomacentridae), but phylogeographic evidence indicates that most of the pomacentrids in this region belong to a single lineage that diverged 12-18 million years ago. A strong majority of these species can only be found in coral communities, and this clade represents a major radiation of coral reef fishes within the IWP. Although these fishes constitute approximately half of the damselfishes (183 of 376 species), the results of morphometric analyses indicate they do not possess any unique cranial shapes, and the results of rarefaction analyses reveal that their skull morphology is significantly less disparate than the cranial diversity of the other damselfish clades. The pomacentrid skull shapes that are not represented within this lineage belong to fishes that inhabit rocky reefs. If only species from predominantly coral reef genera are compared, then there are no significant differences in skull shape disparity between these two groups. The Pomacentridae exhibit numerous examples of morphological and trophic convergence, and this tendency towards repeatedly evolving similar ecotypes is exemplified by the finding that a major expansion among the coral reefs of the IWP has produced no unique examples of damselfish skull anatomy.

Key words: Damselfish; Pomacentridae; Functional morphology; Fish feeding; Biogeography

Introduction

The Indo-West Pacific contains the planet's greatest diversity of coral reef fishes (Bellwood and Wainwright 2002a; Carpenter and Springer 2005; Mora et al. 2003) and deciphering the historical patterns of community assemblage in this region is a major goal for marine biologists. The damselfishes represent a significant component of the near-shore reef fish communities throughout the tropics (Bellwood and Hughes 2001; Floeter et al. 2008), and approximately 300 pomacentrid species inhabit the IWP (Allen 1991). In order to understand how the current patterns of IWP coral reef fish diversity have formed, it is therefore necessary to understand the historical biogeography of the Pomacentridae.

Until recently, very few studies have used well-supported phylogenies of large numbers of species to address questions of reef fish biogeography (Bellwood 1997), but fortunately there has been a marked increase in such efforts during the past several years (e.g., Bellwood et al. 2004; Fessler and

Westneat 2007; Floeter et al. 2008; Strelman et al. 2002; Westneat et al. 2005). These studies are associated with a recent surge in molecular phylogenetic investigation, and multiple examinations of damselfish relationships have been an important part of this rapidly expanding body of work (e.g., Cooper et al. 2009; Jang-Liaw et al. 2002; McCafferty et al. 2002; Quenouille et al. 2004; Santini and Polacco 2006; Tang 2001; Tang et al. 2004). The most recent of these examines 104 species representing all 28 pomacentrid genera (previously 29), reorganizes portions of the taxonomy, and raises certain questions about the biogeographical history of damselfishes in the IWP (Cooper et al. 2009).

The Pomacentridae can be divided into 5 major clades, each of which now constitutes a separate subfamily (Fig. 1; Cooper et al. 2009). Of these clades, the sister lineages that have diverged most recently are the Abudedefdufinae and the Pomacentrinae (Fig. 1). Although relatively recent in origin compared to the rest of the pomacentrid crown group,

the Pomacentrinae have undergone a tremendous amount of diversification, and they now encompass 16 genera, almost exactly half of the damselfishes, and nearly 10 times the number of species as their sister taxon (Fig. 1). Their distribution also spans a massive portion of the globe, with the extremes of their range defined by the eastern coast of South Africa, the Red Sea, the Ryukyu islands of southern Japan, New South Wales and New Zealand, and Easter Island (Allen 1991). Despite the fact that they have radiated over such vast distances, they have not colonized the Atlantic (ATL) or the Eastern Pacific (EP; Allen 1991).

In light of their obvious ability to radiate over large areas that contain warm coastal waters, the absence of the Pomacentrinae from the ATL and EP suggests that their access to these regions has been blocked by dispersal barriers. The most likely of these are the cool ocean waters south of Africa, the geological barrier presented by Africa and the Red Sea landbridge, and the East Pacific Barrier (EPB), which is a large expanse of deep open ocean (~5,000 km) with very little habitat suitable for near-shore fishes (Grigg and Hey 1992). Of these three, only the landmasses can be considered impermeable or "hard" barriers to coastal reef-fish dispersal, while the two purely oceanic barriers in question are "soft" barriers that have been shown to limit, but not prevent, colonization of adjacent ocean regions by reef fishes (Bowen et al. 2006; Briggs 1995; Díaz de Astarloa et al. 2003; Fessler and Westneat 2007; Floeter et al. 2008; Grigg and Hey 1992; Hadley-Hansen 1986; Lessios et al. 1998; Lessios and Robertson 2006; Robertson et al. 2004; Rocha et al. 2005).

The geological barrier was not in place until the closing of the Tethys Seaway that once connected the ATL and Indian Oceans. This warm water marine dispersal route was blocked by the northward movement of the African and Arabian plates somewhere between 12-18 mya, an occurrence that is referred to as the terminal Tethyan event (TTE; Adams 1981; Bellwood and Wainwright 2002b; Blum 1989). The biogeography of the Pomacentrinae and the Abudefdufinae suggests that they diverged shortly before the TTE, with enough time elapsing between their split and the formation of the Red Sea landbridge for the Abudefdufinae to divide into ATL/EP and IWP lineages (Fig. 1-2; Cooper et al. 2009; Quenouille, et al. 2004). The Abudefdufinae also invaded the ATL/EP a second time, with this colonization occurring more recently, but before the final closure of the Panamanian isthmus 3.1 mya (Coates and Obando 1996). It is possible, but unlikely, that the TTE did not occur until after this second incursion of the Abudefdufinae into the ATL/EP,

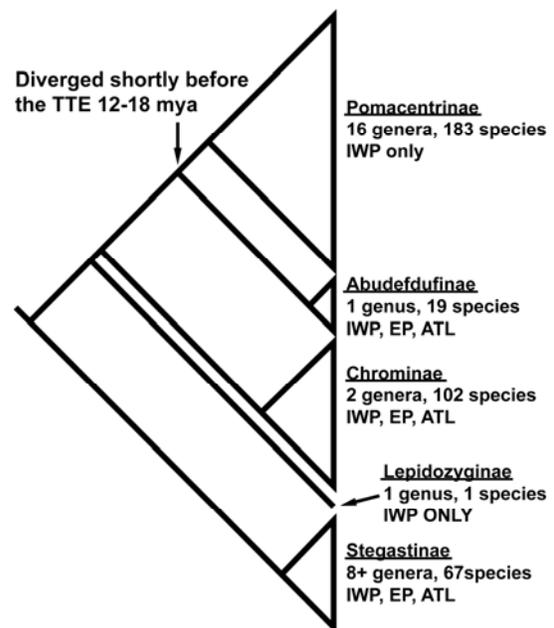


Figure 1. Phylogeography of the damselfish subfamilies. The listing of "8+" genera for the Stegastinae refers to the fact that "*Abudefduf luridus*" lies within this clade, and not with its current congeners in the Abudefdufinae. IWP = Indo-West Pacific; EP = Eastern Pacific; ATL = Atlantic. Phylogeny and taxonomy after Cooper et al. (2009).

but such a scenario would make it difficult to explain why the Pomacentrinae failed to invade the same region during this time. A more likely explanation is that the most recently derived species of *Abudefduf* in the ATL and EP colonized this region after the TTE by passing through one of the soft dispersal barriers listed above.

Regardless of the timing of their divergence, the Pomacentrinae represent a major radiation of reef fishes in the IWP that began relatively recently in comparison to the initial divergence of the damselfish crown group. Since the lineage is young (relative to the rest of the Pomacentridae), and since it contains such a large percentage of the damselfish diversity (>48.6 of the species, and >57.0 % of the genera), it is very likely that it has experienced rapid rates of speciation in comparison to the other pomacentrid clades. In order to determine if this lineage's rapid speciation and colonization of a large portion of the world's tropical oceans has been associated with the evolution of derived trophic morphologies, we chose to compare the functional anatomy of pomacentrid feeding between the Pomacentrinae and all other damselfishes.

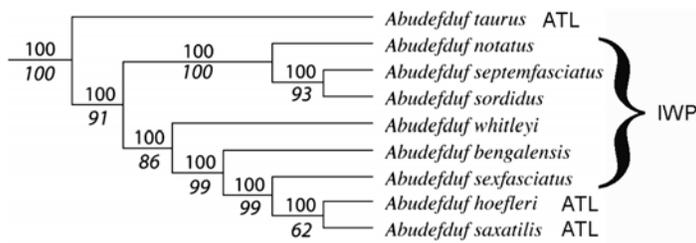


Figure 2. Biogeographic distributions of those species of the Abudefdufinae examined by Cooper et al. (2009). IWP = Indo-West Pacific; ATL = Atlantic. Upper numbers = Bayesian posterior support values. Lower numbers = MP bootstrap support values

Materials and Methods

Specimens

The heads of specimens (N=106) that represent all damselfish subfamilies, genera, and trophic classes (Allen 1999; Allen 1991; Cooper et al. 2009) were dissected in order to expose morphological landmarks of functional importance for fish feeding (Fig. 3). All specimens were adults except in the case of the genus *Altrichthys*, where only juveniles were available. Dissections were digitally photographed in lateral view, and 18 morphological landmarks (LM; Figure 3) were plotted on the image of each specimen using the program tpsDig (Rohlf 2006). This program was also used to determine the Cartesian coordinates of each landmark, and to establish the scale of all images.

Shape analyses

A relative warp (RW) analysis was used to display and quantify patterns of damselfish head shape diversity. The program tpsRelw (Rohlf 2007) was used to perform both a Procrustes superimposition of the data, and a RW

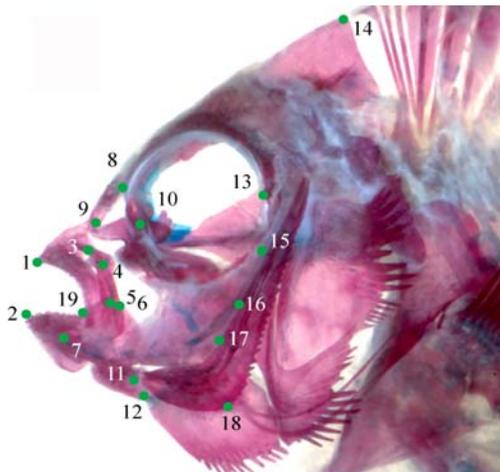


Figure 3. LM examined using RW analysis on a cleared and stained head of *Amphiprion akindynos*.

analysis of the Procrustes transformed coordinates. Procrustes methods remove differences due to size, orientation and translation without distorting shape information. The RW scores of each specimen were used to map their location on RW axes. Distributions of the specimens in this “shape space” were used to describe relative morphological differences among individual skulls.

Comparisons of morphological disparity

In order to statistically compare differences in morphological diversity (shape disparity), a series of 4 different disparity metrics were calculated based on the scores for each specimen on the two largest relative warps (RW1 and RW2). These metrics were: sum of variances, product of variances, sum of ranges and geometric mean range (Stayton and Ruta 2006). Rarefaction of these calculations was then performed using the software application Rarify2 (Stayton 2006) in order to compare members and non-members of the Pomacentrinae using each type of disparity value. All groups were sub-sampled at sample sizes that ranged from 2 specimens to N-2 specimens (N = the number of specimens in each group). All 4 disparity metrics were calculated for 1000 iterations at each sampling level. Since almost all members of the Pomacentrinae are inhabitants of coral reefs (Allen 1991), a second series of rarefaction analyses were performed in order to examine the morphological evolution of only those damselfishes that utilize this habitat.

Results

Inspection of a RW score plot that displays the distribution of damselfish skull shapes along RW1 and RW2 indicates that the diversity of skull form exhibited by the Pomacentrinae is lower than the combined skull shape disparity of the more basal damselfish subfamilies (Fig. 4). The results of rarefaction analyses show that this difference in shape diversity is significant for all 4 disparity metrics at almost every sampling level (Fig. 5). The Pomacentrinae also appear to have evolved no unique skull shapes, since the region of shape space that they inhabit is almost entirely a subset of the region occupied by specimens from the other subfamilies (Fig. 4). Most of this difference is due to the head shapes of relatively large rocky reef inhabitants that evolved within the Abudefdufinae, Chrominae, and Stegastinae, and the exclusion of these specimens from the rarefaction analyses resulted in the elimination of significant differences (Fig. 4-5).

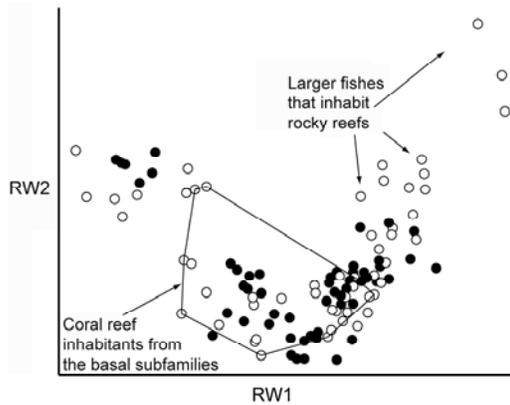


Figure 4. RW score plot of damselfish skull shapes. ● = the Pomacentrinae. ○ = specimens from the remaining damselfish subfamilies.

Discussion

The pomacentrinine damselfishes have undergone an extensive, and presumably rapid, increase in species diversity that has not generated any distinct skull morphologies. Since the anatomical landmarks examined in this study are components of the functional morphology of damselfish feeding, our results strongly suggest that this massive IWP radiation has not been associated with an expansion into completely new trophic niches. These findings therefore raise questions about how we can account for the success of the Pomacentrinae.

The results of investigations into the evolution of damselfish skull biomechanics using comparative phylogenetic methods (Cooper and Westneat 2009) indicate that the answers to some of these questions can be provided by observing how frequently damselfishes switch back and forth between a limited number of trophic niches. Almost all pomacentrids feed via herbivory, planktivory, or a limited type of omnivory that very rarely involves preying upon organisms that are highly elusive, durable or difficult to subdue. Although the variety of niches that they occupy is low, pomacentrids are able to quickly transition between them. The evolution of damselfish feeding is therefore characterized by rapid and repeated shifts between this limited set of ecological states, a pattern that has been described as a *reticulate adaptive radiation* (Cooper and Westneat 2009).

This propensity for convergence also applies to pomacentrids at the community level, since those fishes that inhabit coral reefs have repeatedly evolved similar trophic morphologies. The damselfish example, among others (e.g., Adams et al. 2009), demonstrates that evolutionary success need not be limited to lineages that continuously increase their anatomical diversity, but that it can also be achieved by organisms that do a limited number of things, but which somehow manage to do them very well.

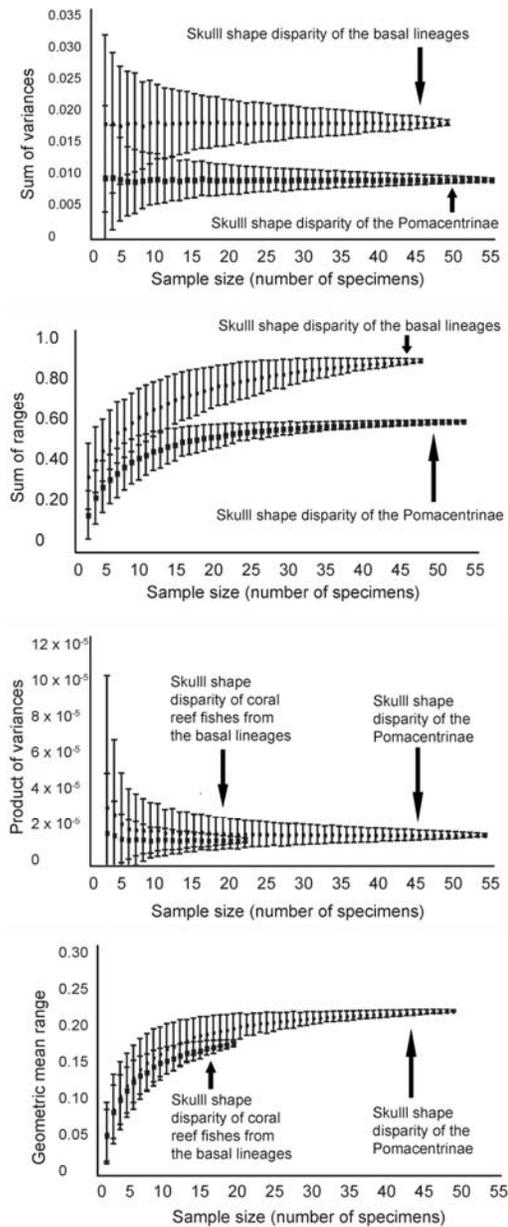


Figure 5. Examples of the rarefaction results.

Acknowledgements

I would like to thank Mark Westneat, Tristan Stayton, Aaron Rice, Mike LaBarbera, Jennifer Fessler, and Lydia Smith for their generous assistance with this research. I would also like to thank the curators and staff of the Field Museum, the Australian Museum, the Scripps Institution of Oceanography and the United States National Museum of Natural History for supplying pomacentrid specimens. This work was supported by NSF Doctoral Dissertation Improvement Grant IBN-0308977 to W. J. Cooper and M. Westneat.

References

- Adams CG (1981) An outline of tertiary palaeogeography. In: Cocks LRM (ed.) The evolving earth. British Museum of Natural History, London, UK
- Adams DC, Berns CM, Kozak KH, Wiens JJ (2009) Are rates of species diversification correlated with rates of morphological evolution? *Proc R Soc Biol Sci Ser B* doi: 10.1098/rspb.2009.0543
- Allen GR (1999) *Altrichthys*, a new genus of damselfish (Pomacentridae) from Philippine seas with description of a new species. *Rev Fr Aquariol* 26: 23-28
- Allen GR (1991) *Damselfishes of the World*. Aquarium Systems, Mentor, Ohio (271)
- Bellwood DR (1997) Reef fish biogeography: habitat associations, fossils and phylogenies. *Proc 8th Int Coral Reef Sym* 1: 397-384
- Bellwood DR, Herwerden Lv, Konow N (2004) Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). *Mol Phylogenet Evol* 33: 140-155
- Bellwood DR, Hughes TP (2001) Regional-Scale Assembly Rules and Biodiversity of Coral Reefs. *Science* 292: 1532-1535
- Bellwood DR, Wainwright PC (2002a) The history and biogeography of fishes on coral reefs. In: Sale PF (ed.) *Coral Reef Fishes*. Academic Press, New York (pp 5-32)
- Bellwood DR, Wainwright PC (2002b) The History and Biogeography of Fishes on Coral Reefs. In: Sale PF (ed.) *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, London (pp 5-32)
- Blum SD (1989) Biogeography of the Chaetodontidae - an Analysis of Allopatry among Closely Related Species. *Enviro Biol Fish* 25: 9-31
- Bowen BW, Muss AJ, Rocha LA, Grant WS (2006) Shallow mtDNA coalescence in Atlantic pygmy angelfish (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *J Hered* 97: 1-12
- Briggs JC (1995) *Global Biogeography*. Elsevier, New York (472)
- Carpenter KE, Springer VG (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Enviro Biol Fish* 72: 467-480
- Coates AG, Obando JA (1996) The geologic evolution of the Central American isthmus. In: Jackson JBC, Budd AF, Coates AG (eds.) *Evolution and environments in tropical America*. University of Chicago Press, Chicago (pp 21-56)
- Cooper WJ, Smith LL, Westneat MW (2009) Exploring the radiation of a diverse reef fish family: Phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. *Mol Phylogenet Evol* 52:1-16
- Cooper, W. J. & M. W. Westneat. 2009. Form and Function of Damselfish Skulls: Rapid and Repeated Evolution into a limited Number of Trophic Niches. *BMC Evol Biol* 9:24 doi:10.1186/1471-2148-9-24
- Díaz de Astarloa JM, Figueroa DE, Reta R (2003) First documented occurrence of the starry toadfish *Arothron firmamentum* (Teleostei: Tetraodontidae) in the south-west Atlantic. *J Mar Biol Assoc U K* 83: 879-880
- Fessler JL, Westneat MW (2007) Molecular phylogenetics of the butterflyfishes (Chaetodontidae): Taxonomy and biogeography of a global coral reef fish family. *Mol Phylogenet Evol* 45: 50-68
- Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcon JM, Bowen BW, Bernardi G (2008) Atlantic reef fish biogeography and evolution. *J Biogeogr* 35: 22-47
- Grigg RW, Hey R (1992) Paleocceanography of the Tropical Eastern Pacific-Ocean. *Science* 255: 172-178
- Hadley-Hansen PE (1986) Revision of the tripterygiid fish genus *Helcogramma*, including descriptions of four new species. *Bull Mar Sci* 38: 313-354
- Jang-Liaw NH, Tang KL, Hui CF, Shao KT (2002) Molecular phylogeny of 48 species of damselfishes (Perciformes : Pomacentridae) using 12S mtDNA sequences. *Mol Phylogenet Evo* 25: 445-454
- Lessios HA, Kessing BD, Robertson DR (1998) Massive gene flow across the world's most potent marine biogeographic barrier. *Proc R Soc Biol Sci Ser B* 256: 583-588
- Lessios HA, Robertson DR (2006) Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proc R Soc Biol Sci Ser B* 273: 1471-2954
- McCafferty S, Bermingham E, Quenouille B, Planes S, Hoelzer G, Asoh K (2002) Historical biogeography and molecular systematics of the Indo-Pacific genus *Dascyllus* (Teleostei: Pomacentridae). *Mol Ecol* 11: 1377-1392
- Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA (2003) Patterns and processes in reef fish diversity. *Nature* 421: 933-936
- Quenouille B, Bermingham E, Planes S (2004) Molecular systematics of the damselfishes (Teleostei : Pomacentridae): Bayesian phylogenetic analyses of mitochondrial and nuclear DNA sequences. *Mol Phylogenet Evo* 31: 66-88
- Robertson DR, Grove JS, McCosker JE (2004) Tropical Transpacific Shore Fishes. *Pac Sci* 58
- Rocha LA, Robertson DR, Rocha CR, Van Tassell JL, Craig MT, Bowen BW (2005) Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. *Mol Ecol* 14: 3921-3928
- Rohlf FJ (2006) tpsDig2 [<http://life.bio.sunysb.edu/morph/>]
- Rohlf FJ (2007) tpsRelw [<http://life.bio.sunysb.edu/morph/>]
- Santini S, Polacco G (2006) Finding Nemo: Molecular phylogeny and evolution of the unusual life style of anemonefish. *Gene* 385: 19-27
- Stayton CT (2006) *Rarify 2*. Available from the author (tstayton@bucknell.edu) Bucknell University, Bucknell, PA
- Stayton CT, Ruta M (2006) Geometric morphometrics of the skull roof of stereospondyls (Amphibia : Temnospondyli). *Palaeontology* 49: 307-337
- Streelman JT, Alfaro M, Westneat MW, Bellwood DR, Karl SA (2002) Evolutionary history of the parrotfishes: Biogeography, ecomorphology, and comparative diversity. *Evolution* 56: 961-971
- Tang KL (2001) Phylogenetic relationships among damselfishes (Teleostei : Pomacentridae) as determined by mitochondrial DNA data. *Copeia*: 591-601
- Tang KL, McNyset KM, Holcroft NI (2004) The phylogenetic position of five genera (*Acanthochromis*, *Azurina*, *Chrysiptera*, *Dischistodus*, and *Neopomacentrus*) of damselfishes (Perciformes : Pomacentridae). *Mol Phylogenet Evo* 30: 823-828
- Westneat MW, Alfaro ME, Wainwright PC, Bellwood DR, Grubichl JR, Fessler JL, Clements KD, Smith LL (2005) Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proc R Soc Biol Sci Ser B* 272: 993-1000