



Patterns of morphological evolution of the cephalic region in damselfishes (Perciformes: Pomacentridae) of the Eastern Pacific

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Pomacentridae are one of the most abundant fish families inhabiting reefs of tropical and temperate regions. This family, comprising 29 genera, shows a remarkable diversity of habitat preferences, feeding, and behaviours. Twenty-four species belonging to seven genera have been reported in the Eastern Pacific region. The present study focuses on the relationship between the diet and the cephalic profile in the 24 endemic damselfishes of this region. Feeding habits were determined by means of underwater observations and the gathering of bibliographic data. Variations in cephalic profile were analyzed by means of geometric morphometrics and phylogenetic methods. The present study shows that the 24 species can be grouped into three main trophic guilds: zooplanktivores, algivores, and an intermediate group feeding on small pelagic and benthic preys. Shape variations were low within each genus except for *Abudefduf*. Phylogenetically adjusted regression reveals that head shape can be explained by differences in feeding habits. The morphometric phylogeny recovered the subfamily Stegastinae and the relationship between *Abudefduf troschelii* and *Chromis* species. The cephalic profile of damselfishes contains a clear and strong phylogenetic signal. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 102, 593–613.

ADDITIONAL KEYWORDS: Gulf of California – head shape – phylogenetic morphometrics – reef fishes – trophic niche.

INTRODUCTION

The damselfishes (Pomacentridae) are a species-rich (approximately 360), worldwide distributed family of marine fishes that inhabit tropical and temperate waters (Allen, 1991). Most inhabit tropical coral reefs, although a number of species live in rocky reefs of cooler temperate waters. They have been present within these ecosystems for 50 million years (Bellwood, 1996; Bellwood & Sorbini, 1996). In the Eastern Pacific, their range extends from Monterey Bay

(California, USA) in the north to the south of Chile, including all the oceanic islands of this region (Fig. 1). In this part of the Pacific, Pomacentridae is one of the most abundant families, having radiated in coral reefs, rocky reefs, and kelp forests. Twenty-four species belonging to seven genera (i.e. *Stegastes*, *Microspathodon*, *Hypsypops*, *Nexilosus*, *Chromis*, *Azurina*, and *Abudefduf*) have been reported in the Eastern Pacific and all are endemic to this region (Robertson & Allen, 2008). The genera *Azurina*, *Hypsypops*, and *Nexilosus* are solely present in this part of the Pacific, whereas the genus *Microspathodon* contains two species in the Eastern Pacific and

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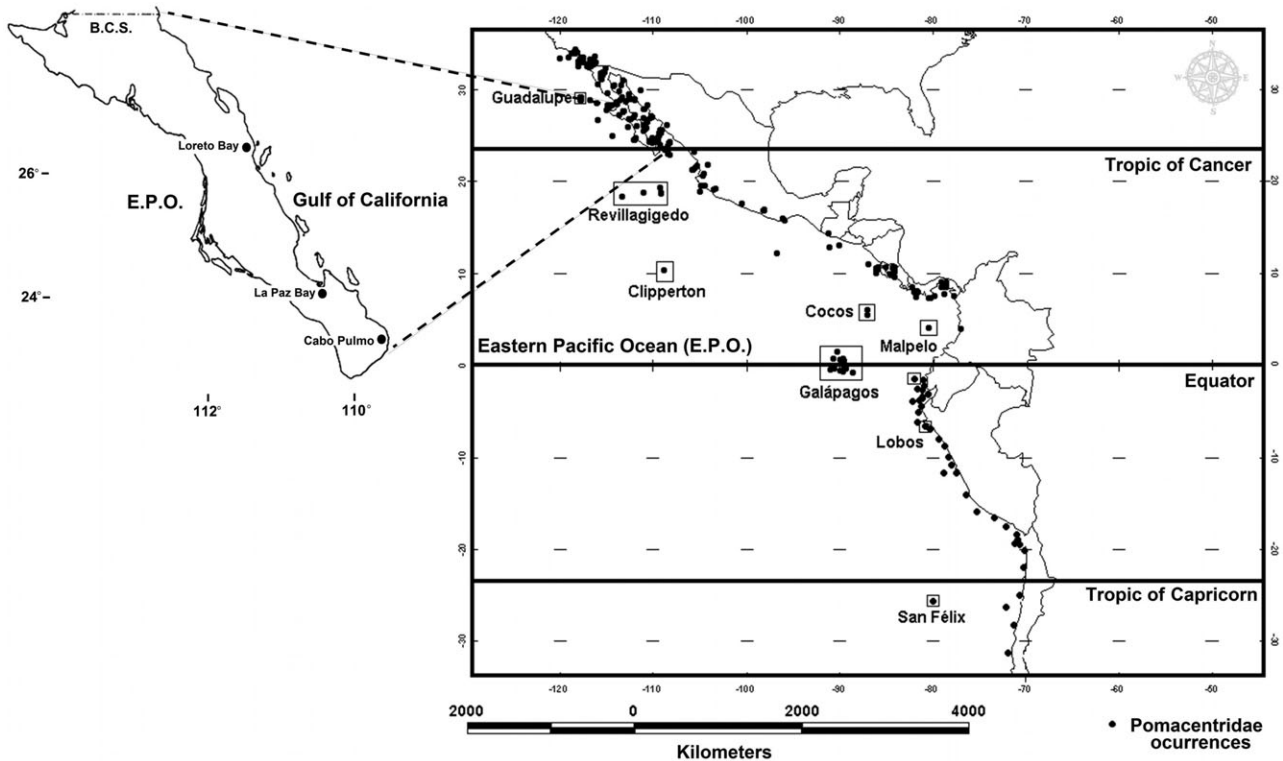


Figure 1. Distribution of damselfish species in the coast and islands of the Eastern Pacific Ocean. Left: localities of underwater observations in the Gulf of California: National Marine Park of Loreto, La Paz Bay, and National Marine Park of Cabo Pulmo.

two others in the Atlantic Ocean. On the other hand, the genera *Abudefduf*, *Chromis*, and *Stegastes* are distributed worldwide (Allen, 1991). All genera represented in this region belong to the basal groups of the family Pomacentridae (i.e. the subfamilies Stegastinae, Chrominae and Abudefdufinae; as defined by Cooper, Smith & Westneat, 2009) (Fig. 2). The members of the most derived subfamily Pomacentrinae have radiated in the Indo-West Pacific region only (Cooper *et al.*, 2009). Despite the use of numerous molecular data, the phylogenetic relationships within the family Pomacentridae are not fully resolved (Tang, 2001; Quenouille, Bermingham & Planes, 2004; Cooper *et al.*, 2009).

The damselfishes of the Eastern Pacific display a remarkable diversity with regards to habitat preferences, feeding habits, and behaviours. Their coloration is highly variable, ranging from drab hues of brown, grey, and black to brilliant combinations of orange, yellow, and neon blue (Robertson & Allen, 2008). Generally speaking, the damselfishes living in coral reefs of the Indo-West Pacific region feed mainly on filamentous algae as well as small planktonic and benthic invertebrates (Allen, 1991; Kuo & Shao, 1991; Frédérick *et al.*, 2009). The drab-coloured species feed mainly on algae, whereas most

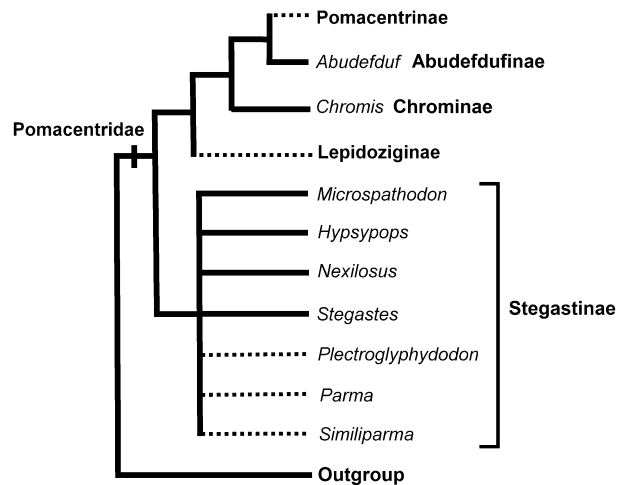


Figure 2. Phylogeny of Pomacentridae family *sensu* Cooper *et al.* (2009). Dotted lines refer to groups not represented in the Eastern Pacific region.

of the brightly patterned species (e.g. members of the genus *Chromis*) obtain their nourishment from the current-borne plankton (Allen, 1991). To our knowledge, the trophic ecology of only two damselfish species from the Eastern Pacific has

been studied in detail: *Stegastes rectifraenum* and *Microspathodon dorsalis* (Montgomery, 1980).

Ecomorphological studies attempt to understand the relationships between the morphological variation among species and their corresponding ecological variation (Norton, Luczkovich & Motta, 1995; Wainwright, 1996; Costa & Cataudella, 2007). For example, head morphology is subject to various constraints dealing with the strategy of feeding and the type of ingested food (Liem, 1979, 1993; Wainwright & Richard, 1995). The relationship between cephalic morphology and diet has been broadly studied in freshwater fishes such as perches (Svanbäck & Eklöv, 2002), centrarchids (Collar, Near & Wainwright, 2005), and cichlids (Barel, 1983; Albertson, Streelman & Kocher, 2003), as well as marine fishes such as sparids (Costa & Cataudella, 2007) and labrids (Westneat, 1995; Streelman & Karl, 1997; Wainwright *et al.*, 2004). The first ecomorphological studies in Pomacentridae (Emery, 1973; Gluckmann & Vandewalle, 1998) suggested that a detailed study of cephalic morphology could reveal different trophic groups. Using geometric morphometrics (Rohlf & Marcus, 1993; Lawing & Polly, 2009), Frédérich *et al.* (2008) highlighted strong size and shape variations in four skeletal units of the damselfish skull among species living in the Indo-West Pacific region and belonging to different trophic groups. Recently, Cooper & Westneat (2009) investigated the evolution of skull shape within Pomacentridae and showed that planktivory has involved important changes in damselfish head morphology. In this latter study, the authors used only one species per genus to infer morphological evolution. Consequently, the inference of intra-generic variation in trophic morphology was not possible. Recently, Barneche *et al.* (2009) confirmed the applicability of Bergmann's rule to the family Pomacentridae, stating that the larger species are found at higher latitudes. The damselfishes of the Eastern Pacific are distributed along a wide range of latitudes (–33°N to 35°S; Fig. 1) and show a great variation of body size among species (standard length in the range 11–36 cm; Table 1). Moreover, the genera *Chromis*, *Hypsypops*, *Nexilosus* and *Microspathodon* contain the largest damselfishes (Allen, 1991). This axis of body size variation could have promoted morphological variation within this group of endemic species.

In the present study, we collect trophic data about all endemic damselfish species of the Eastern Pacific region and apply geometric morphometric techniques and phylogenetic methods to the cephalic region of these damselfishes. The main goal of the study is to provide an overview of the trophic diversity of damselfishes in the Eastern Pacific and to determine whether variations in cephalic shape can be explained by size variation (i.e. allometry), feeding behaviour,

and/or phylogeny. In particular, we investigate the ecomorphological hypothesis that cephalic shape variation is associated with dietary differences in damselfishes of the Eastern Pacific. On the basis of previous analyses in damselfishes (Emery, 1973; Gluckmann & Vandewalle, 1998; Frédérich *et al.*, 2008; Cooper & Westneat, 2009), we predict that diet is correlated to shape variations. We also test the presence of phylogenetic signal (i.e. the expectation that the phylogenetic relatedness is associated with shape similarity) (Cardini & Elton, 2008) in the cephalic region of damselfishes. We have no a priori hypothesis regarding this relationship because such studies are limited in fishes (Guill, Heins & Hood, 2003).

MATERIAL AND METHODS

TROPHIC DATA

Underwater observations (UO) were carried out in three areas in the Gulf of California, Mexico (Fig. 1): (1) National Marine Park of Loreto Bay; (2) La Paz Bay; and (3) National Marine Park of Cabo Pulmo. The National Marine Park of Loreto Bay is located at 26°07' to 25°43'N and 111°21' to 111°13'W. Coronado, Carmen and Danzante islands delimit this area where the substrate composition varies from fine sand to cobbles, boulders, and rocks (Campos-Dávila *et al.*, 2005). La Paz Bay is located at 24°07' to 24°21'N and 110°17' to 110°40'W, the reef presents fine sand, big (30 m) and small (12 m) boulders, big walls (15 m), and rocky reef (Aburto-Oropeza & Balart, 2001). The National Marine Park of Cabo Pulmo is the northernmost coral reef in the Eastern Pacific and is located near the entrance of the Gulf of California in a transitional zone between the tropical and temperate Pacific at 23°50'N, 109°25'W (Alvarez-Filip, Reyes-Bonilla & Calderon-Aguilera, 2006). This park presents a barrier reef and a lagoon composed of small boulders with sandy areas. The UO were carried out during January, May, and August 2008, and January and March 2009, by scuba diving and snorkeling. Observations of territorial species were carried out for 2 min per organism; for fishes in constant movement (e.g. planktivorous), a maximum of 10 min were devoted per organism. Observations were conducted on 20–100 individuals per species, according to the availability. During these observations, we mainly focused on two main components of their trophic ecology: (1) social behaviour: territorial and solitary species versus species forming groups and (2) feeding habit: feeding areas (especially for territorial, algivorous species), feeding strategy (i.e. biting, grazing or feeding in the water column), and type of prey. Fourteen damselfish species were

Table 1. List of studied damselfish species

Species	Loreto Bay	La Paz Bay	Cabo Pulmo	N	N _M	N _{ew}	SL A (cm)	SL B (cm)	SL C (cm)
<i>Abudefduf concolor</i> (Gill, 1862)				8	8	0	13	15	19
<i>Abudefduf declivifrons</i> (Gill, 1862)	x	x	x	12	5	7	13	16	18
<i>Abudefduf troschelii</i> (Gill, 1862)	x	x	x	39	13	26	13	16	23
<i>Azurina eupalama</i> Heller & Snodgrass, 1903				8	8	0	10	11	16
<i>Azurina hirundo</i> Jordan & McGregor, 1898 en Jordan & Evermann, 1898				25	25	0	13	15	17
<i>Chromis alta</i> Greenfield & Woods, 1980	x	x	x	12	11	1	10	15	15
<i>Chromis atrilobata</i> Gill, 1862	x	x	x	28	4	24	8	10	13
<i>Chromis crusma</i> (Valenciennes, 1833 en Cuvier & Valenciennes, 1833)				16	16	0	13	16	19
<i>Chromis intercrusma</i> Evermann & Radcliffe, 1917				15	15	0	16	17	28
<i>Chromis limbaughi</i> Greenfield & Woods, 1980	x			25	13	12	11	14	12
<i>Chromis meridiana</i> Greenfield & Woods, 1980				25	25	0	10	12	11
<i>Chromis punctipinnis</i> (Cooper, 1863)			x	23	23	0	19	25	25
<i>Hypsypops rubicundus</i> (Girard, 1854)			x	25	19	6	20	23	36
<i>Microspathodon bairdii</i> (Gill, 1862)	x	x	x	20	5	15	21	25	31
<i>Microspathodon dorsalis</i> (Gill, 1862)	x	x	x	25	6	19	18	22	31
<i>Nexilosus latifrons</i> (Tschudi, 1846)				16	16	0	22	27	30
<i>Stegastes acapulcoensis</i> (Fowler, 1944)		x	x	27	26	1	12	18	18
<i>Stegastes arcifrons</i> (Heller & Snodgrass, 1903)				15	15	0	11	18	16
<i>Stegastes baldwini</i> Allen & Woods, 1980				10	10	0	8	9	13
<i>Stegastes beebei</i> (Nichols, 1924)				10	10	0	11	12	17
<i>Stegastes flavilatus</i> (Gill, 1862)	x	x		26	21	5	11	14	15
<i>Stegastes leucurus</i> (Gilbert, 1892)	x	x	x	25	3	22	12	15	17
<i>Stegastes rectifraenum</i> (Gill, 1862)	x	x	x	24	0	24	10	12	13
<i>Stegastes redemptus</i> (Heller & Snodgrass, 1903)			x	23	23	0	12	15	15
<i>Zalambius rosaceus</i> (Jordan & Gilbert, 1880)				27	27	0	14	17	20

Sites of underwater observation in the Gulf of California, Mexico.

N, number of specimens used for the geometric morphometric analysis; N_M, number of specimens from museum collections; N_{ew}, number of specimens collected in the wild; SL, standard length; SL A, average SL of the fishes used in the present study; SL B, maximum SL of the fishes used in present study; SL C, maximum SL reported by Allen (1991).

directly observed and studied (Table 1). Consequently, the diet of all Eastern Pacific species was described by means of our UO and completed by a review of results from previous general studies. Using all these data, an alimentary item matrix of the 24 endemic damselfishes of the Eastern Pacific was built (Table 2). It was analyzed for the redundancy of the 16 alimentary items in all the species using the Kendall correlation index for presence–absence data; this analysis was conducted to group the alimentary items and reduce the main matrix. All alimentary items with a correlation higher than 0.80 were grouped (Table 2).

Additionally, the data of diet composition were also used for the estimation of the trophic level of each damselfish species. The TROPH index, initially used for Mediterranean fishes (Stergiou & Karpouzi, 2002), expresses the position of organisms within the food webs that largely define aquatic ecosystems. Real consumers do not usually have TROPHs with integer values and the definition of TROPH for any consumer species (1) is:

$$\text{TROPH} = 1 + \sum_{j=1}^G \text{DC}_{ij} \cdot \text{troph}_j$$

where G is the total number of prey species, DC_{ij} represents the fraction of j in the diet of i and troph_j is the fractional trophic level of prey j . The TROPH value was calculated from the dataset using TROPHLAB (Pauly *et al.*, 2000), which is a stand-alone application for estimating TROPH and its standard error using qualitative information from the list of items known to occur in the diet of each species. If such trophic levels are missing, TROPHLAB uses default troph values for various prey (based on data in FISHBASE; Froese & Pauly, 2000). TROPH values were used as feeding habit data, allowing the study of the relationships between head shape of damselfishes and their trophic ecology in a quantitative way, and giving an ecomorphological meaning to shape differences (see methods below) (Costa & Cataudella, 2007).

GEOMETRIC MORPHOMETRICS AND PHYLOGENETIC ANALYSIS

The sample comprised 509 specimens belonging to all 24 damselfishes of the Eastern Pacific (Table 1). Additionally, the embiotocid *Zalembeius rosaceus* (Jordan & Gilbert, 1880) (family Embiotocidae) was used as an ‘outgroup’. The Embiotocidae are now recognized as the sister group of Pomacentridae (Streelman & Karl, 1997; Mabuchi *et al.*, 2007), *Zalembeius rosaceus* is a small benthic carnivorous fish distributed inside the same area of the studied pomacentrids. Some specimens were speared during the field studies and the others came from the museum collections of CIBNOR

(La Paz, BCS, México), CICIMAR (La Paz, BCS, México), SIO (San Diego, CA, USA), LACM (Los Angeles, CA, USA), and USNM (Washington, DC, USA) (Table 1). The list of museum specimens used in this study is available upon request from the first author (R.A.-M.).

The specimens were photographed in lateral view with a camera (Kodak $\times 4$ optical and 4 mega pixels) and the x - and y -coordinates of 18 homologous landmarks (Fig. 3) were digitized from the left side of each individual using TPSDIG, version 2.05. Superimposition of landmark data was achieved using a generalized procrustes analysis (Rohlf & Slice, 1990) which aligned landmark configurations such that the sum of squared distances between corresponding landmarks was minimized by scaling, translating, and rotating specimens with respect to a mean consensus configuration. The consensus configuration (‘the grand mean’) was obtained and used as the reference. Partial warp scores (PWs) including both uniform and non-uniform components were calculated and used as descriptors of shape variation (Bookstein, 1991; Rohlf, 1993).

A principal components analyses (PCA) was used to find hypothetical variables (components) that account for as much of the variance in the morphological data (Davis, 1986). Subsequently, two kinds of discriminant analyses were carried out. Differences among species were tested by means of analyses of variance (ANOVA), the Tukey–Kramer test and multivariate analyses of variance (MANOVA). Then, a canonical variance analysis (CVA) was performed to compare cephalic profile among groups. Indeed, CV axes allow us to maximize the differences in shape among groups relative to within group variance. MANOVA and CVA were computed using all shape variables (PWs). Deformation grids using the thin-plate spline (TPS) algorithm were used to visualize the patterns of shape variations along PC axes and CV axes (Thompson, 1917; Bookstein, 1991; Rohlf, 1993).

To determine whether shape data are hierarchically clustered, we applied phenetic and phylogenetic parsimony methods for grouping. Phenetic distance methods are based upon a different conceptual framework of grouping than parsimony. We included a phenogram to determine whether there was evidence for the assertion that similarity in morphometric data is not the result of a phylogenetic signal. Phenetic relationships were summarized using a cluster analysis on the matrix of mean shape. Phenogram of the 25 species was calculated using the unweighted pair-group method algorithm, and the Procrustes distance as measure of the similarity. The goodness of fit of the cluster analysis was measured by the coefficient of cophenetic correlation (Cardini & Elton, 2008). The

Table 2. Diet and trophic index of all pomacentrids living in the Eastern Pacific

Species	Diet																TROPH index Mean ± SE	References									
	Benthic						Pelagic				Other																
	A	B	C	D	E	F	G	H	I	J	K	L	M	A	B	C			D	E	F	G	H	I	J	K	L
<i>Abudefduf concolor</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.38	Robertson & Allen, 2008
<i>Abudefduf declivifrons</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.6 ± 0.52	UO; Robertson & Allen, 2008
<i>Abudefduf troschelii</i>	0	1	0	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	3.9 ± 0.61	UO; Hobson, 1965; Petersen & Marchetti, 1989; Grove & Lavenberg, 1997
<i>Azurina eupalama</i>	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4 ± 0.66	Robertson & Allen, 2008
<i>Azurina hirundo</i>	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3.8 ± 0.58	Robertson & Allen, 2008
<i>Chromis alta</i>	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4 ± 0.65	Robertson & Allen, 2008
<i>Chromis atrilobata</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.9 ± 0.61	UO; Hobson, 1965; Espinoza & Salas, 2005; Robertson & Allen, 2008
<i>Chromis crusma</i>	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4 ± 0.65	Núñez & Vásquez, 1987; Angel & Ojeda, 2001
<i>Chromis intercrusma</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4 ± 0.65	Robertson & Allen, 2008
<i>Chromis limbaughi</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.38	UO; Robertson & Allen, 2008
<i>Chromis meridiana</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.38	Greenfield & Woods, (1980)
<i>Chromis punctipinis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.4 ± 0.45	Bray <i>et al.</i> , 1988; Rothans & Miller, 1991
<i>Hypsypops rubicundus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.6 ± 0.21	Hixon, 1981; Robertson & Allen, 2008
<i>Microspathodon bairdii</i>	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.8 ± 0.36	UO; Robertson & Allen, 2008
<i>Microspathodon dorsalis</i>	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.8 ± 0.36	UO; Espinoza & Salas, 2005; Robertson & Allen, 2008
<i>Nexilosus latifrons</i>	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.9 ± 0.32	Grove & Lavenberg, 1997; Angel & Ojeda, 2001; Robertson & Allen, 2008
<i>Stegastes acapulcoensis</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.40	UO; Espinoza & Salas, 2005; Robertson & Allen, 2008
<i>Stegastes arcifrons</i>	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.1 ± 0.38	Grove & Lavenberg, 1997; Robertson & Allen, 2008
<i>Stegastes baldwini</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.40	Robertson & Allen, 2008
<i>Stegastes beebei</i>	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.2 ± 0.38	Grove & Lavenberg, 1997; Robertson & Allen, 2008
<i>Stegastes flavilatus</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.38	UO; Petersen & Marchetti, 1989; Espinoza & Salas, 2005; Robertson & Allen, 2008
<i>Stegastes leucurus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.40	UO; Robertson & Allen, 2008
<i>Stegastes rectifraenum</i>	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2.9 ± 0.34	UO; Hobson, 1965; Petersen & Marchetti, 1989; Robertson & Allen, 2008
<i>Stegastes redemptus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 ± 0.40	Robertson & Allen, 2008
<i>Zalambius rosaceus</i>	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.3 ± 0.47	Robertson & Allen, 2008

Benthic diet: A, sponges; B, macroalgae, microalgae, crustaceans, and sessile worms; C, sessile mollusks; D, mobile crustaceans; E, mobile worms; F, anemones; G, gastropods; H, fish eggs. Pelagic diet: I, zooplankton; J, crustaceans; K, fish larvae. Other: L, detritus; M, ectoparasites. UO, Underwater observations.

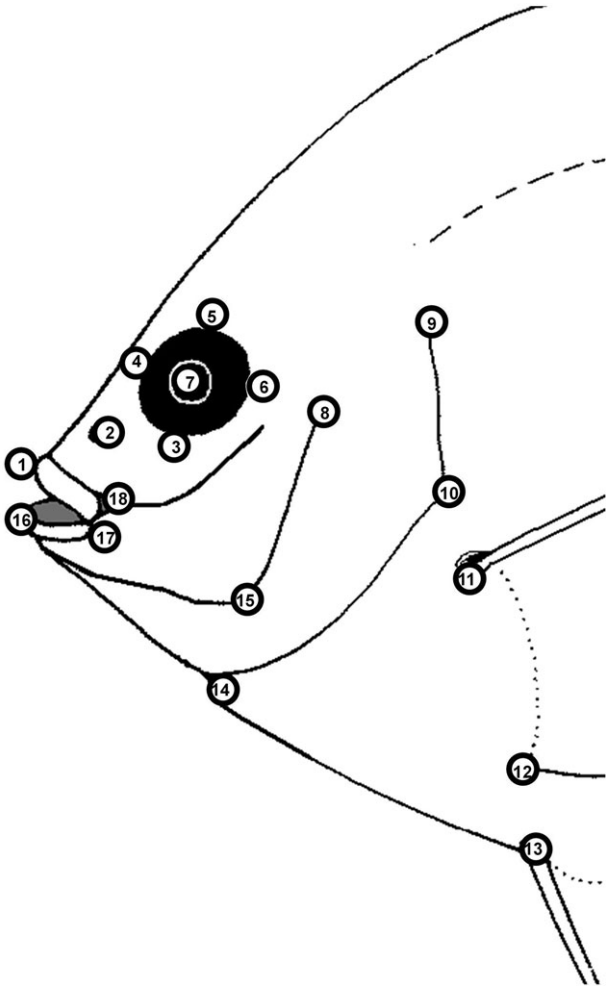


Figure 3. Anatomical landmarks used in geometric morphometric analyses: (1) tip of the premaxilla; (2) nostril; (3–6) inferior, anterior, superior, and posterior margin of the eye; (7) center of the eye; (8) superior tip of the preopercular; (9) superior tip of the operculum; (10) posterior tip of the operculum; (11, 12) superior and inferior insertion of the pectoral fin; (13) insertion of the pelvic fin; (14) insertion of the operculum on the body profile; (15) postero-ventral corner of the preopercular; (16, 17) anterior and posterior extremity of the dentary; (18) posterior extremity of the premaxilla.

morphological phylogenetic analysis was executed using the 32 shape variables (RWs) as characters for all studied species. For each species, we scored either RW intervals, RW means or both. Phylogenetic analyses were performed using new algorithms for the direct optimization of continuous characters in TNT (Goloboff, Mattoni & Quinteros, 2006). We used a combination of ratchet, sectorial search, tree drifting, and tree fusing search algorithms for the selection of optimal trees and for the estimation of Jackknife values as a measure of support.

The molecular phylogenetic hypothesis by Cooper *et al.* (2009) and our morphological phylogeny were used for phylogenetic adjusted regressions of the shape variables on the TROPH index, centroid size (CS), and standard length (SL) using the module PDAP in MESQUITE (Midford, Garland & Maddison, 2009). Our morphological and molecular phylogenies were used to obtain an estimate of character distribution and correlation along a phylogeny (Garland *et al.*, 1993). Phylogenetic regression analyses to test interspecific allometry were performed using the mean values of CS and SL versus the 32 shape variables. Similarly, we performed phylogenetic regression analysis using the mean values of the 32 shape variables and the TROPH index to test the relationship between feeding habit and cephalic shape. Additionally, we compared these results with conventional nonphylogenetic regression analyses performed in TPSREGRES, version 1.37.

Geometric morphometric analyses were performed using computer programs from the TPS series (TpsDig, TpsRegres) written by F. J. Rohlf (<http://life.bio.sunysb.edu/morph/>), and the IMP series (PCAGen, CVAGEN), created by H. D. Sheets (<http://www2.canisius.edu/~sheets/morphsoft.html>). Multivariate analyses (correlation analyses, ANOVA, PCA, CVA, MANOVA) were computed with the statistical packages: PAST, version 1.74 (Hammer, Harper & Ryan, 2001; <http://folk.uio.no/ahammer/past>), Statistica, version 8.0 (<http://www.StartSoft.com>) and JMP, version 8.0 (SAS Institute Inc.). Phylogenetic analysis was computed in TNT, version 1.1 (Goloboff, Farris & Nixon, 2008; <http://www.zmuc.dk/public/phylogeny>). Phylogenetic regressions were performed in the PDAP package (Midford, Garland & Maddison, 2010; http://mesquiteproject.org/pdap_mesquite/) for MESQUITE, version 2.73 (Maddison & Maddison, 2010; <http://mesquiteproject.org/mesquite/mesquite.html>).

RESULTS

TROPHIC AND BEHAVIOURAL DATA

Chromis limbaughi, *Chromis punctipinnis*, *Hypsypops rubicundus*, and *Stegastes redemptus* were only observed at one locality (Table 1), whereas the trophic behaviours were always consistent among sites in the other species. Unfortunately, *Chromis alta* was never observed at any location, maybe as a result of its depth preferences (down to 150 m; Allen, 1991). Generally, the underwater observations corroborate data obtained from the literature related to diet of each studied species. However, some new trophic behaviours were also observed. For example, the mainly algivorous *S. rectifraenum* was observed recurrently picking feces from zooplankton feeders (e.g. *Abudefduf troschelii*) directly in the water column.

The trophic behaviour appeared relatively constant within all genera, except within the genus *Abudefduf* (Table 2). *Abudefduf troschelii* mainly fed on planktonic preys in the water column, whereas *Abudefduf concolor* and *Abudefduf declivifrons* mainly grazed algae or fed on some small sessile animals attached to the rocks.

The analysis of alimentary items shows a strong relationship ($r > 0.80$) between four items: macroalgae, microalgae, sessile crustaceans, and worms. Consequently, these prey items were grouped in Table 2. Thus, a mainly algivorous species such as all *Stegastes* species, *Microspathodon* species, *Nexilosus latifrons*, and *H. rubicundus* may be considered as a benthic feeder grazing on algae and feeding on small benthic invertebrates. On the basis of a review of the published results and our UO, four alimentary items are species-specific (Table 2): sponges (A): *H. rubicundus*; detritus (L): *S. rectifraenum*; gastropods (G): *Z. rosaceus*; and ectoparasites (M): *A. troschelii*. *Abudefduf troschelii* showed the largest diet of the damselfish investigated in the present study, feeding in benthic and pelagic areas. All seven species of *Chromis* and the two species of *Azurina* mainly feed on zooplankton. *Zalembius rosaceus* is considered as a benthic carnivorous species, feeding only on mobile benthic crustaceans (shrimps, small crabs), worms, gastropods, and bivalves (Table 2).

As for the diet, the social behaviour was conserved within genera. *Hypsypops rubicundus* and *Stegastes* species are solitary, protecting small territories, forming couples only during the reproductive season. *Hypsypops rubicundus* showed a preference for small caves around big rocks and all *Stegastes* species prefer small rocks. Both *Microspathodon* species are solitary or live in pairs and protect big rocks with high vertical walls. *Nexilosus latifrons* was not observed in the wild, although some authors (Grove & Lavenberg, 1997; Angel & Ojeda, 2001; Robertson & Allen, 2008) reported that it is a grazing species living close to the rocks in small groups (up to ten individuals). All *Abudefduf*, *Azurina*, and *Chromis* species live in groups (i.e. schooling species) and are territorial only during the reproductive season. The main difference between these species is the number of integrants in the groups (*Abudefduf* species: 5–30 individuals versus *Chromis* species: 10–60 individuals), although it proved complicated to achieve a good description of these numbers because they changed according to the study area and the habitat. Neither *Azurina* species were observed in wild; thus, we do not have any estimation of the number of fish per group. Specimens of *A. declivifrons* and *A. concolor* could also be found solitary.

GEOMETRIC MORPHOMETRICS

The main shape variations across species can be examined by a distribution of specimens in the PC figure defined by the axis PC1 and axis PC2 (Fig. 4). The first two PCs account for 70% of the total shape variance (PC1 = 58.41% and PC2 = 10.32%). Shape variation was relatively low within each genus except for *Abudefduf*. This genus could be clearly divided into two groups, one comprising *A. concolor* and *A. declivifrons* and the other comprising *A. troschelii*. PC1 allowed a clear distinction between mainly benthic feeders (low PC1 values) and mainly zooplankton feeders (high PC1 values). The main morphological variation along axis PC1 is related to the snout length, the cephalic depth, and the eye size and position. The benthic feeders, especially *Microspathodon* species, were characterized by a very short snout and small eyes; the pelagic feeders (*Azurina* species, *Chromis* species, and *A. troschelii*) were characterized by relatively larger eyes and longer cephalic profile. Along axis PC2, the main shape variation was related to the position of the mouth and the pectoral fin, and explains the variation within some genera such as *Stegastes* and *Chromis*.

When species were used as grouping factor, the MANOVA revealed significant differences among them ($\lambda_{\text{WILKS}} = 2.36 \times 10^{-5}$, $F = 42.02$, d.f.₁ = 256, d.f.₂ = 3665.2; $P < 0.001$) and pairwise comparisons supported that all species showed significant differences in mean shape ($P < 0.05$). MANOVA was repeated using genus as grouping factor, and the results also show significant differences among all genera; however, *Abudefduf* genus show a strong pattern of segregation into two groups. According to the trophic data, the feeding habit is consistent within genera except for the genus *Abudefduf*. The segregation pattern of *Abudefduf* was tested by exploratory analyses (ANOVA, PCA, and CVA). Because the pattern was repeated in all analyses, the final MANOVA was performed using genera as grouping factor, with the genus *Abudefduf* split into two groups: (1) *A. concolor* and *A. declivifrons* and (2) *A. troschelii*. The results of MANOVA show significant differences among all groups ($\lambda_{\text{WILKS}} = 0.0000263$, $F = 41.23$, d.f. = 265, $P < 0.001$), and all pairwise comparisons based on Mahalanobis distances show significant differences ($P < 0.05$).

Discrimination among groups can be also interpreted by examining the ordination of specimens in the morphospace defined by the CV axes (Fig. 5). The first three CV axes accounted for 84% of the total shape variation in the dataset and allow the discrimination of five main groups. The axis CV1 distinguishes three groups (Table 3): (A) *Microspathodon* species; (B) *A. concolor*, *A. declivifrons*, *H.*

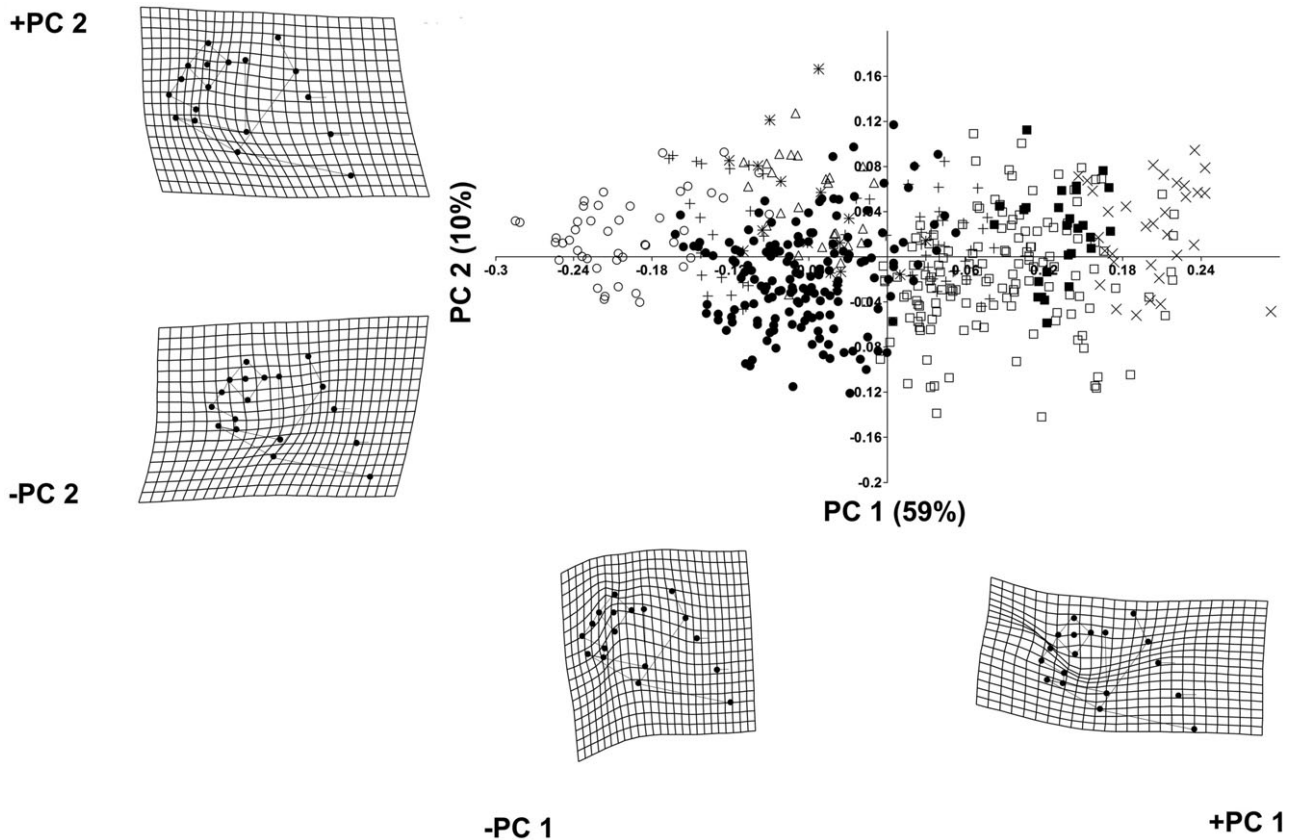


Figure 4. Scatterplot of principal components (PC) 1 and 2. Cross, *Abudehdud*; equis, *Azurina*; square, *Chromis*; triangle, *Hypsypops*; circle, *Microspathodon*; asterisk, *Nexilosus*; black circle, *Stegastes*; black square, *Zalemibus*. Thin plate spline deformation grids for the extreme points of each axis are shown; these are superimposed on the shapes predicted when the average landmark configuration of all specimens is deformed into that of a hypothetical specimen positioned at the extreme point of an ordination axis.

rubicundus, *N. latifrons* and *Stegastes* species; (C) *Azurina* species, *Chromis* species, *A. troschelii* and *Z. rosaceus*. This last group (group C) could be subdivided into three groups in the morphospace defined by CV1 and CV3: *Z. rosaceus* in the extreme high values, *Azurina* species in the middle values, and *A. troschelii* and *Chromis* species in the extreme low values (Fig. 5, Table 3).

In general, the CVA strengthened the profile and the position of the eye and the mouth. Having the lowest scores of CV1, the two species of *Microspathodon* showed a higher and flatter cephalic profile; *Chromis* species, *Azurina* species, *A. troschelii*, and *Z. rosaceus* present a lengthened cephalic profile with big eyes; *H. rubicundus*, *N. latifrons*, *Stegastes* species, *A. concolor*, and *A. declivifrons* showed an intermediate shape. Along CV2, the main shape variation was related to the position of the mouth and of the pectoral fin. The two *Microspathodon* species showed a more horizontally oriented pectoral fin, the cephalic profile is high and the mouth is small

(+CV2). The eye of the two *Azurina* species and *Z. rosaceus* was in a more forward and lower position, and the snout region is also longer than in all *Chromis* species and *A. troschelii* (CV3; Fig. 5). The phenogram shows a segregation of four morphological groups (Fig. 6): (1) all species of the genus *Stegastes*, *A. concolor*, and *A. declivifrons*, which are mainly algal feeders; (2) all species of the genus *Chromis* and *A. troschelii*, which are mainly zooplankton feeders; (3) both *Microspathodon* species are algal feeders, with an extremely flat cephalic shape; and (4) both *Azurina* species, which are zooplanktivorous, and *Z. rosaceus*, which is carnivore benthic feeder, form a group having a highly sharp cephalic profile. The coefficient of cophenetic correlation is relatively high ($r = 0.76$).

PHYLOGENETIC ANALYSIS

The morphological phylogenetic hypothesis (Fig. 6) shows a grouping pattern with a high degree of

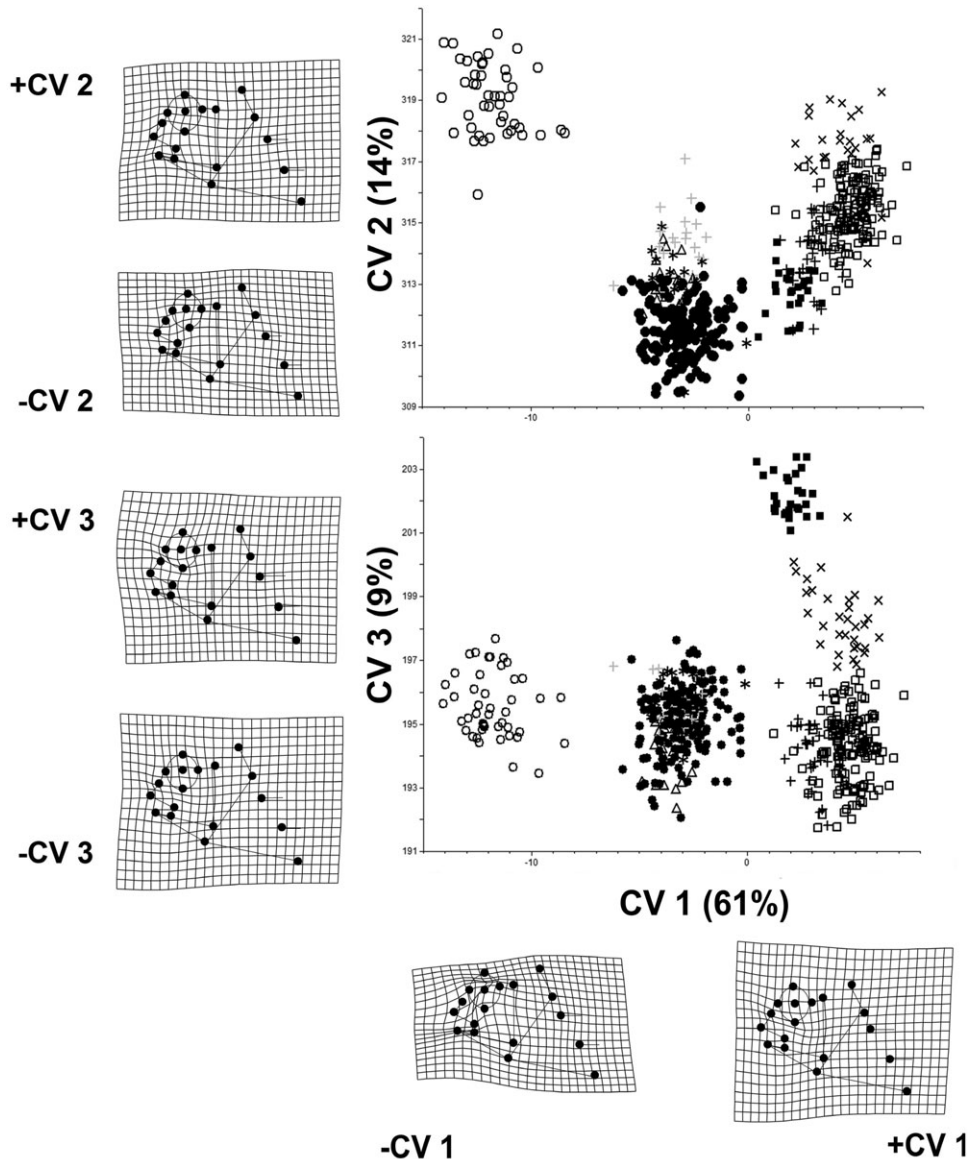


Figure 5. Scatterplot of canonical variates (CV): CV1 versus CV2 and CV1 versus CV3. Black cross, *Abudefduf concolor* and *A. declivifrons*; grey cross, *Abudefduf troschelii*; equis, *Azurina*; white square, *Chromis alta*, *C. crusma*, *C. intercrusma*, *C. limbaughi*, *C. meridian* and *C. punctipinnis*; grey square, *Chromis atrilobata*; triangle, *Hypsypops*; circle, *Microspathodon*; asterisk, *Nexilosus*; black circle, *Stegastes*; black square, *Zalembius*. For both plots, thin plate spline deformation grids for the extreme points of each axis are shown; these are superimposed on the shapes predicted when the average landmark configuration of all specimens is deformed into that of a hypothetical specimen positioned at the extreme point of an ordination axis.

correlation between head morphology and feeding habits. The morphological phylogeny is not totally congruent with the molecular phylogeny, except in that the subfamily Stegastinae is recovered with the genus *Stegastes*, *Nexilosus*, *Hypsypops*, and *Microspathodon*. This clade presents moderate support values (Jackknife = 63). However, our morphometric phylogeny includes two species of

Abudefduf that belong to the Abudefdufinae subfamily according to the molecular phylogeny. Within this group, the clade of two species of *Abudefduf* is highly supported (Jackknife = 96). The subfamilies Chrominae and Abudefdufinae are not recovered as monophyletic groups in our morphometric phylogeny. Rather, the Chrominae is a partially resolved grade that also includes *A. troschelii*.

Table 3. Analysis of variance and Tukey–Kramer test of the three first axes of canonical variance analysis

	A	B	C	D	E	F	G	H	I	
CV 1	A		5.694	7.324	7.605	0.743	8.480	0.143	0.118	4.959
	B	< 0.0001		1.630	1.910	6.437	14.175	5.837	5.576	0.735
	C	< 0.0001	< 0.0001		0.280	8.067	15.805	7.467	7.206	2.365
	D	< 0.0001	< 0.0001	0.876		8.348	16.085	7.747	7.487	2.646
	E	0.246	< 0.0001	< 0.0001	< 0.0001		7.737	0.600	0.861	5.702
	F	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001		8.338	8.598	13.439
	G	1.000	< 0.0001	< 0.0001	< 0.0001	0.631	< 0.0001		0.261	5.102
	H	1.000	< 0.0001	< 0.0001	< 0.0001	0.002	< 0.0001	0.986		4.841
	I	< 0.0001	0.083	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	
CV 2	A		0.443	2.710	1.015	1.418	4.645	1.408	2.889	1.692
	B	0.799		3.153	1.458	0.975	5.088	0.965	2.446	1.249
	C	< 0.0001	< 0.0001		1.695	4.127	1.935	4.118	5.599	4.402
	D	0.001	< 0.0001	< 0.0001		2.432	3.630	2.423	3.904	2.707
	E	< 0.0001	0.005	< 0.0001	< 0.0001		6.063	0.010	1.471	0.275
	F	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001		6.053	7.534	6.337
	G	< 0.0001	0.033	< 0.0001	< 0.0001	1.000	< 0.0001		1.481	0.284
	H	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001		1.197
	I	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.987	< 0.0001	0.993	< 0.0001	
CV 3	A		1.33	2.82	1.20	1.13	0.11	0.54	0.35	6.72
	B	< 0.0001		4.15	0.13	0.20	1.44	1.87	0.98	8.05
	C	< 0.0001	< 0.0001		4.02	3.95	2.71	2.28	3.17	3.90
	D	< 0.0001	1.00	< 0.0001		0.07	1.31	1.74	0.85	7.92
	E	0.01	1.00	< 0.0001	1.00		1.24	1.67	0.78	7.85
	F	1.00	< 0.0001	< 0.0001	< 0.0001	< 0.0001		0.43	0.46	6.62
	G	0.80	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.86		0.89	6.18
	H	0.86	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.14	0.02		7.07
	I	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.01	< 0.0001	< 0.0001	< 0.0001	

A: *Abudefduf concolor*, *Abudefduf declivifrons*; B: *Abudefduf troschelii*; C: *Azurina* spp.; D: *Chromis* spp.; E: *Hypsypops rubicundus*; F: *Microspathodon* spp.; G: *Nexilosus latifrons*; H: *Stegastes* spp.; I: *Zalembeius rosaceus*. Above the diagonal: difference degree of Tukey–Kramer; below the diagonal: *P*-value.

RELATIONSHIP BETWEEN CEPHALIC SHAPE AND SIZE

Interspecific allometry was tested using linear regressions analyses. The relationship between shape and size (CS and SL) is low ($r^2 \leq 0.4$; Table 4). The lowest r^2 -values were found with the nonphylogenetic regression analysis and the highest ones with the phylogenetic regression analyses (Table 4). However, shape always showed a stronger relationship with CS than with SL.

RELATIONSHIP BETWEEN CEPHALIC SHAPE AND TROPHIC DATA

Both nonphylogenetic regression analyses and the equivalent with phylogenetically independent contrasts show a significant positive relationship between the TROPH index and shape variables (Table 4). Values of the coefficient of determination (r^2) were lower in the phylogenetic regression analysis than in the nonphylogenetic analysis. These tests and mirror trees analyses clearly demonstrate that

the main shape variation among the studied damselfishes is related to their feeding habit (Fig. 7). Cephalic shapes are more related to trophic levels than to the phylogenetic relationships (Fig. 7, Table 4). Trophic data group the 24 damselfishes in three main groups: mainly algal feeders, mainly zooplankton feeders, and an intermediate group feeding on small pelagic and benthic preys. CVA and cluster analysis allow the discrimination of the three main trophic groups and also show a clear degree of variation between two extremes of cephalic shape (i.e. zooplankton feeders, *Azurina* species, with highly sharpness cephalic shape and algal feeders, *Microspathodon* species, with highly flattened cephalic shape). On the other hand, the phylogenetic hypothesis constructed with shape data produces two monophyletic groups: (1) subfamily Stegastinae, which group mainly algal feeders and (2) a group composed of *A. troschelii*, *Chromis meridiana*, and *C. limbaughi*, which are mainly zooplanktivorous, feeding also on fish eggs.

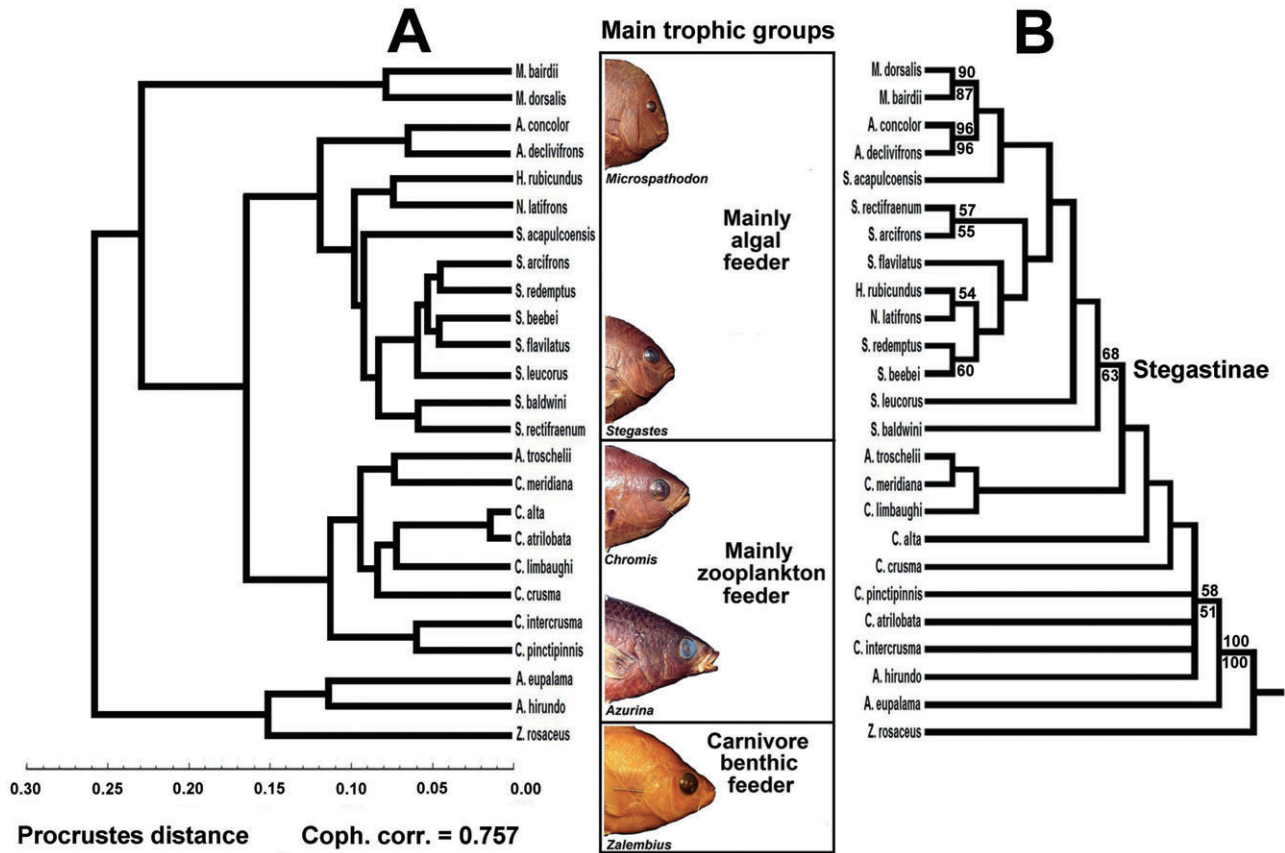


Figure 6. Comparison of two hierarchical models. Phenogram (A) and morphometric phylogeny (B) compared to main trophic groups of damselfish. Images of some species are added to help to visualize the pattern of cephalic shape variation in relation to each trophic group. In the phylogeny, the number on branches are support values (jackknife, 1000 replicates, cut = 50, jackknifing $P = 36$). Coph. Corr., coefficient of cophenetic correlation.

Table 4. Phylogenetic and nonphylogenetic regression analysis for testing interspecific allometry and the relationship between morphology and trophic data

Least square regression	Variables	r^2	F	d.f.	P
Phylogenetic	CS versus shape variables (molecular and morphological phylogeny)	0.41	16.32	23	0.0005
	SL versus shape variables (molecular and morphological phylogeny)	0.17	4.64	23	0.042
	TROPH index versus shape variables (molecular phylogeny)	0.51	23.16	23	< 0.0001
	TROPH index versus shape variables (morphological phylogeny)	0.51	23.16	23	< 0.0001
Nonphylogenetic	CS versus shape variables	0.20	6.22	32–736	< 0.0001
	SL versus shape variables	0.09	2.44	32–736	< 0.0001
	TROPH index versus shape variables	0.36	13.17	32–736	< 0.0001

CS, centroid size; SL, Standard length.

The optimization of the TROPH index and morphology in the molecular phylogeny revealed that all species of the genus *Stegastes* and *N. latifrons* are highly similar with respect to morphology and feeding habits. The subfamily Stegastinae show a high correlation between morphology and feeding habits,

although some shape variation can be observed among all *Stegastes* species, *N. latifrons*, and the two *Microspathodon* species. Morphological phylogeny highlighted a pattern of convergence with two members of *Abudefduf* genus (*A. concolor* and *A. declivifrons*). Although *A. concolor* and *A. declivifrons*

Character: TROPH Index
 Parsimony reconstruction
 Squared length: 0.1650

Character: Morphology
 Parsimony reconstruction
 Squared length: 7.6695

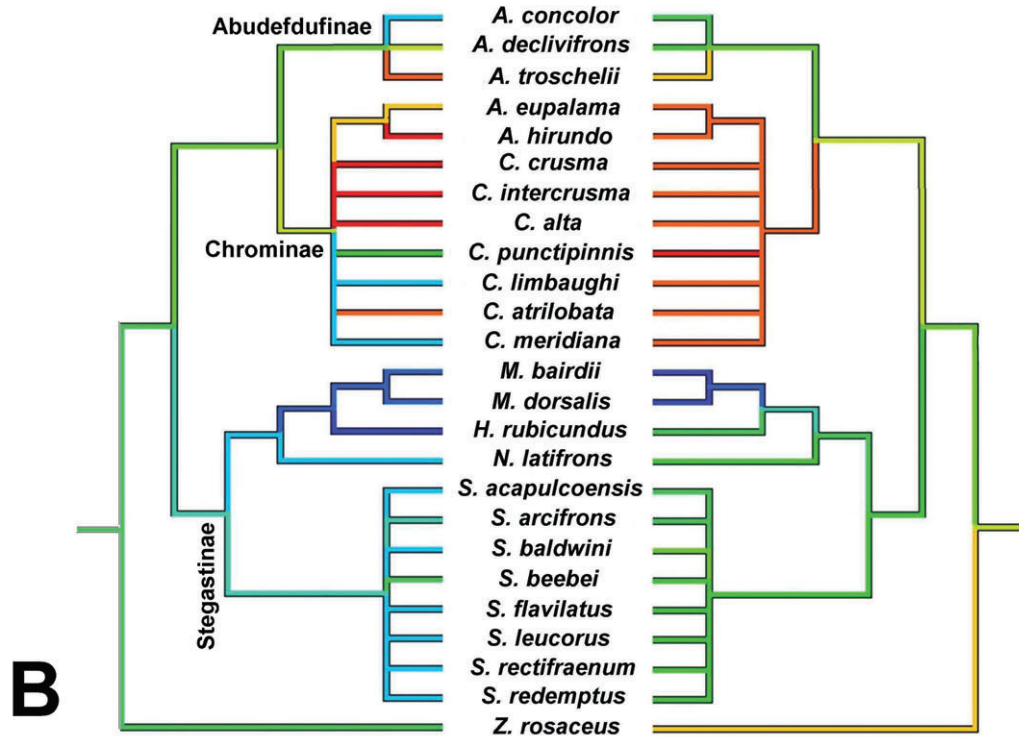
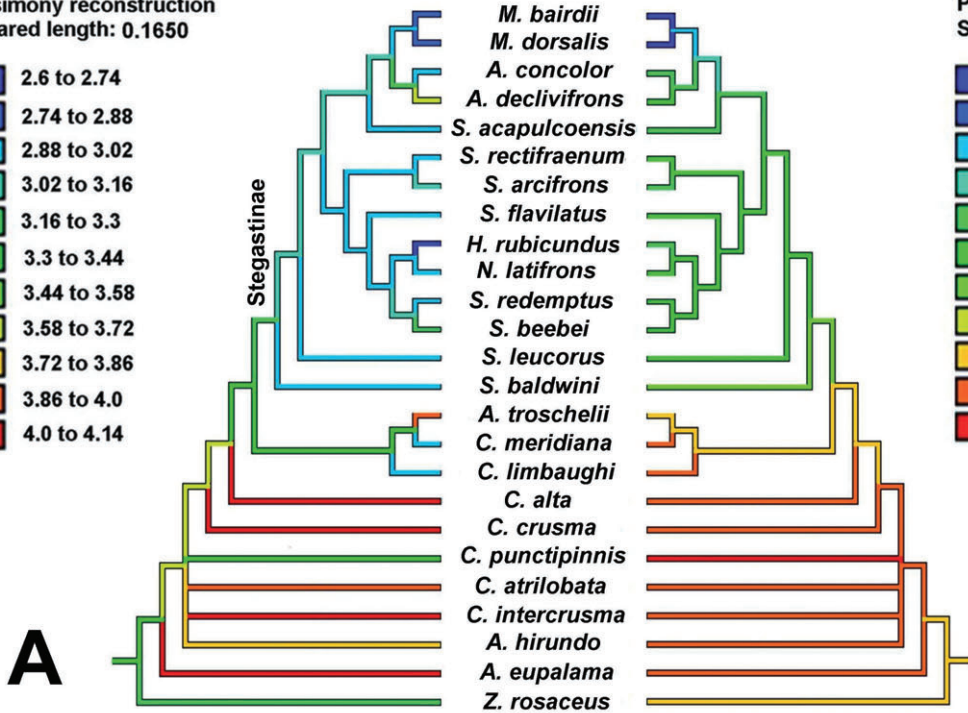
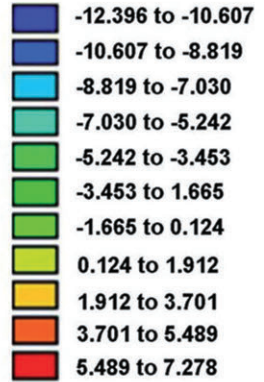


Figure 7. Mirror tree optimization of the TROPH index (left) and morphology (right). A, morphological hypothesis; B, molecular hypothesis.

are close according to the morphological phylogeny, the feeding habit of *A. declivifrons* is different and more similar to that of members of the Chrominae subfamily. Both *Microspathodon* species and *H. rubicundus* are close according to their feeding habits. The cephalic shape is highly conserved in the subfamily Stegastinae through both phylogenies. According to the categories of the TROPH index (Fig. 7), the Chrominae subfamily shows five categories distributed between medium and high values of the TROPH index. On the other hand, the range of morphological variation of this group is low (i.e. only two extreme morphological categories of colour code; Fig. 7). According to the morphological phylogeny, *A. troschelii* is closely related to the Chrominae. The convergence pattern of *A. troschelii* introduces a new morphology within this group. The Abudefdufinae subfamily is highly diverse. Two morphological categories were found in this subfamily (Fig. 7); (1) *A. troschelii* is more similar in shape to the outgroup (*Z. rosaceus*) and (2) *A. concolor* and *A. declivifrons* show similar values to the Stegastinae subfamily members. Each *Abudefduf* species has a different colour code for its trophic index (Fig. 7).

DISCUSSION

TROPHIC DIVERSITY OF DAMSELFISHES

The trophic data obtained in the present study confirm the division of damselfishes of the Eastern Pacific into three main trophic groups, as reported for species living in the Indo-West Pacific region (Allen, 1991; Kuo & Shao, 1991; Frédérick *et al.*, 2009): (1) the pelagic feeders mainly sucking zooplanktonic preys (e.g. *Chromis* spp., *Azurina* spp.); (2) the benthic feeders mainly grazing filamentous algae and picking small invertebrates (e.g. *Stegastes* spp., *Nexilosus latifrons*, *Hypsypops rubicundus*, *Microspathodon* spp.); and (3) an intermediate group gathering species feeding both on small pelagic and benthic preys (e.g. *Abudefduf* spp.).

The social behaviour of damselfishes is constant in the whole Indo-Pacific, Western Atlantic, and Eastern Pacific region (Emery, 1973; Frédérick *et al.*, 2009; present study): species mainly feeding on benthic prey are solitary, whereas zooplanktivorous species live in groups. However, *N. latifrons* is relatively atypical because it is a grazing species living in small groups (up to ten individuals) (Grove & Lavenberg, 1997; Angel & Ojeda, 2001; Robertson & Allen, 2008).

In general, the diet is consistent within damselfish genera. However, our ecomorphological approach indicated that the three *Abudefduf* species should be grouped into two different trophic guilds. Consistent

with the trophic data (Table 2), the cephalic profile of *A. troschelii* is more similar to that of *Chromis* and *Azurina*, suggesting that this species should be considered as an omnivorous species mainly feeding on zooplankton. On the other hand, *A. declivifrons* and *A. concolor* are more similar to *Stegastes*, *Hypsypops*, and *Nexilosus*, showing that they should be considered as omnivorous species and mainly benthic feeders.

To our knowledge, *H. rubicundus* is the only damselfish feeding on sponges. No damselfish of the Indo-West Pacific is known to be a common consumer of such kind of prey (Allen, 1991; Frédérick *et al.*, 2009). The angelfishes (Pomacanthidae) is specialized in such prey catching in coral reef environments (Konow & Bellwood, 2005). According to Robertson & Allen (2008), one Pomacanthidae, *Pomacanthus zonipectus*, is distributed in the cooler temperate regions and lives sympatrically with *H. rubicundus*. However, this angelfish achieves its maximum population density in the Tropical Eastern Pacific and is scarce in cooler temperate regions. Consequently, a lower competition level could permit an extension of the trophic width of damselfishes such as *H. rubicundus* in temperate regions.

ECOMORPHOLOGY AND MORPHO-FUNCTIONAL IMPLICATIONS

The bucco-pharyngeal cavity of a fish has been modelled as a truncate cone, whose small base comprises the circular opening of the mouth and whose large base is located behind the branchial basket on the level of the opercles (Alexander, 1967; Lauder, 1980; Lauder & Lanyon, 1980; Liem, 1993). The efficiency of the cone depends on various factors such as the morphology of the skull and particularly the bucco-pharyngeal cavity (Liem, 1990). There are three basic modes of feeding according to the degree of truncation of the cone (Liem, 1980, 1993): suction feeding, ram feeding, and biting. However, a mode of prey capture is not exclusive; many teleosts are able to modulate their feeding mode and to move from one category to another (Liem, 1980, 1993; Ferry-Graham *et al.*, 2002). If the head morphology of damselfishes prompts the consideration that they are good suction feeders (Emery, 1973; Frédérick *et al.*, 2008; Cooper & Westneat, 2009; present study), geometric morphometric analyses allow a deeper understanding of the different ways of feeding and reveal functional differences among species.

The main difference between morphological groups is the degree of sharpness of the cephalic shape, which goes from a long angular cephalic profile as in *Z. rosaceus*, both *Azurina* species, *A. troschelii*, and all *Chromis* species; followed by angular but shorter

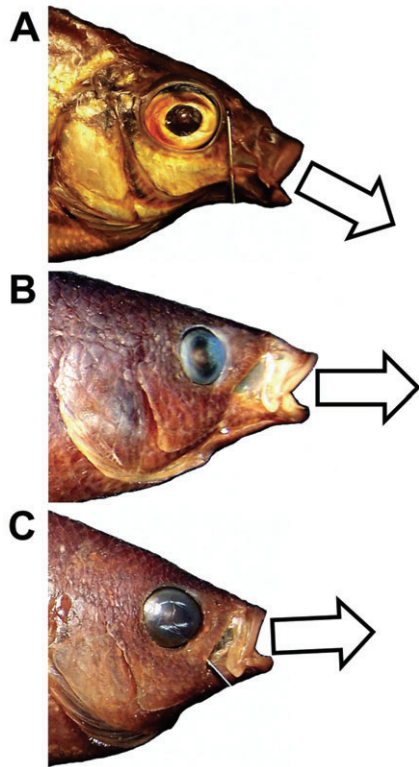


Figure 8. Difference in the mouth orientation when it is open in (A) *Zalembeius rosaceus*, (B) *Azurina hirundo*, and (C) *Chromis atrilobata*.

cephalic profiles as in *A. concolor*, *A. declivifrons*, *H. rubicundus*, *N. latifrons*, and all *Stegastes* species; and, finally, to an almost flat cephalic profile as in both *Microspathodon* species (Fig. 6). The benthic carnivorous *Z. rosaceus* feeds mainly on gastropods, mobile worms, and crustaceans (Table 2). As observed in some cichlids (Liem, 1993), a long angular cephalic profile may facilitate the catching of these items. Despite a similar angular cephalic profile as in both *Azurina* species and *Chromis* species, *Z. rosaceus* shows a great morpho-functional difference compared to these zooplanktivorous species, which was not indicated by our geometric morphometric analyses. Indeed, this difference is solely observed when the mouth is extended (i.e. during mouth protrusion) (Fig. 8). During feeding, the mouth is oriented more ventrally in *Z. rosaceus*, optimizing the capture of benthic animal preys, whereas the mouth is directed rostrally in *Azurina* and *Chromis* species, facilitating prey capture in the water column. Further morpho-functional studies should precisely address the differences in the degree of protrusion of the premaxillary bones during feeding among these species. Zooplanktivorous damselfishes such as the *Azurina* and *Chromis* species can be described as being particulate

feeding in that they attack the individual planktonic preys they select visually. The possession of relatively large eyes (Fig. 5) should increase their ability to find and target planktonic preys, as exemplified in cichlids (Barel, 1983). Their elongated head profile facilitates the capture of these organisms using ram-suction feeding (Coughlin & Strickler, 1990), although further functional studies should aim to test whether the differences in cephalic profile between *Chromis* and *Azurina* species (Fig. 5) could be related to differences in feeding strategy and performance. For example, the contribution of ram (i.e. the predator movement towards the prey) and suction (i.e. the prey movement towards the predator as a result of aspiration) during feeding may differ between both genera (Wainwright *et al.*, 2001).

Abudefduf troschelii is an omnivorous species feeding mainly on zooplankton (Grove *et al.*, 1986; present study). Robertson & Allen (2008) considered this species to comprise two feeding groups: omnivorous and planktivorous. *Abudefduf troschelii* shows a very similar cephalic profile to the almost exclusive zooplanktivorous *Chromis* and *Azurina* genera. Similarly, *A. troschelii* mainly occurs along rocky shores or coral reefs, in shallow waters, foraging on zooplankton in aggregations. By contrast, *A. concolor*, *A. declivifrons*, *H. rubicundus*, *N. latifrons*, all *Stegastes* species and both *Microspathodon* species mainly graze filamentous algae growing on rocks. Within this trophic group, the two *Microspathodon* species present a highly different morphology. Our underwater observations revealed that the way of feeding in both *Microspathodon* species differ from that of the others. Indeed, all *Stegastes* species grazed algae or picked up small invertebrates on small, mainly horizontal rocks or rubble, whereas the two *Microspathodon* species scraped on big rocks with high vertical walls. This type of feeding is probably facilitated by an almost flat cephalic profile in *Microspathodon* species. Moreover, the premaxillary bones on their anterior region reveal a loose connective tissue where teeth are continuously produced (Ciardelli, 1967). When the fish scrapes the rocky wall, the teeth are continuously eroded and, consequently, need to be produced constantly (Trapani, 2001). Furthermore, this connective tissue that supports and nurtures the teeth could act as a buffer, supporting the movement of the teeth and the premaxillary bones on the rock. Although, when the food items are similar, the morphological pattern could diverge if the methods of prey catching differs.

The results of the present study indicate that damselfishes from the Eastern Pacific show strong differences with respect to their cephalic profile. These differences are mainly related to the degree of sharpness and the position of the eye and the mouth. A

pattern of relationship between head morphology and diet was found, as in previous analysis (Frédérich, Parmentier & Vandewalle, 2006; Frédéric *et al.*, 2008; Cooper & Westneat, 2009). However, the relationship between the cephalic profile and feeding habit found in damselfishes extends beyond this. In the present study, head morphology was observed to be related to the way that the food resource is extracted: two species can use the same food resource (*Stegastes* species and *Microspathodon* species) and present a different head morphology, and these respond to the way that each species extracts the resources of the environment.

EVOLUTIONARY CONSIDERATIONS

The shape data of the present study confirm a morphological group composed by *Z. rosaceus*, our chosen outgroup (Figs 4, 5). The family Embiotocidae includes mainly carnivorous (zoobenthos) species with a pointed cephalic profile. Interestingly, *Z. rosaceus* shows a cephalic profile more similar to the most derived zooplanktivorous damselfishes (i.e. *Chromis* and *Azurina*) (Fig. 2). The similarity among these three genera is a convergence in the cephalic profile. The present study confirms the results reported by Frédéric *et al.* (2008), who stated that shape variation is not correlated with size variation in damselfishes. Interspecific allometry is low and size does not predict convergent shapes. Consequently, variations in size and shape may be viewed as two independent evolutionary factors explaining the diversification of the family Pomacentridae. When the relationships between CS, SL, and shape variables are analyzed through nonphylogenetic analyses, r^2 -values are lower than when they are analyzed through phylogenetic analyses, indicating that size is related to the phylogeny.

The morphometric results of the present study show *Azurina* to be very similar in cephalic shape to *Chromis*. In a Euclidean plane, the slender *Azurina* species lie at the extreme point of the *Chromis* distribution along an axis of cephalic length (Figs 4, 5). According to the morphological phylogeny, *Azurina* species are closely related to *Chromis* species (Fig. 6); this relationship is also reported by Cooper *et al.* (2009), who proposed synonymizing the genus *Azurina* with *Chromis* and re-classifying the two species of *Azurina*. Their proposal was based on a strong phylogenetic relationship between *Azurina hirundo* from the Eastern Pacific and *Chromis multilineata* from the Atlantic.

The genus *Abudefduf* had been traditionally segregated into two groups. According to our morphometric analyses, the main difference between these groups is the position of the mouth, which clearly corresponds

to two different feeding habits. In *A. troschelii*, the mouth is superior (omnivorous, feeding mainly on zooplankton); this shape is very similar to that of *C. meridiana* and *C. limbaughi* (Fig. 6). By contrast, the mouth of *A. concolor* and *A. declivifrons* is inferior (omnivorous, feeding mainly on benthic preys); thus, the shape is similar to *Microspathodon bairdii* and *Microspathodon dorsalis* (Fig. 6). The molecular phylogenetic analysis of Quenouille *et al.* (2004) considered 16 *Abudefduf* species, and found three main clades within this genus: *A. declivifrons*, *A. concolor*, and *Abudefduf taurus* are the sister group to the two principal groups. *Abudefduf taurus* is a mainly herbivorous fish (Randall, 1967; Allen, 1991), with similar behaviour to *A. concolor* and *A. declivifrons*, showing strong preference for limestone shorelines and tide pools in regions with surf (Allen, 1991; R. Aguilar-Medrano, pers. observ.). The second group comprises *Abudefduf sordidus*, *Abudefduf septemfasciatus*, and *Abudefduf notatus*, which are also mainly algal feeders (Allen, 1991). All *Abudefduf* species of these two groups possess a dark body with clear vertical bars and have a strong preference for very shallow areas (0–4 m) with surf (Allen, 1991; R. A.-M. & B. F. pers. observ.). Their mouth is placed in a lower position than the others. The third cluster of Quenouille *et al.* (2004) includes *A. troschelii*, these group present species which show an overall lighter body with dark vertical bars and are laterally compressed; all are omnivorous, feeding mainly on zooplankton (Emery, 1973; Frédéric *et al.*, 2009; present study). They are gregarious, their mouth is in a superior position, their habitat distributions are in a water depth in the range 1–15 m, and they are associated with rocky and coral reefs (Emery, 1973; Allen, 1991; Frédéric *et al.*, 2009; present study).

Previous molecular phylogenetic analyses found that *Microspathodon*, *Hypsypops*, *Nexilosus*, and *Stegastes* are closely related genera belonging to the subfamily Stegastinae (Tang, 2001; Quenouille *et al.*, 2004; Cooper *et al.*, 2009), although relationships are not fully resolved (Fig. 2). The trophic data of the present study revealed that all these species are benthic feeders, mainly grazing filamentous algae. Our geometric morphometric analyses and phenogram clearly distinguish the two *Microspathodon* species from the other species belonging to this trophic group (i.e. *H. rubicundus*, *N. latifrons*, and all studied *Stegastes* species) based on their highly flattened cephalic profile. *Hypsypops rubicundus* and *N. latifrons* are predominantly found in temperate waters, in the extreme north and south, respectively, of the Eastern Pacific damselfish distribution. Their cephalic profiles are relatively similar to those of *Stegastes* species, although geometric data show some differences among these three genera. In the

morphospace, *H. rubicundus* and *N. latifrons* species are placed peripheral of the *Stegastes* morphological distribution (Fig. 5) and a schematic representation of the observed differences within this group is illustrated in Figure 9. If we hypothesize that *Nexilosus*, *Hypsypops*, and *Microspathodon* are derived from the genus *Stegastes* (Cooper *et al.*, 2009), the results of the present study demonstrate that the main shape variation during the evolutionary process was related to the form of the cephalic profile (pointed versus flattened), the size of the eye, and the position of the eye and mouth. From a *Stegastes* ancestor, a first evolutionary step could produced two new forms (Fig. 9): (1) *H. rubicundus* with an pointed profile, a long horizontal distance between the mouth and the eye, and a short vertical distance between the mouth and the eye, and (2) *N. latifrons* with a more rounded profile, a short horizontal distance between the mouth and the eye, and a long vertical distance between the mouth and the eye. The possible next evolutionary step from the *Nexilosus* brand produced a strongly specialized cephalic profile: both *Microspathodon* species present a highly flattened profile, no horizontal space between the eye and the mouth and high vertical distance between the mouth and the eye (Fig. 9).

The molecular data reported by Tang (2001) showed that *Hypsypops* is closer to *Parma* (Subfamily Stegastinae) than to *Stegastes*. Indeed, when the genus *Parma* was first described, *H. rubicundus* was included as one of its members (Tang, 2001). These two genera are predominantly distributed in temperate cool water and rocky reefs; furthermore, *Parma* includes some species that can be found in kelp forests, such as *H. rubicundus* (Allen, 1991; Buckle & Booth, 2009). Future geometric studies should include *Parma* species to obtain a good overview of the phenotypic differences or similarities among *Parma*, *Hypsypops*, and *Stegastes*. The phylogenetic position of *N. latifrons* is unknown (Cooper *et al.*, 2009), although the data of the present study strongly suggest that *N. latifrons* is closely related to *Stegastes* species in morphology and ecology, even though the former lives in small groups. According to Robertson & Allen (2008), the main differences between this genus and *Stegastes* are that the margins of the preopercle and infraorbital bones are smooth in *Nexilosus* and serrated in *Stegastes*. Both genera present a single row of teeth and the number of dorsal fin spines of *Nexilosus* (XIII) is included in the range of *Stegastes* (XII to XIV) (Allen, 1991). Similar to the question of synonymy between the genus *Azurina* and *Chromis*, the close relationship between *Nexilosus*, *Stegastes*, and *Hypsypops* allows us to question whether *Nexilosus* and *Hypsypops* (both monospecific genera: *N. latifrons* and *H. rubicundus*, respectively)

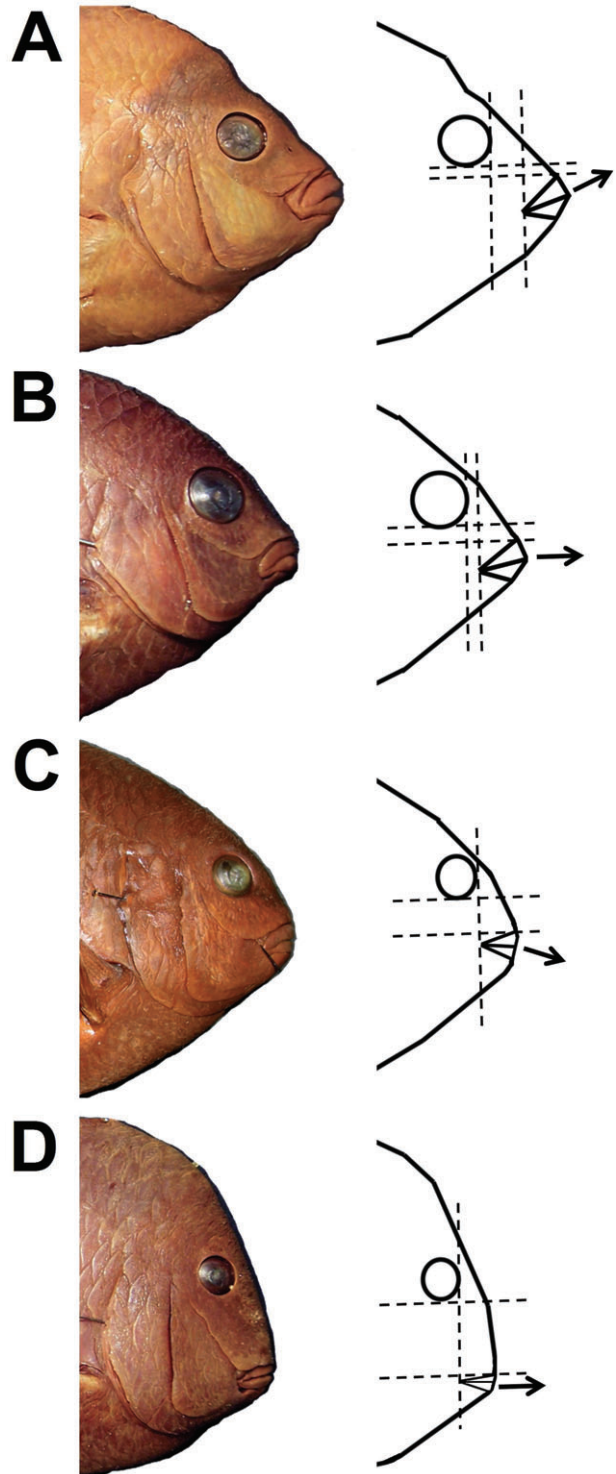


Figure 9. Schematization of the variation related to the position of the eye and mouth in the cephalic profile of (A) *Hypsypops rubicundus*, (B) *Stegastes flavilatus*, (C) *Nexilosus latifrons*, and (D) *Microspathodon dorsalis*.

should be considered as valid genera. Further exhaustive phylogenetic studies are needed to better understand the phyletic relationships among *Microspathodon*, *Hypsypops*, *Nexilosus*, *Stegastes*, and *Parma*.

Our morphometric and phylogenetic analyses of the cephalic region show that the subfamilies Stegastinae and Chrominae present a specific morphological pattern, but not Abudefdufinae (Fig. 7). The morphological average appeared twice throughout the molecular phylogeny (Fig. 7B): (1) Stegastinae subfamily, in *Stegastes* genus, *N. latifrons*, and *H. rubicundus*, and (2) in Abudefdufinae subfamily, in *A. concolor* and *A. declivifrons*. In these groups, the mean cephalic shape is related to medium-high values of the TROPH index. Nevertheless, species of the genus *Chromis* showed the same TROPH values. Consequently, *A. concolor* and *A. declivifrons* present convergent morphological adaptations to the members of the subfamily Stegastinae in the family in the Eastern Pacific.

In conclusion, the present study shows that variation in the cephalic shape of Pomacentridae of the Eastern Pacific can be clearly explained by differences in diet and trophic behaviour. Shape and size may be viewed as two independent evolutionary factors explaining the diversification of Pomacentridae. Cephalic shape is a significant predictor of trophic habit. Finally, the morphological groups discovered by our morphometric analyses partially agree with the main clades delimited by molecular phylogenetic hypothesis. Consequently, the cephalic profile of damselfishes shows a clear and strong historical (phylogenetic) signal only for the Stegastinae and partially for Chrominae. Members of the subfamily Abudefdufinae show convergences of cephalic shape. The mainly zooplanktivorous *A. troschelii* is very similar to *Chromis* species (Chrominae), and the mainly algal feeders *A. concolor* and *A. declivifrons* are very similar to *Microspathodon* species (Stegastinae).

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