Zoomorphology (2018) 137:315–327
https://doi.org/10.1007/s00435-017-0391-6

ORIGINAL PAPER

Ecomorphological trajectories of reef fish sister species (Pomacentridae) from both sides of the Isthmus of Panama

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Received: 5 July 2017 / Revised: 21 November 2017 / Accepted: 27 November 2017 / Published online: 22 December 2017

Abstract

The vicariance model of biogeography focuses on allopatric speciation through fragmentation from an ancestral biota via a barrier that interrupts gene flow between populations. The evolutionary processes that occur over time in sister species on each side of the vicariance event influence their traits by a compromise between divergence and conservatism. The eastern Pacific and the Caribbean Sea were separated by the Isthmus of Panama ~ 3–6 Mya and allopatric speciation occurred on either side of the isthmus. Differences in ecological conditions on each side of the Isthmus of Panama separating the sister species may have shaped their niches and morphologies over evolutionary time. The objectives of this study were to: (1) analyze the variation in niche, morphology, and size in each pair of sister damselfish species on both sides of the Isthmus of Panama, (2) determine whether these variables show specific patterns on each side of the isthmus, and (3) determine whether these variables are correlated through evolution. The results showed no relationship between morphology and niche, however, size was related to both niche and morphology. Sister damselfish species on either side of the Isthmus of Panama differ in terms of niche, morphology, and size. Nevertheless, they also show similarities, indicating environmental constraints and conservatism. This study describes a model in which adaptation or divergence and conservatism shaped the evolution of sister damselfish species on both sides of the Isthmus of Panama. These mechanisms are fundamental to population biology, and they act in opposite directions.

Keywords Damselfish · Reef fish · Vicariance · Isthmus of Panama · Niche · Morphology

Introduction

According to the vicariance model of biogeography, ancestral biota separated by a barrier interrupting interpopulation gene flow results in allopatric speciation (Croizat et al. 1974; Rosen 1976, 1978; Nelson and Platnick 1981; Wiley 1988; Humphries and Parenti 1999). Speciation on each side of the barrier occurs from the interaction between conservatism (Peterson et al. 1999; Webb et al. 2002; Wiens 2004; Kozak and Wiens 2006; Wiens et al. 2010) and divergence (Rissler and Apodaca 2007; Pyron and Burbrink 2009). These two processes are rooted in population biology and act in opposite directions. Conservatism limits adaptation, whereas divergence enables adaptation to a new environment (Wiens 2004; Pyron and Burbrink 2009). These processes influence morphology, habitat use, migratory capacities, longevity, and speciation rate, and are limited by external processes such as the environment, climate, predation and competition (Fransen 2002, 2007). Consequently, ecological variation on each side of a barrier could affect the traits of the taxa differently over evolutionary time.

The eastern Pacific (EP) and the Caribbean Sea (CBS) were separated around 3–6 Mya by the closure of the Central American Seaway when the Isthmus of Panama finally rose (Duque-Caro 1990; Coates and Obando 1996; Glynn and Ault 2000; Bellwood and Wainwright 2002; Steeves et al. 2005; Bacon et al. 2015; Montes et al. 2015; O'Dea et al. 2016; Jaramillo et al. 2017). This event caused allopatric separation and, eventually, speciation (Glynn and Ault 2000). Six pairs of damselfish (Pomacentridae) sister species on each side of the Isthmus of Panama have been identified.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00435-017-0391-6) contains supplementary material, which is available to authorized users.

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It was estimated that they diverged ~ 2–18 Mya (Frédérich et al. 2013), which is consistent with the period of the final rise of the Isthmus of Panama.

Ecological variables such as habitat, food availability, ocean temperature, and productivity strongly influence the distribution and evolution of marine organisms (Grove et al. 1986; Bellwood et al. 2004; Price et al. 2011; Lobato et al. 2014). Pomacentrids inhabit a wide range of habitats (Clarke 1971; Grove et al. 1986; Robertson and Allen 2015; Aguilar-Medrano et al. 2015, 2016). In the eastern Pacific (EP), 24 species of damselfish have been recorded between Monterey Bay, California in the North and the coast of Valdivia, Chile in the South (Cooper 1863; Allen 1991; Pequeño et al. 2005). In the EP, damselfish are distributed mainly in the rocky reefs and kelp forests of tropical- and temperate waters. In the Caribbean Sea (CBS), Gulf of Mexico (GM), and Atlantic Ocean (ATL), 31 species of damselfish have been recorded from Bermuda Island in the North, along the coasts of North- and South America and Africa, to Uruguay (South America) and Angola (South Africa) (Allen 1991; Rocha and Myers 2015). In the CBS and ATL, most of the damselfish are distributed in tropical coral reefs.

Among damselfish species, there is a strong relationship between habitat use, feeding, behavior, and morphology (Emery 1973; Fulton 2007; Frédérich et al. 2008, 2013; Aguilar-Medrano 2013, 2017; Aguilar-Medrano and Barber 2016; Aguilar-Medrano et al. 2011, 2013, 2016). The ecological conditions that each species are exposed to since their separation by the Isthmus of Panama may have shaped their niche and morphology over time. The objectives of this study were to: (1) analyze the variation in niche, morphology, and size of the sister species, (2) determine whether these variables differ on either side of the Isthmus of Panama, and (3) determine whether these variables are correlated with the evolution of damselfish sister species.

Materials and methods

Sampling

Six pairs of damselfish sister species were considered in this study. According to Frédérich et al. (2013), the estimated time for the divergence of these sister species pairs are: *Abudefduf hoefleri* and *A. trochelii*: ~ 1–3 Mya; *A. taurus* and *A. concolor*: ~ 1–4 Mya; *Chromis enchrysura* and *Ch. alta*: ~ 6 Mya; *Microspathodon chrysurus* and *M. dorsalis*: ~ 2.5–12 Mya; *Stegastes imbricatus* and *S. rectifraenum*: ~ 2.5–10 Mya. According to Quenouille et al. (2004), *Ch. atrilobata* is the sister species of *Ch. multilineata*. Frédérich et al. (2013) found that the most recent common ancestor of *Ch. atrilobata* and *Azurina hirundo* is the sister species of *Ch. multilineata*. However, this relationship would change if *Azurina eupalama* was added to the phylogeny. (The genus *Azurina* consists of only two species). In this study, *Ch. atrilobata* was used as the sister species of *Ch. multilineata* (~ 7.5–19 Mya).

Provinciality

The provinciality of each species was determined by cluster analyses based on the presence or absence of the species on each side of the Isthmus of Panama. The CBS, GM, and ATL were segregated into eight zones according to Allen (1991): Gulf of Mexico; Florida; Bermuda; North Caribbean Sea; South Caribbean Sea; St. Helena/Ascension; Cape Verde Islands; and West Africa. The EP was segregated into six zones according to Aguilar-Medrano et al. (2015): North (Revillagigedo, Gulf of California, Mexican Province, and Guatemala); Center (El Salvador, Nicaragua, Panama, Costa Rica, and Colombia); eastern Pacific Equatorial Islands (Galapagos, Malpelo, and Coco); South (Ecuador, Peru, and Chile); California Province; and Clipperton Island.

The provinciality was determined from species occurrence data (Table 1). The presence/absence database was analyzed with three cluster linkage methods: Jaccard similarity, Bray–Curtis similarity, and Ward's method. The first two do not treat absences as evidence of similarity between groups. They use the average linkage method to compare the average similarities of all segment pairs within a cluster (Clarke 1993; Kosman and Leonard 2005; Robertson and Cramer 2009). Ward's method optimizes using within-group variance rather than raw distance (Ward 1963; Sneath and Sokal 1973; Kuiper and Fisher 1975; Mojena 1977; Glynn and Ault 2000; Goswami and Polly 2010). The cophenetic correlation coefficient (CCC) was applied to all three cluster linkage methods to evaluate the goodness-of-fit of the dendrogram to the original data (Sokal and Rohlf 1962).

Niche

Five variables were used as the niche dimensions. These are defined here as the multidimensional space of resources used by a species and with which it maintains viable populations (Hutchinson 1957). (1) The geographic range (GR) is the number of zones in which each species occurs and is calculated based on the provinciality analysis data (Table 1). (2) The number of habitat types (NHT) wherein the species were recorded was obtained from the published literature for (a) coral reefs, (b) rocky reefs, and (c) kelp forests. The NHT were encoded as follows: 1—present in one type of ecosystem; 2—present in two types; 3—present in three ecosystems; etc. (3) Diet (TI) was derived from the trophic index available in FishBase (Froese and Pauly 2014). (4) Depth range (DR) is the distance from the upper- to the lower depth limit of the water column wherein the species was recorded.

Table 1 Ecological data and distribution of damselfish on both sides of the Isthmus of Panama

	SL	TI	DR	SE	PWC	GC	GR	NHT	Caribbean, Gulf of Mexico and Atlantic								Eastern Pacific					
									GM	FL	BE	NC	SC	SH	CV	WA	CP	N	C	S	EI	CI
Abudefduf hoefleri	155	2.7	20	1	2	1	25	1							1	1						
Abudefduf taurus	200	2.1	4	2	1	2	100	2	1	1	1	1	1	1	1	1						
Chromis enchrysura	100	3.4	141	1	2	1	75	2	1	1	1	1	1	1								
Chromis multilineata	86	3	60	1	3	2	75	1		1	1	1	1	1		1						
Microspathodon chrysurus	124	2.1	10	1	1	2	63	2	1	1	1	1	1									
Stegastes imbricatus	100	2	25	1	1	1	25	1							1	1						
Abudefduf concolor	100	2.7	5	2	1	1	67	2										1	1	1	1	
Abudefduf troschelii	135	3	11	1	3	1	100	3									1	1	1	1	1	1
Chromis alta	100	3.4	120	1	1	1	34	2										1			1	
Chromis atrilobata	108	3.4	74	1	3	1	67	2										1	1	1	1	
Microspathodon dorsalis	204	2.1	4	1	2	1	67	2										1	1	1	1	
Stegastes rectifraenum	90	2	9	1	1	2	34	2									1	1				
Habitat type									cr-rr	cr	cr	cr	cr	cr	cr	cr	kf-rr	rr	rr-cr	rr	cr-rr	cr

SL (mm) standard length (not considered in the niche analyses), *TI* trophic index, *DR* (m) depth range, *SE* surge exposure, *PWC* position in the water column in relation to the substrate, *GC* geographic climate, *GR* (%) geographic range, *NHT* number of habitat types occupied

Distribution in the Caribbean Sea, Gulf of Mexico and Atlantic, *GM* Gulf of Mexico, *FL* Florida, *BE* Bermuda, *NC* North Caribbean Sea, *SC* South Caribbean Sea, *SH* St. Helena, *CV* Cape Verde Islands, *WA* West Africa

Distribution in the eastern Pacific, *CP* California Province, *N* North (Revillagigedo, Gulf of California, Mexican Province and Guatemala), *C* center (El Salvador, Nicaragua, Panama, Costa Rica and Colombia), *S* South (Ecuador, Peru and Chile), *EI* Eastern Pacific Equatorial Islands (Galapagos, Malpelo and Coco), *CI* Clipperton Island

Habitat type, *cr* coral reef; *rr* rocky reef; *kf* kelp forest

(5) Surge exposure (SE) was encoded either as (a) lagoon (1) or (b) surge (2). (6) Position in the water column (PWC) was encoded as follows: (a) over the substrate (1); (b) over the substrate and close to the surface (2); or (c) close to the surface (3). (7) Geographic climate (GC) was encoded as (a) tropical (1) or (b) subtropical (2).

All variables were log-transformed. They were used in a principal component analysis (PCA) on the correlation matrix to find the main axes of the interspecies niche variations. To determine the relationship between species based on niche variables, three cluster analysis linkage methods were used: Jaccard similarity, Bray–Curtis similarity, and Ward's method. The cophenetic correlation coefficient (CCC) was used to measure the goodness-of-fit of the dendrogram to the original data (Sokal and Rohlf 1962).

Geometric morphometrics

Geometric morphometric analyses were conducted on 161 lateral-view photographs of adult damselfish representing the 12 species of the EP, CBS, GM, and ATL (supplementary online material). For each specimen, 15 landmarks (LMs) and 34 semilandmarks (SMLs; Fig. 1) were digitized. Landmark- and semilandmark data were superimposed with a generalized Procrustes analysis (Rohlf and Slice 1990). Relative warp scores (RWs) were calculated and used as shape variation descriptors (Bookstein 1991; Rohlf 1993). The main axes of morphological variation were analyzed by principal component analysis (PCA) on the landmark and semilandmark data.

The morphological independence of each species was evaluated by running multivariate analysis of variance (MANOVA) on the RW values to compare all species. Sister species were then compared by one-way NPMANOVA, which is a non-parametric test of significant differences between two or more groups based on any distance measure (Anderson 2001). Three algorithms were run to compare the results: (a) Euclidian distance; (b) Spearman's rho; and (c) Gower distance. To determine the morphological distances among species, the Procrustes distance (PD) was calculated for each pair of species (Rohlf and Slice 1990). Thin-plate spline algorithms were run to calculate the deformation grids and visualize the shape variation patterns along the main morphological axes (Bookstein 1991; Rohlf 1993). All geometric morphometric analyses were performed on the TPS series (Rohlf 2015). All

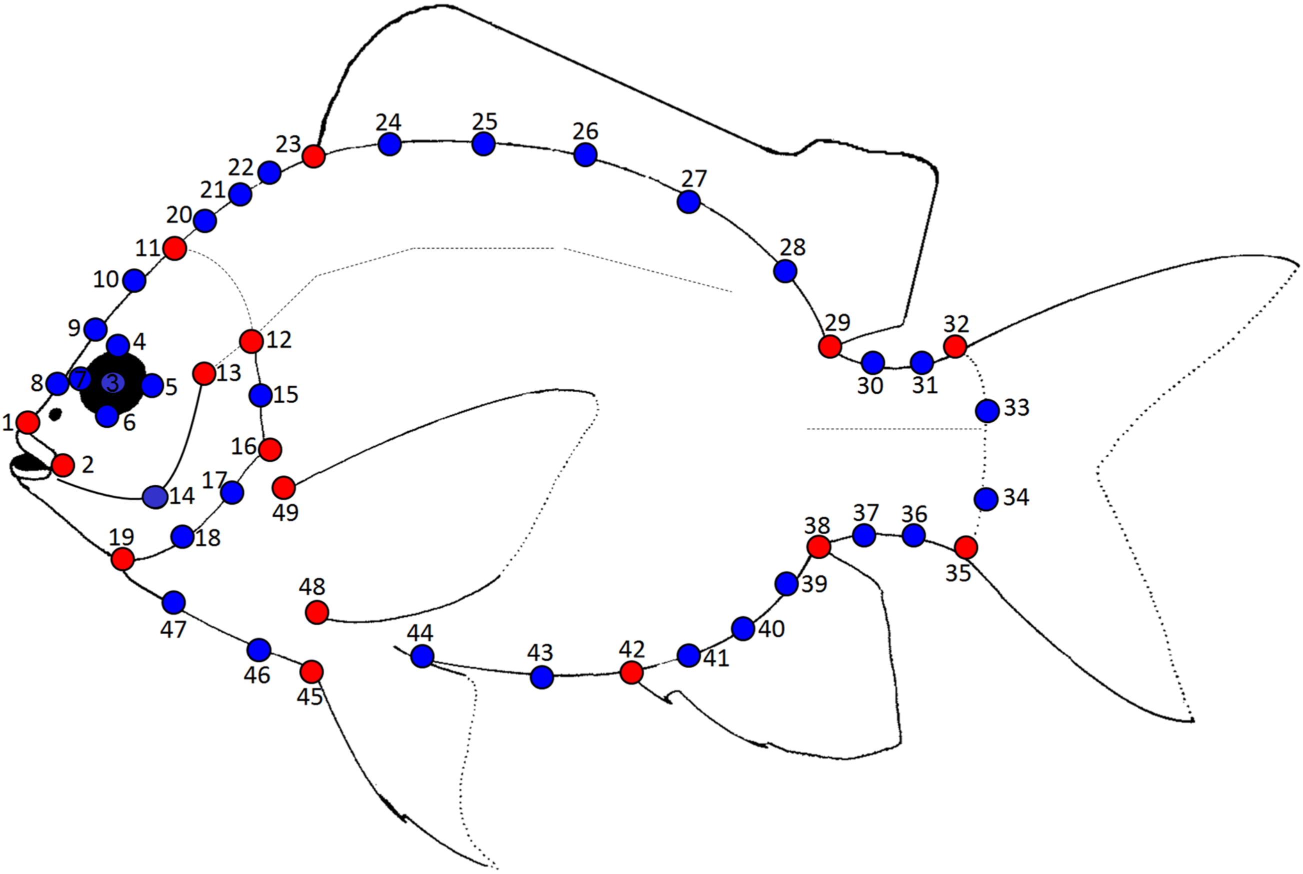


Fig. 1 Landmarks (LMs, red dots) and semilandmarks (SMLs, blue dots) used in the geometric morphometric analyses

statistical analyses were computed in PAST v. 3.11 (Hammer et al. 2001).

Allometric variation

The relationship between shape and size across species was tested by a multivariate regression of the shape variables (RWs) onto the centroid size (CS) (Bookstein 1991; Monteiro 1999) in TpsRegr v. 1.41 (Rohlf 2014a, b).

Phylogenetic comparative methods

To test the correlation between niche, morphology, and size, the phylogenetic generalized least square method (PGLS) was applied to the Pomacentridae phylogeny of Frédérich et al. (2013). Principal components were used wherever needed as morphology and niche descriptors and to account for the majority of the variation. The average standard length was also included as a size descriptor. Two trait evolution models were used to test correlations: (1) Brownian motion (BM1), in which disparity increases with time (Harmon et al. 2003), and (2) the Ornstein–Uhlenbeck model (OU1), which incorporates ≥ 1 optimum trait values and the selection strength (Beaulieu et al. 2012). The fit of each model was tested using Akaike's information criterion (AIC), which measures the trade-off between the fit and the complexity of the model (Akaike 1973). It was expected that the OU model would fit better than the BM model if the variables affected each other during evolution because the former should have lower AIC values (Wiens et al. 2010). PGLS was analyzed with the following packages in R v. 3.0.3 (R Core Team 2013): APE (Paradis et al. 2004); GEIGER (Harmon et al. 2008), NLME (Pinheiro et al. 2014); PICANTE (Kembel et al. 2010), CAPER (Orme et al. 2011); and PHYTOOLS (Revell 2012).

Results

Provinciality

Both Jaccard (CCC: 0.985) and the Bray–Curtis (CCC: 0.978) cluster analyses produced the same arrangement. The zones on the eastern side of the Isthmus of Panama were segregated into four provinces: (1) African, including West Africa and the Cape Verde Islands; (2) St. Helena, including St. Helena/Ascension Islands; (3) Gulf of Mexico, including the Gulf of Mexico; and (4) the Caribbean Sea, including Florida; Bermuda; the North Caribbean Sea; and the South Caribbean Sea. The EP was also segregated into four provinces: (1) California, including California Province and Clipperton Island; (2) North; (3) Equatorial Islands; and (4) Center and South. Ward's method showed the lowest fit (CCC: 0.87) and integrated St. Helena/Ascension Islands to the clade of Cape Verde Islands and West Africa. In the EP, the Equatorial Islands were integrated to the North Province (Fig. 2).

Niche

The two first axes of the PCA explain 85.3% of the total variation. PC1 represents 70.7% of the total variation and is mainly represented by the depth range. PC2 represents 14.6% of the total variation and is mainly represented by the geographic range and position in the water column (Fig. 3). *Chromis* species are at one extreme of the first axis (+ PC1) due to a wider range of depths, positional versatility in the water column, and higher trophic indices. *Abudefduf taurus, A. concolor*, and *Microspathodon dorsalis* are at the other extreme of the first axis (− PC1), presenting with limited depth ranges, distribution close to the substrate, and low trophic indices. The second axis of variation segregates species such as *A. troschelii* (+ PC2) with wider geographic ranges and positional versatility in the water column from species such as *Stegastes imbricatus* (− PC2; Fig. 3) with limited geographic range and fixed positions in the water column.

The cophenetic correlation coefficient fit better on the Jaccard similarity cluster (CCC: 0.83) than it did on the Bray–Curtis similarity cluster (CCC: 0.81) or using Ward's method (CCC: 0.81). The Jaccard similarity cluster showed a clear segregation of sister species on both sides of the Isthmus of Panama. The outlying cluster grouped the species distributed in most or all the provinces on the eastern side of the Isthmus of Panama. The second cluster grouped two species present only in the African Province. The third cluster grouped all the eastern Pacific species (Fig. 4).

Morphological variation

The two first PCA axes explained 62% of the total variation (PC1 = 52%; PC2 = 10%). The first axis segregated *Microspathodon dorsalis* at one extreme (+ PC1) because this species has a deep body, flattened cephalic profile, wide vertical distance between mouth and eyes, small eyes, and small terminal mouth. *Chromis atrilobata* and *Ch. multilineata* were segregated at the other extreme of the first axis (− PC1) because they have elongated bodies, angular cephalic profiles, eyes close to the mouth, large eyes, and large superior mouths. *Abudefduf concolor, A. taurus*, and *M. chrysurus* were correlated with the right side of the first axis (+ PC1). *A. troschelii, A. hoefleri*, and *Stegastes spp*. were in the center of the PC1. The second axis segregated *Microspathodon* species, *Ch. alta* and *Ch. enchrysura* at one extreme (− PC2) because they have rounded cephalic profiles, wide vertical distances between eyes and mouth,

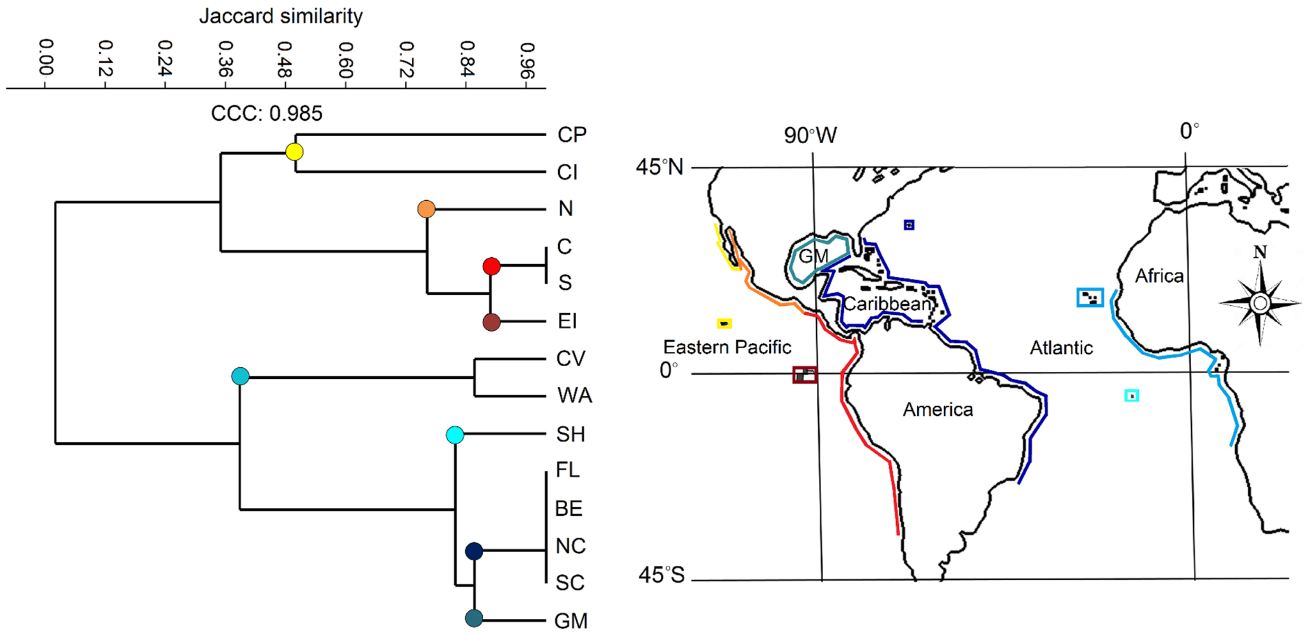


Fig. 2 Analysis of provinciality of damselfish sister species from both sides of the Isthmus of Panama. Jaccard similarity cluster analysis on the geographic distribution of damselfish sister species. Yellow: California Province; bronze: North Province; red: Center and South Province; brown: Equatorial Islands Province; Blue: African Province; Turquoise: St. Helena Province; Cadet blue: Gulf of Mexico Province; Navy blue: Caribbean Sea Province. CCC: cophenetic correlation coefficient

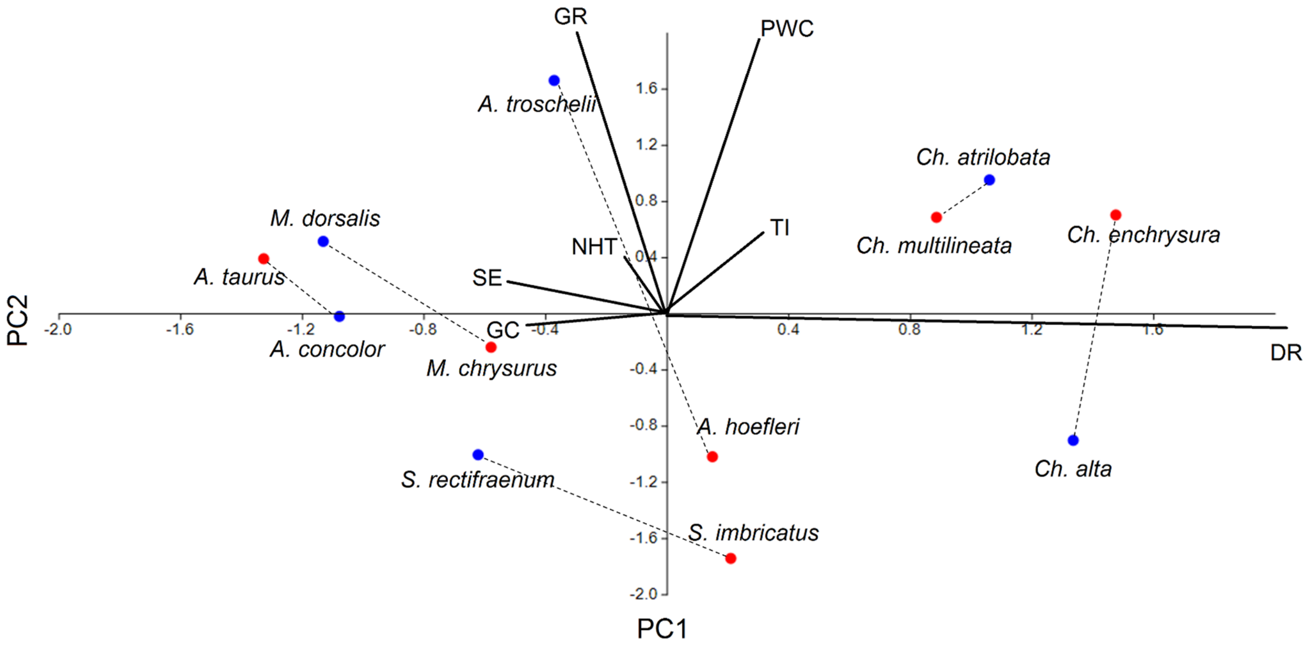


Fig. 3 Principal components analysis (PCA) on the ecological variables. Red dots: Caribbean Sea, Gulf of Mexico and Atlantic species. Blue dots: eastern Pacific species. *GR* geographic range; *NHT* number of habitat types were the species were recorded; *TI* trophic index; *DR* depth range; *SE* surge exposure; *PWC* position in the water column; *GC* Geographic climate. Dotted lines connect sister species

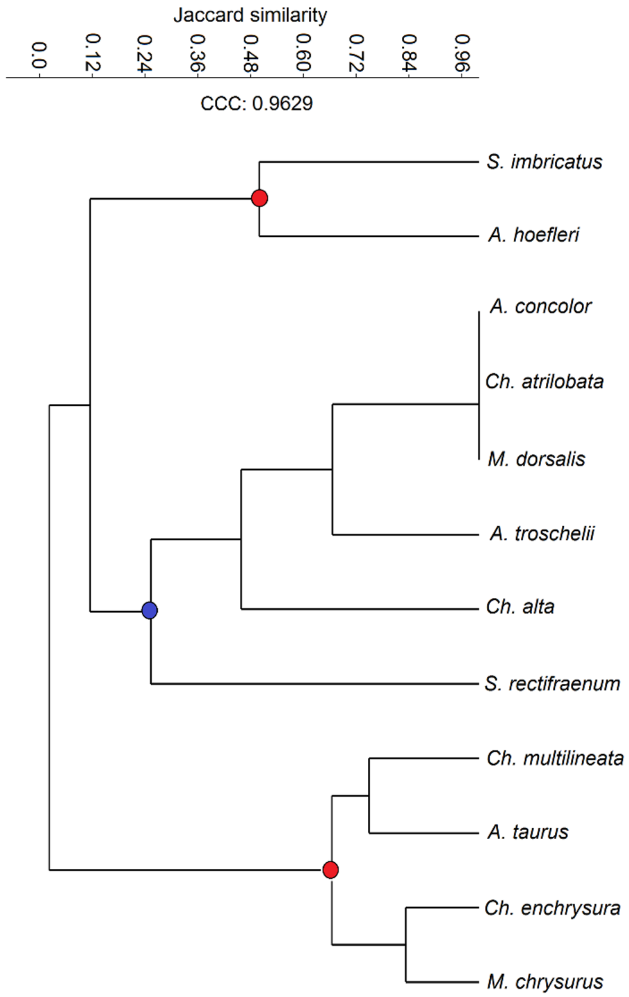


Fig. 4 Jaccard similarity cluster analysis on the niche variables. Red dots: Caribbean Sea, Gulf of Mexico and Atlantic species. Blue dots: eastern Pacific species. *CCC* cophenetic correlation coefficient

smaller eyes, and wider mouths. *Abudefduf spp*. were segregated at the alternate extreme (+PC2) because they have angular cephalic profiles, larger eyes, and narrower mouths (Fig. 5).

MANOVA indicated differences between species (Wilk's lambda = 3.637e − 12, $F_{1034-632} = 6.19$; $p = 5.637e-114$; Pillai trace = 9.367, $F_{1034-704} = 3.904$, $p = 3.274e-75$). One-way NPMANOVA (Table 2) showed significant differences among all sister species. *Abudefduf hoefleri* and *A. troschelii, Chromis multilineata* and *Ch. atrilobata*, and *Microspathodon chrysurus* and *M. dorsalis* differed significantly in all algorithms. *Ch. enchrysura* and *Ch. alta* differed in two of the three algorithms. *A. taurus* and *A. concolor*, and *Stegastes imbricatus* and *S. rectifraenum* differed in only one of the three algorithms.

The Procrustes distance test determined that the shortest morphological distance between *A. taurus* and *A. concolor* was 0.0270 PD and the distance between *M. chrysurus* and *M. dorsalis* was longer (0.06 PD). The cephalic region is where most of the variation occurred. The mouths of the species on the eastern side of the Isthmus are in higher positions than those of their sister species on the EP (Fig. 6).

Allometry

There is a weakly significant correlation between size and morphology ($r^2 = 0.024$, $F_{94-14,758} = 3.84$, $p = 0.000$). The morphological variations related to size are expressed mainly in the form of as relative differences in mouth position, eye size, and body depth. Smaller species (such as *Chromis spp*.) tend to have larger eyes and superior mouth positions. In contrast, larger species (such as *Microspathodon spp*.) have smaller eyes, terminal mouth positions, and are deep bodied (Fig. 7).

Diversification

The PGLS showed no evolutionary correlation between niche and morphology. Size was significantly correlated with morphology and niche in both models. Morphology fit better in the BM model, and niche fit well in both models (Table 3).

Discussion

The morphology and niche of the sister species on each side of the Isthmus of Panama differ significantly. All the species on the eastern side of the Isthmus of Panama possess upward-oriented mouths, indicating that they tend to feed in the pelagic zone (Liem 1993; Pavlov and Kasumyan 2002; Aguilar-Medrano et al. 2011). They have bigger eyes which are closer to their mouths, suggesting a tendency towards visually selective feeding (Barel 1983; Wainwright and Bellwood 2002; Schmitz and Wainwright 2011; Aguilar-Medrano et al. 2011). The angles of their pectoral fin attachments are somewhat horizontal, which facilitates long-distance swimming (Wainwright et al. 2002; Walker and Weastneat 2002; Aguilar-Medrano et al. 2013). This morphological pattern indicates that these species more actively pursue their prey in the water column than their sister species in the eastern Pacific. This pattern is observed in all pairs of sister species, independent of their respective trophic guilds. Therefore, the environment has strong effects on the morphology of its inhabitants.

Pomacentrid species have inhabited reef ecosystems for > 50 Mya (Bellwood 1996; Bellwood and Sorbini 1996). Nevertheless, the published data has indicated that damselfish are highly opportunistic and use a wide range of resources according to their availability (Emery 1973; Greenfield and Woods 1980; Grove et al. 1986; Allen 1991;

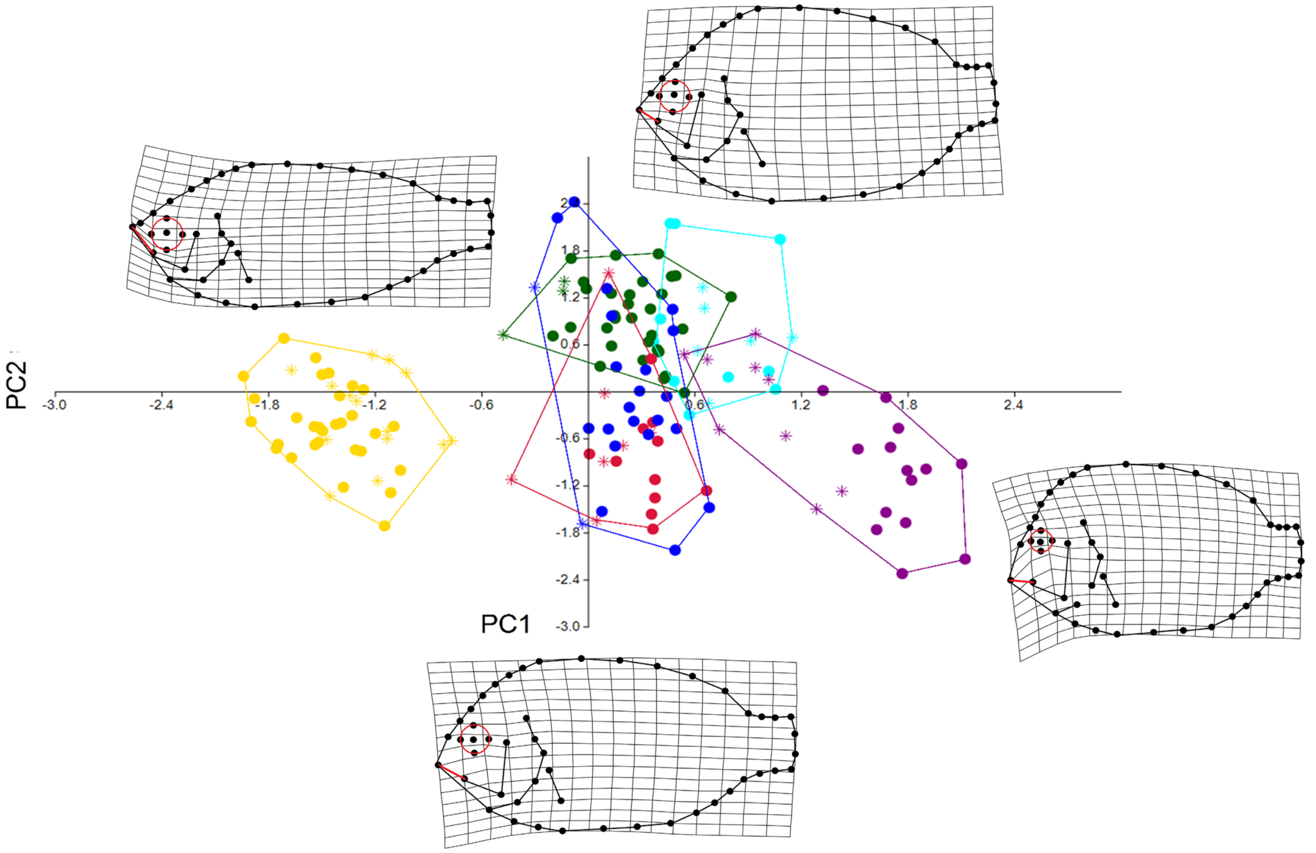


Fig. 5 Principal components analysis (PCA) on the geometric morphometric data. Deformation grids represent the deformation of each extreme of the axis versus the grand mean. Highlighted in red the eye and mouth. Yellow: *Chromis atrilobata* (dot) and *Ch. multilineata* (star); pink: *Ch. alta* (dot) and *Ch, enchrysura* (star); purple: *Microspathodon dorsalis* (dot) and *M. chrysurus* (star); blue: *Stegastes rectifraenum* (dot) and *S. imbricatus* (star); green: *Abudefduf troschelii* (dot) and *A. hoefleri* (star); aqua: *A. concolor* (dot) and *A. taurus* (star)

Table 2 Analyses of morphological variation between sisters species

Algorithm	Euclidian			S. Rho		Gower	
Sister species	Permutation	*F*	*p*	*F*	*p*	*F*	*p*
A. taurus							
A. concolor	9999	0.951	0.4552	1.786	**0.0216**	1.165	0.1441
A. hoefleri							
A. troschelii	9999	4.795	**0.0009**	2.481	**0.0004**	1.754	**0.0002**
Ch. multilineata							
Ch. atrilobata	9999	5.67	**0.0003**	3.658	**0.0001**	1.671	**0.0001**
Ch. enchrysura							
Ch. alta	9999	1.549	0.1135	2.309	**0.0052**	1.528	**0.0006**
M. chrysurus							
M. dorsalis	9999	8.552	**0.0001**	4.877	**0.0001**	1.654	**0.0001**
S. imbricatus							
S. rectifraenum	9999	1.342	0.1942	1.414	0.0735	1.234	**0.0473**

One-way NPMANOVA using three algorithms to compare results, Euclidian distance Spearman's Rho and Gower distance in bold significant differences

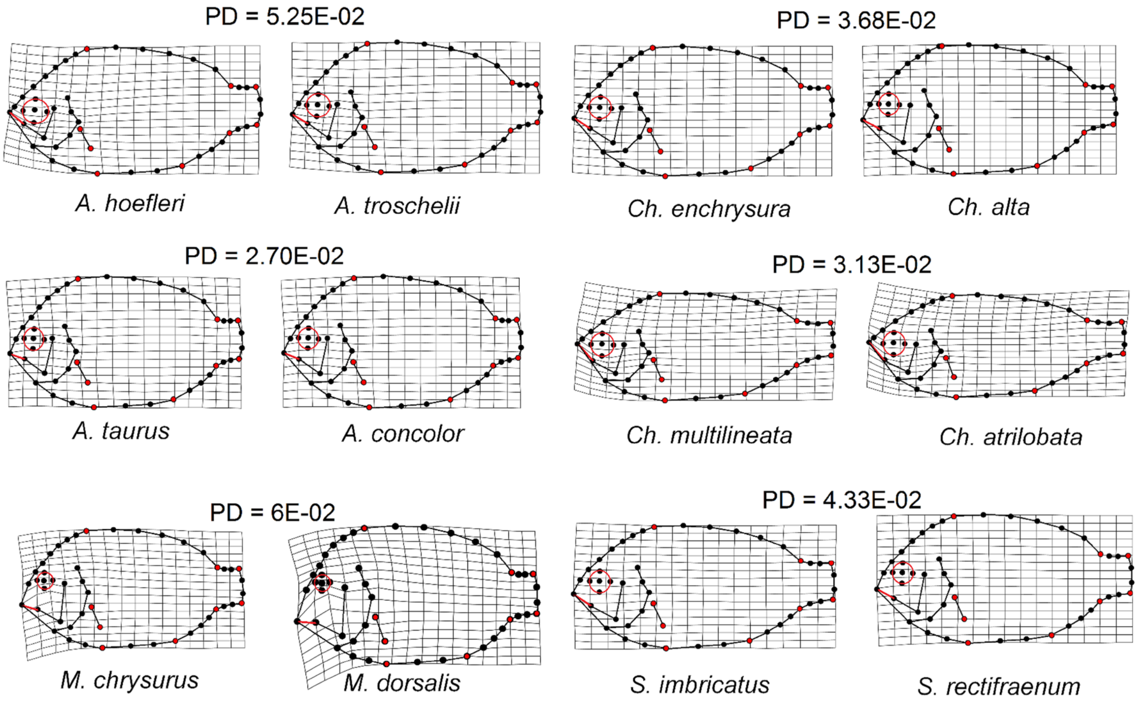
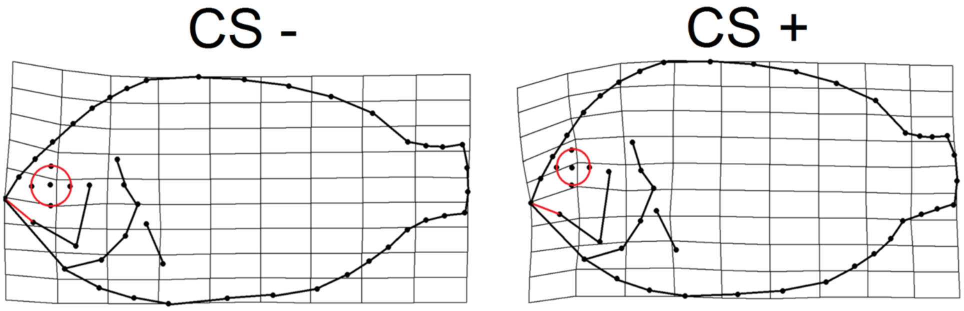


Fig. 6 Deformation grids represent the deformation of each sister species versus the grand mean. Highlighted in red the eye, mouth and base of all fins. *PD* Procrustes distance

Fig. 7 Size related to morphological variation. Deformation grids represent the deformation of each extreme of the axis versus the grand mean. CS – represent the morphology associated to smaller organisms, CS + represent the morphology associated to larger organisms



Frédérich et al. 2008; Cooper and Westneat 2009; Aguilar-Medrano et al. 2011, 2017). Species in the Caribbean Sea, Gulf of Mexico, and the Atlantic use mainly coral reefs. In contrast, the eastern Pacific species can also be found in rocky reefs and kelp forests. Damselfish widen their niches in response to ecological opportunity without undergoing significant morphological changes. This behavior may explain why no correlation was found between niche and morphology over evolutionary time.

Divergence was observed on each side of the Isthmus of Panama. On the other hand, most of the sister species also showed phylogenetic conservatism. The principal component analyses run on the ecological and morphological data indicated that sister species tend to resemble each other more than non-sister species (Figs. 3, 4, 5). Thus, divergence increased variation, while conservatism minimized it. The mechanisms underlying adaptive diversification and conservatism, however, are based on population biology; thus, both are outcomes of the same underlying factors, but they act in opposite directions (Holt 1987; Schluter 2000; Ackerly 2003, 2016).

The results demonstrated that, via evolution, size was correlated with both niche and morphology (Table 3). Therefore, size is an important trait influencing damselfish evolution. Larger species tend to inhabit shallow environments and possess narrow mouth and deeper bodies. Examples are *Microspathodon dorsalis* and *Abudefduf taurus*. Smaller species such as *Stegastes spp*. (the smallest studied here) tend to exhibit average morphological and ecological characteristics. *Chromis*, the second smallest group, has a relatively wider depth range, large mouth and fusiform body (Table 1; Fig. 7).

Table 3 Results of phylogenetic generalized least squares analyses testing correlated evolution between morphology, niche and size

		AIC	Value	Std. error	*t* value	*p* value	Correlation
RW1/PCN1	BM	105.41	523.35	353.17	– 1.48	0.17	– 0.002
	OU	**117.92**	– 758.82	455.31	– 1.67	0.13	0.002
RW1/PCN2	BM	117.87	745.82	658.33	1.32	0.31	– 0.002
	OU	**105.39**	276.35	243.39	1.21	0.30	0.002
RW1/SL	BM	**– 19.88**	0.000	0.000	0.65	0.53	– 0.49
	OU	– 17.99	0.001	0.000	2.24	**0.05**	0.95
RW2/PCN1	BM	**105.32**	195.30	1079.75	0.21	0.86	– 0.08
	OU	118.59	371.58	1188.20	0.31	0.76	– 0.02
RW2/PCN2	BM	116.71	– 1116.44	1906.72	– 0.59	0.57	– 0.08
	OU	**104.61**	– 338.81	590.29	– 0.58	0.58	– 0.02
RW2/SL	BM	**– 19.88**	0.000	0.000	0.65	0.53	– 0.49
	OU	– 17.99	0.001	0.000	2.24	**0.05**	– 0.95
PCN1/SL	BM	**117.36**	– 0.35	0.13	– 2.71	**0.02**	– 0.49
	OU	129.88	– 1.05	0.47	– 2.25	**0.05**	– 0.95
PCN2/SL	BM	114.56	0.89	0.2	8.01	**0.00**	– 0.49
	OU	**110.82**	0.71	0.2	4.01	**0.00**	– 0.95

BM Brownian motion model, *OU* Ornstein–Uhlenbeck model, *AIC* Akaike's information criterion, *RW* relative warps of morphological data, *PCN* principal component of niche breadth, *SL* standard length

p value in bold statistically significant values

AIC in bold better model fit

There are several hypotheses about the timing of the closure of the Central American Seaway. The phylogenetic hypothesis of Frédérich et al. (2013), however, is consistent with the most highly supported hypothesis on the final rise of the Isthmus of Panama ~ 3–6 Mya (Duque-Caro 1990; Coates and Obando 1996; Glynn and Ault 2000; Bellwood and Wainwright 2002; Steeves et al. 2005; Bacon et al. 2015; Montes et al. 2015; O'Dea et al. 2016; Jaramillo et al. 2017). Nevertheless, the diversification times of sister species indicates that some of them actually started their differentiation before the isthmus rose. Examples include *Chromis atrilobata* and *Ch. multilineata* (~ 7.5–19 Mya), *Microspathodon* species (~ 2.5–12 Mya), and *Stegastes* (~ 2.5–10 Mya). Others, such as *Abudefduf hoefleri* and *A. troschelii*, may have diverged after the fact (~ 1–3 Mya).

The provinciality analysis corroborated some of the findings reported by Allen (1991) and Aguilar-Medrano et al. (2015), who also cited the Equatorial Islands, St. Helena Island, and the Gulf of Mexico. Therefore, these provinces are highly unique. St. Helena Island seems to be the contact point between the Caribbean Sea Province and the African Province.

Certain distribution patterns appear to be correlated with divergence time. For example, *Stegastes spp.* are distributed in the most remote province from the Isthmus of Panama, which might indicate either narrowing of distribution or colonization after divergence. In either case, the time of divergence (~ 2.5–10 Mya) is concordant. On the other hand, *Abudefduf troschelii* is distributed in all the provinces of the eastern Pacific, while *A. hoefleri* is found only in the African Province. The divergence time, however, suggests post-divergence contact (~ 1–3 Mya). These results require further analysis using the techniques of population genetics.

It is expected that the morphological and ecological differences between species decrease as the amount of time since the species shared a common ancestor increases (Blomberg and Garland 2002; Losos 2008; Pyron and Burbrink 2009). Nevertheless, the results of the present study indicate a diverse evolutionary process in damselfish. Certain damselfish species might have traits amenable to rapid adaptation (Cooper and Westneat 2009; Frédérich et al. 2013; Aguilar-Medrano et al. 2016). For example, the sister species with the shortest time since divergence are *Abudefduf hoefleri* and *A. troschelii* (~ 1–3 Mya). *A. hoefleri* is found only in the African Province, whereas *A. troschelii* is present in all localities of the eastern Pacific. Their niche variations are correlated with depth range, water column position, and geographic range. Their morphologies vary significantly in terms of eye and snout position and body depth. Therefore, these two species have the second largest Procrustes distance. On the other hand, the sister species with the second longest time since divergence are *Microspathodon* (~ 2.5–12 Mya). They are restricted to the central provinces near the Isthmus. Their niche variation is related to depth range, water column position, and geographic climate. Their morphologies vary significantly in terms of eye and snout position and body depth. Therefore, these two species present with the largest Procrustes distance. They also show size variation, with *M. dorsalis* being the largest species.

The successful response to a vicariant event depends on the ability of a taxon to persist, adapt, and disperse. These capacities are contingent upon the biological traits of the population in that environment. Vicariant events affecting ancestral biota triggered differential evolutionary processes on each side of the barrier (Bermingham and Lessios 1993; Bermingham et al. 1997; Knowlton and Weigt 1998; Lessios 1998; Lessios et al. 2001; Marko 2002; Marko and Moran 2002). The results of this study indicate that sister species underwent post-vicariance evolutionary processes, which are trade-offs between conservatism and divergence. In the case of damselfish sister species separated by the Isthmus of Panama, the observed variations indicate different trends and significant environmental influences in the evolution of the species on each side of the barrier.

Acknowledgements This study was partially funded by the Universidad Autónoma de Tamaulipas (project PFI2015-06). I am in debt and grateful to all my colleagues in the fish collections. Lucia Campos and Eduardo F. Balart at CIBNOR, La Paz, BCS, Mexico; Victor Cota and José De La Cruz-Agüero at CICIMAR, La Paz, BCS, Mexico; Rick Feeney at LACM, Los Angeles, CA, USA; H.J. Walker and Phil Hastings at SIO, San Diego, CA, USA; and Zachary Randall and Rob Robins at FLMNH, Florida, USA.

Compliance with ethical standards

Conflict of interest The author declares no conflict of interest.

Ethical approval This study did not use live organisms.

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