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ORIGINAL PAPER

Variation of phenotypic disparity over the ontogeny of coral reef fish populations

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Abstract

Phenotypic disparity present within populations is of crucial importance for adaptation and natural selection. To date, few studies have explored how disparity levels vary during fish ontogeny. Many coral reef teleosts experience ecological shifts across life stages, making them ideal models. During the larval stage, individuals are adapted to an oceanic pelagic environment while juveniles and adults have a morphology adapted to the benthic reef environment. We hypothesize that these two environments may exert different selective pressures. Here, we quantify the variation of body shapes over the ontogeny of eight coral reef fish species to test whether (1) the morphology of post-larvae, juveniles and adults differs due to specific habitat adaptations and (2) the level of phenotypic disparity varies among ontogenetic stages. Shape analyses reveal that, in most species, adults have a more streamlined body with proportionally shorter jaws than do post-larvae. The distribution of disparity levels throughout ontogeny does not follow a general trend. Depending on the species, shape disparity may be highest during the post larval stage or during the adult stage, or conversely, may not vary at all during ontogeny. Our results oppose two contrasting scenarios: either post-larvae exhibit reduced morphological disparity due to the homogeneity of pelagic habitats, or life stages associated with the reef environment are less disparate because they experience stronger selective pressures. Further research is certainly needed to determine whether phylogeny or ecology mainly drives ontogenetic changes in phenotypic disparity.

Keywords Habitat shifts · Natural selection · Ontogeny · Shape variation · Guadeloupe · Lesser Antilles

Introduction

An individual's visible characteristics such as its morphology, physiology or behavior define its phenotype, and phenotypic variation refers to the deviation of these characteristics between individuals of a given population. Phenotypic disparity is universal and is mainly induced by environments which vary (Whitman and Agrawal 2009). The variability of some phenotypic components between individuals of a population can be observed during early stages of ontogeny. Indeed, an individual's phenotype at birth is determined in part by the transmission of genes and also by the environmental conditions present during its development (Byers 2008; Plard et al. 2016). However, the variability of phenotypes in a population can also occur during later stages of ontogeny. Abiotic and biotic factors can interact with an individual's development, potentially improving the correspondence between phenotype and environment, in a process known as phenotypic plasticity (DeWitt and Scheiner

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2004). Phenotypic variation within one generation can be highly adaptive, enabling species to cope with environmental modifications (Meyers and Bull 2002; DeWitt and Scheiner 2004).

Ontogenesis itself can therefore be seen as a continuous variation of phenotypes allowing an individual to adapt to the environments in which it evolves (Schlichting and Smith 2002). Phenotypic variation within populations certainly enhances species adaptation. For example, mortality in early life stages varies according to phenotypes: different cohorts may have developed under dissimilar environmental conditions and/or come from genetically different source populations, leading to variation in the distribution of phenotypes and therefore, to their greater or lesser vulnerability in an environment (Johnson et al. 2014). Improved understanding of how this phenotypic disparity is distributed across the different ontogenetic stages would advance understanding of the process of adaptation.

In coral reefs, most teleost fishes have a complex life cycle which, in general, develops over two distinct environments: the pelagic environment where larvae live, and the reef environment for the juvenile and adult life stages (Leis et al. 1996). The transition of the larvae from the pelagic to the reef environment is known as settlement (Dufour and Galzin 1993). During this key period, post-larvae metamorphose into juveniles under the influence of thyroid hormones (Holzer et al. 2017; Roux et al. 2019). This process gives rise to the morphological (*e.g.* body shape, scales), physiological (*e.g.* vision) and behavioral changes necessary for adaptation to the new environment (*e.g.* McCormick et al. 2002; Frédérich et al. 2008; Frédérich et al. 2010; Frédérich et al. 2012; Holzer et al. 2017; Fogg et al. 2022). During the settlement phase, fish larvae are subjected to strong selective pressure, having to cope with competitors and predators as well as search for a suitable reef habitat that will promote their survival and growth (Planes et al. 1993; Doherty 2002). Different strategies of settlement have been highlighted in coral reef fishes: juveniles of some species may use nursery habitats but not join the adult habitat directly, whereas others settle directly into the adult habitat (Kaufman et al. 1992; Nagelkerken et al. 2000; Lecchini and Galzin 2005; Grol et al. 2014).

Varied selective forces may operate during ontogenetic habitat shifts. In the early life stages, the transition from a pelagic oceanic to a benthic reef environment is subject to natural selection: individuals lacking the optimal developmental traits required to withstand the transition between the two environments will generally not survive and are easily preyed upon (Carr and Hixon 1995; Caselle 1999; Searcy and Sponaugle 2001; Gagliano et al. 2007; Dorenbosch et al. 2009). Once on the reef, the choice between different habitats is linked to minimizing the risk of mortality while maximizing the rate of growth (Doherty 2002). The presence of sufficient resources or predation pressure are additional selective forces that influence phenotypic adaptation and habitat choice (Lima and Dill 1990). Thus, due to their complex life cycle with habitat transitions and to the various selective forces to which they are subjected, coral reef fishes offer a unique opportunity to study morphological changes associated with habitat transitions and potential variation in the level of phenotypic disparity throughout ontogeny (Frédérich and Vandewalle 2011). Until now, many studies have been devoted to the description of ontogenetic morphological changes in coral reef fishes (*e.g.* McCormick and Makey 1997; Fulton and Bellwood 2002; McCormick et al. 2002; Frédérich and Vandewalle 2011; Frédérich et al. 2012), but there have been few comparative analyses involving fish species belonging to different taxa and having different ontogenetic ecological strategies, such as the recent study by Goatley et al. (2021). Moreover, there is a lack of clarity regarding the distribution of morphological disparity over the ontogeny of fish populations. Specialized ecomorphs of *Salvelinus alpinus* from Icelandic lakes showed significant reductions in shape variation throughout ontogeny (Parsons et al. 2010). Conversely, the highest level of body shape disparity was observed at the adult stage of sparid fishes (*Diplodus* spp; Colangelo et al. 2019). Finally, a recent study on the surgeonfish *Acanthurus triostegus* revealed a transient increase in body shape disparity during the period of metamorphosis (Reynaud et al. 2023).

Overall, the present study aims to quantify and compare phenotypic variation in coral reef fishes throughout their ontogeny. During the larval stage, individuals are adapted to an oceanic pelagic environment. After metamorphosis, juvenile and adult individuals have a morphology which is adapted to the benthic reef environment. We hypothesize that the morphology of post-larvae, juveniles and adults differs due to specific habitat adaptations. We also expect the level of phenotypic disparity to vary among ontogenetic stages and will attempt to clarify two opposite patterns driven by different ecological factors. Given that the phenotypic diversity, *i.e.* the disparity, present within populations is of crucial importance for their adaptation, and that this disparity is also essential for the operation of natural selection, we hypothesize that a heterogeneous environment may exert different selective pressures on the body shapes of fishes. We may therefore expect that either higher morphological disparity in a population will become more homogenous after settlement, or that low morphological disparity in the ocean will increase after settlement. We thus form two hypotheses: (1) the oceanic environment, which is probably more homogenous than the reef environment in terms of habitat diversity, sustains less phenotypic variation in the larval population of a given fish species than in its juvenile and adult populations, and (2) selective pressure exerted during habitat transitions reduces the level of phenotypic disparity during the ontogeny of a given coral reef fish species (from post-larvae to juvenile and adult stages).

Materials and methods

Fish sampling

The present study was conducted in Guadeloupe Island, Lesser Antilles (16°15’N; 61°30 N).

Eight teleost species belonging to five different families were studied: *Acanthurus chirurgus, Acanthurus tractus* (Acanthuridae), *Lutjanus apodus*, *Ocyurus chrysurus* (Lutjanidae), *Sargocentron coruscum* (Holocentridae), *Scarus iseri* (Labridae), *Sparisoma viride* (Labridae) and *Stegastes leucostictus* (Pomacentridae). *Acanthurus chirurgus* and *A. tractus* are gregarious herbivorous fishes that graze on seagrass epiphytes and on algal turf and macroalgae on the reef, whatever their ontogenetic stage (juvenile or adult) (Cocheret de la Morinière et al. 2003; Nagelkerken and Van Der Velde 2003; Dromard et al. 2015). *Scarus iseri* and *Sparisoma viride* are herbivorous fishes that graze on seagrass epiphytes at the juvenile stage, and on algal turf in reef areas at the adult stage. Both species thus present a habitat shift during their ontogeny and use seagrass meadows as nursery areas (Dromard et al. 2017). They live alone or in small groups (Nagelkerken and Van Der Velde 2003). *Lutjanus apodus* and *Ocyurus chrysurus* are carnivorous fishes, feeding on small invertebrates and fishes. The ontogeny of these two species is also characterized by a habitat shift: juveniles live in seagrass meadows and/or mangroves, and adults inhabit the reef environment (Cocheret de la Morinière et al. 2003). They are solitary, but *Ocyurus chrysurus* may also form groups (Vaslet et al. 2015). *Sargocentron coruscum* is a nocturnal carnivorous species associated to the reef throughout its entire lifespan. *Stegastes leucostictus* is an omnivorous species that feeds on small invertebrates and filamentous algae, and whose territory is established on coral reefs, small patch reefs surrounded by seagrass beds, but also on mangrove roots. Juveniles and adults usually share the same habitat (Vaslet et al. 2015).

Three ontogenetic stages were studied: post-larval (*i.e.*, fish settling on reef habitats), juvenile, and adult stages. Post-larvae and juvenile fishes were collected from January 2022 to March 2023 at eight sites: Anse du Mancenillier, Ilet du Gosier, Ilet à Cochon, Port Louis, Banc Frotte-Ton-Cul, Banc des Anneaux, Anse Bertrand and Vieux Fort (Fig. 1). Post-larvae were collected using crest nets and “CARE” traps (Collected by Artificial Reef Ecofriendly) (Lecaillon and Lourié 2007). Juveniles were collected with a seine net and dip nets. After their capture, post-larvae and juvenile fishes were euthanized by immersion in a solution of eugenol diluted with seawater, and then placed on ice in an ice box. All adult specimens were collected by fishermen in April 2022 and during the ACOBIOM campaign carried out by IFREMER in September 2022. The choice of the eight studied fish species depended on fishery efficiency and the availability of individuals collected for each species at the three ontogenetic stages.

Morphometry and shape analyses

The standard length (SL) of each specimen was measured to the nearest mm using a Vernier caliper (Table 1). Each specimen was then photographed in lateral view using an Olympus Tough TG-6 camera mounted on a stand. Photographs were taken to show a global lateral view with fully extended fins, and the camera was equipped with a level indicator to ensure that the same angle of view was consistently obtained.

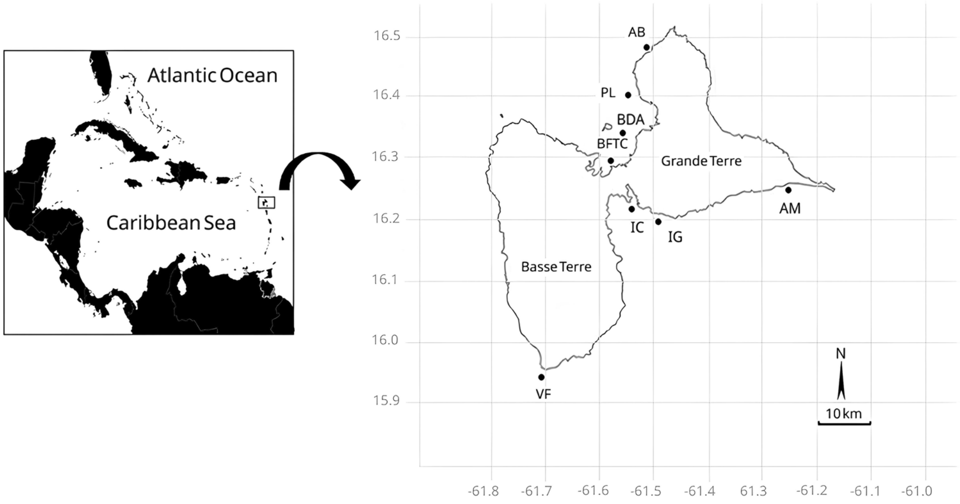


Fig. 1 Location of the sampling sites: Anse du Mancenillier (AM), Ilet du Gosier (IG), Ilet à Cochon (IC), Port Louis (PL), Banc-Frotte-Ton-Cul (BFTC), Banc-des Anneaux (BDA), Anse Bertrand (AB) and Vieux Fort (VF).

Table 1 Name abbreviations, number, and standard length (min-max) of specimens collected for the eight species.

Species	Abbreviations	n			Standard length (mm)		
		Post-larvae	Juvenile	Adult	Post-larvae	Juvenile	Adult
Acanthurus chirurgus	*A. chirurgus*	6	13	20	32–35	35–75	200–225
Acanthurus tractus	*A. tractus*		23	20		30–65	160–190
Lutjanus apodus	*L. apodus*		13	20		21–55	225–340
Ocyurus chrysurus	*O. chrysurus*	22	23	24	16–25	41–138	260–280
Sargocentron coruscum	*S. coruscum*	20	16	12	35–37	40–70	70–80
Scarus iseri	*S. iseri*	21	20	21	24–25	33–37	180–205
Sparisoma viride	*S. viride*		6	12		30–80	295–365
Stegastes leucostictus	*S. leucostictus*	17	16	13	10–20	22–60	60–85

Fig. 2 Lateral view of *Acanthurus chirurgus* (left) and *Sargocentron coruscum* (right) at three ontogenetic stages (post-larva—TOP, juvenile—MIDDLE and adult—BOTTOM), illustrating the landmarks (white dots) used to quantify body shape variation with geometric morphometrics.

Table 2 Description of homologous landmarks to quantify fish body shape.

Landmarks	Position
1	Anterior end of the upper jaw
2	Center of the eye
3	Anterior insertion of the dorsal fin
4	Posterior insertion of the dorsal fin
5	Dorsal insertion of the caudal fin
6	Ventral insertion of the caudal fin
7	Anterior insertion of the anal fin
8	Posterior insertion of the anal fin
9	Insertion of the pelvic fin
10	Inferior insertion of the pectoral fin
11	Superior insertion of the pectoral fin
12	Upper-posterior end of the operculum

We used Procrustes-based geometric morphometric methods (Bookstein 1991; Zelditch et al. 2004) to quantify fish body shape variation and to explore the dynamic of phenotypic disparity over ontogeny. The TPSDig.2 computer program written by F.J. Rohlf (freely available at http://life.bio.sunysb.edu/morph/) was used to digitize 12 homologous landmarks (LMs) to capture body shape (Fig. 2, Table 2). Unlike the other species, *Sargocentron coruscum* has two separate dorsal fins, necessitating the addition of two LMs (LM#13 and LM #14, Fig. 2) to capture morphological variation of these dorsal fin attachments. All specimens were optimally aligned using a generalized Procrustes superimposition method (GPA analysis—Rohlf and Slice 1990), the grand mean (*i.e.*, the consensus of all specimens) was calculated, and shape variables were then generated as partial warp scores (PWs) including both uniform and non-uniform components (Bookstein 1991). These shape variables were then used in the multivariate analyses described below. GPA analysis and the production of shape variables were performed separately for each species.

A set of different statistical analyses was performed to examine the pattern of shape divergence among ontogenetic stages (post-larvae, juveniles, and adults) for the eight fish species. Each species was studied separately. First, a Principal Component Analysis (PCA) was carried out on shape variables to highlight the main axes of shape variation differentiating the ontogenetic stages. PCA plots allowed the representation of a shape space where fish body morphologies are distributed, and the identification of the main axes of shape variation within species. To display shape changes associated with PC axes, we used deformation grids produced by TpsRelw (Rohlf and Slice 1990) to represent the extreme positive and negative deviations along the PC axes.

A visual exploration of the shape space defined by the PC axes allowed for an intuitive identification of differences between ontogenetic stages. In addition to this qualitative assessment, a Procrustes ANOVA (permutation test, 9999 iterations) followed by pairwise comparisons of Procrustes distances were performed to test if body shape was different between ontogenetic stages (larvae, juvenile and adult) for each species. Procrustes distance is a univariate metric defining shape dissimilarity in the Kendall shape space (Bookstein 1996). We used this metric to quantify the amount of shape variation between two respective ontogenetic stages. Procrustes ANOVA, pairwise comparisons and information about Procrustes distances between the mean shape of ontogenetic stages were obtained using the *procD.lm* function from the R-package geomorph (version 4.0.7; Adams and Otárola-Castillo (2013)) and the *pairwise* function.

Allometric variation is present during the growth of reef fishes (e.g. Frédérich and Vandewalle 2011; Frédérich et al. 2012), so the extent of size variation within ontogenetic stages (i.e. post-larvae, juvenile and adult) may explain a fraction of the shape disparity. Levene tests revealed that the variance of body size was dissimilar between ontogenetic stages for most studied species (Table 3). Accordingly, we performed and duplicated the following statistical analyses using raw shape data and size-corrected shape data. Size correction of the shape data was performed by a linear regression of all shape variables on the logarithm of size, expressed as centroid size (Bookstein 1991) for each species, and the residuals of regressions were used as new datasets in the statistical analyses.

Table 3 Levene tests assessing the homogeneity of variances among ontogenetic stages for each species. Significant P-values are indicated in bold.

Species	Levene test		
	df	F	p-value
Acanthurus chirurgus	2	1.997	0.151
Acanthurus tractus	1	3.196	0.081
Lutjanus apodus	1	9.419	**0.004**
Ocyurus chrysurus	2	12.107	**$3.3*10^{-05}$**
Sargocentron coruscum	2	6.298	**0.004**
Scarus iseri	2	24.043	**$2.3*10^{-08}$**
Sparisoma viride	1	0.246	0.627
Stegastes leucostictus	2	6.028	**0.005**

The disparity of morphologies for each species at each ontogenetic stage was examined by quantifying shape disparity. The level of shape disparity was calculated based on Procrustes variance, and pairwise comparisons (permutation test, 9999 iterations) between ontogenetic stages were performed using the *morphol.disparity* function in the R-package geomorph to test for variation between ontogenetic stages.

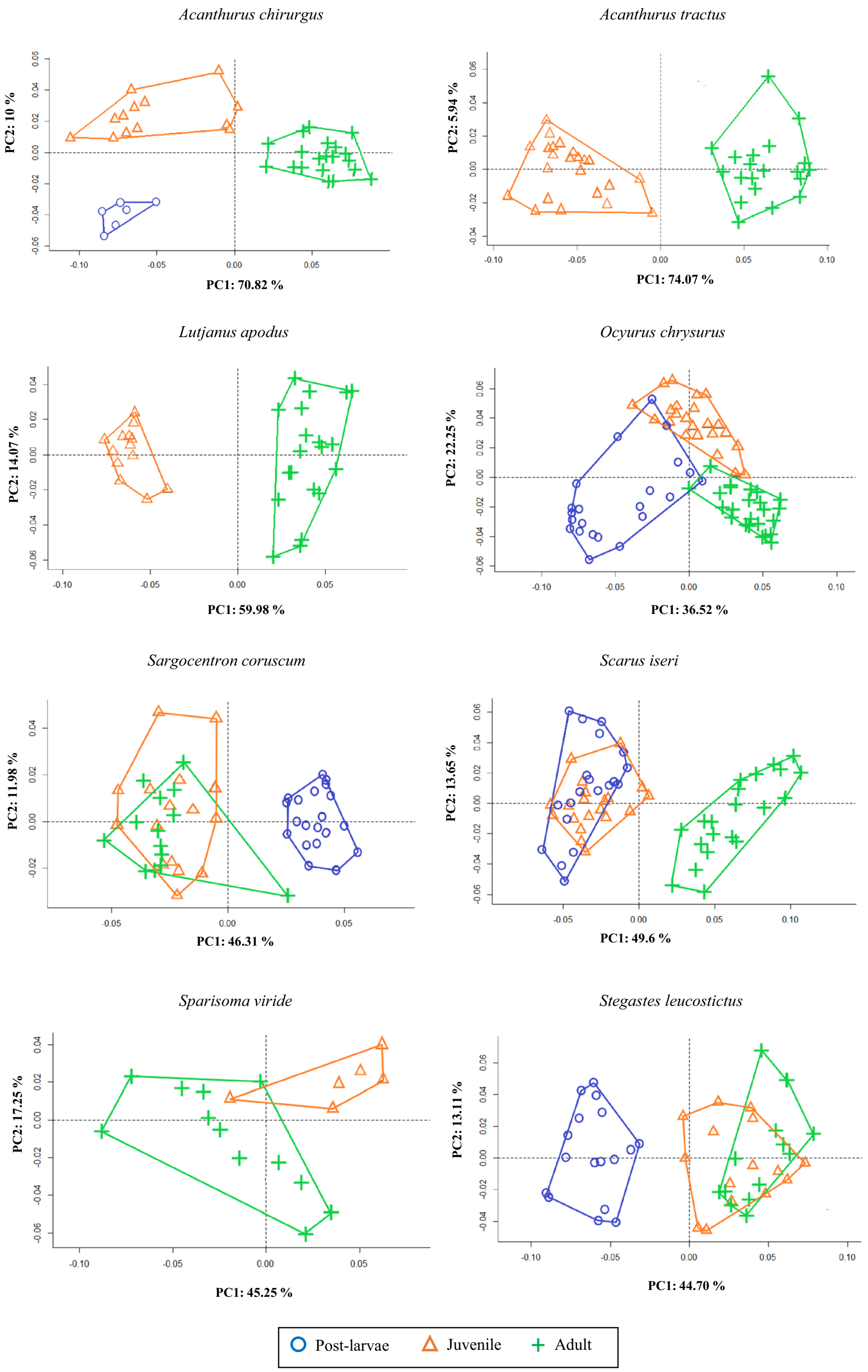
Results

A total of 358 specimens were studied (Table 1). No post-larval individuals of *Acanthurus tractus*, *Lutjanus apodus* and *Sparisoma* viride (Table 1) could be collected.

The body shape of each fish species varied during growth. In the great majority of the studied species, the ontogenetic stages occupied different subspaces of the shape space (Fig. 3). However, some overlaps between stages were observed in *Ocyurus chrysurus*, *Sargocentron coruscum*, *Scarus iseri* and *Stegastes leucostictus* (Fig. 3). Significant differences in body shape between ontogenetic stages were confirmed by Procustes-ANOVAs ($p < 0.001$, Table 4). The use of Procrustes distances allowed a simple, univariate quantification of overall body shape variation between pairs of ontogenetic stages. In *A. chirurgus* and *S. iseri*, the largest differences in body shape were observed between the juvenile and the adult stages, whereas shape differences between the post-larval and the juvenile stages were not even significant (Fig. 4, Table 4). On the other hand, the largest Procrustes distance value was observed between the post-larval and the juvenile stages in *S. coruscum* and *S. leucostictus* (Fig. 4), while shape divergence between juveniles and adults was not significant in these two species (Table 4).

For all species, scatterplots were produced with the first two principal components (PC1 and PC2) and provided an illustration of the distribution of fish in the shape space and associated variations (Fig. 3). The deformation grids (Fig. 5) produced by the thin-plate spline (TPS) algorithm were used to illustrate maximum shape changes associated with PC1 and/or PC2. For each of the eight species studied, the main morphological variations observed visually on the first two PC axes concerned the anterior part of the head (LMs 1 and 2) and the relative position of dorsal, caudal, anal, pelvic, and pectoral fins (LMs 3 to 11; Fig. 5). Shape variation associated with PC1 was relatively similar in every species

Fig. 3 Principal component analysis (PCA) of the variation in body shape of the ontogenetic stages, for each species. Ontogenetic stages are indicated by different symbols and colors, and illustrated by convex envelopes.



and consisted of variation of the head length and the overall body length. In all species studied, growth was characterized by a shortening of the nasal and ethmoid regions of the head (LMs 1 and 2) and by a proportional lengthening of the overall body shape (LMs 3 to 11) (Fig. 5). Adults possessed more streamlined bodies with shorter jaws and cheeks in comparison with juveniles and post-larvae (Fig. 5). However, the proportional lengthening of the body in *O. chrysurus* was accompanied by a heightening of the anterior body region (LM 3, Fig. 5). *Ocyurus chrysurus* and *L. apodus* tended to have greater body lengthening than other species. The general pattern of ontogenetic shape changes in *S.*

Table 4 Pairwise comparisons of the differences in body shape among the ontogenetic stages for the eight studied species, using raw shape data. See Table 1 for the abbreviations of species.

		Post-larvae	Juvenile	Adult
A. chirurgus	Post-larvae		ns	< 0.001
	Juvenile			< 0.001
	Adult			
A. tractus	Juvenile			< 0.001
	Adult			
L. apodus	Juvenile			< 0.001
	Adult			
O. chrysurus	Post-larvae		< 0.001	< 0.001
	Juvenile			< 0.001
	Adult			
S. coruscum	Post-larvae		< 0.001	< 0.001
	Juvenile			ns
	Adult			
S. iseri	Post-larvae		ns	< 0.001
	Juvenile			< 0.001
	Adult			
S. viride	Juvenile			< 0.01
	Adult			
S. leucostictus	Post-larvae		< 0.001	< 0.001
	Juvenile			ns
	Adult			

coruscum differed from the other species, and rather than a proportional lengthening of the whole body during growth, the body shape of juveniles and adults appeared more massive than in post larvae (Fig. 5). Shape variation associated with the PC2 axis concerned all ontogenetic stages and was mainly associated with body height (Fig. 5).

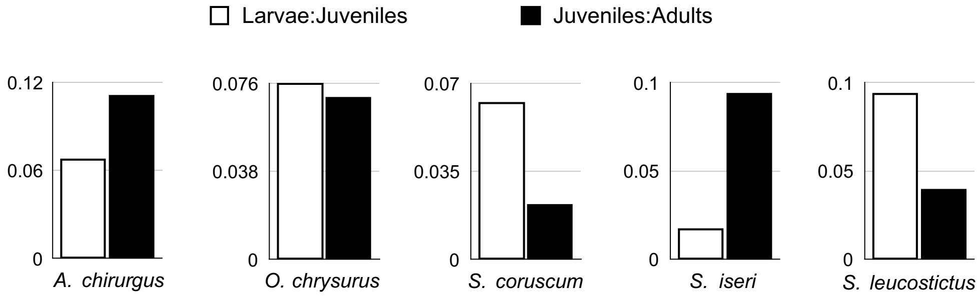
The level of body shape disparity varied significantly throughout the ontogeny of the great majority of studied species (Fig. 6 and Table 5). However, no variation was detected between the juvenile and the adult stages for *A. tractus* and *S. viride*. These results were consistent when using raw shape data and size-corrected shape data. The post-larval stage of *O. chrysurus* and *S. leucostictus* was the most disparate (Fig. 6). In *L. apodus, A. chirurgus* and *S. coruscum*, the largest shape disparity was at the adult stage (Fig. 6). Interestingly, the lowest body shape disparity was detected at the juvenile stage of *S. iseri* instead of in the larvae and adults.

Discussion

For each of the studied species, the post-larvae—whose morphology is optimized for life in a pelagic environment–were seen to differ significantly from their adult counterparts in terms of body shape. Moreover, the dynamic of the variation in body shape disparity over ontogeny was observed to differ among species. *Ocyurus chrysurus* and *S. leucostictus* exhibited greater disparity at the post-larval stage, whereas *L. apodus*, *A. chirurgus* and *S. coruscum* showed greater disparity at the adult stage. The level of disparity did not vary between life stages for *A. tractus* and *S. viride*.

Species differ in the dynamic of changes to their body shape during ontogeny via a phenomenon probably related to the presence or absence of ontogenetic shifts in their ecology. Body shape differences appear, at the least, between the two extreme stages: post-larval and adult. Adults have a more streamlined body with shorter jaws and cheeks, whereas post-larvae exhibit wider, shorter bodies and more elongated jaws and cheeks. Only *S. coruscum* stands apart from the other species, with juveniles and adults having a more rounded body shape than post-larvae. At the post-larval stage, newly settled individuals are not yet totally metamorphosed and therefore retain body characteristics associated with the pelagic environment. In the open ocean, larvae must move horizontally and vertically in the water column to feed and to avoid being preyed upon. They then return to the reef for colonization (Leis et al. 1996). Older larvae have considerable swimming capabilities (Stobutzki and Bellwood 1994; Dudley et al. 2000) and, according to a study carried out on damselfishes (Pomacentridae), the critical swimming speed of individuals seems to decrease when they are settled in the reef environment (Stobutzki and Bellwood 1994). Accordingly, variation in body shape observed between the post-larval stage and the other two stages may therefore be linked to changes in swimming performance. Moreover, the coral reef fish larvae diet is made up of planktonic preys (Llopiz 2013). Juveniles and adults often adopt a different diet from that of larvae (*e.g.,* herbivory, piscivory, corallivory), which translates into necessary morphological adaptations for the exploitation of new food resources (Frédérich et al. 2008; 2012). Indeed, a head with

Fig. 4 Procrustes distances between stages for the five species, having three studied ontogenetic stages (larvae, juveniles and adults). The calculation of Procrustes distance was performed when using raw shape data.



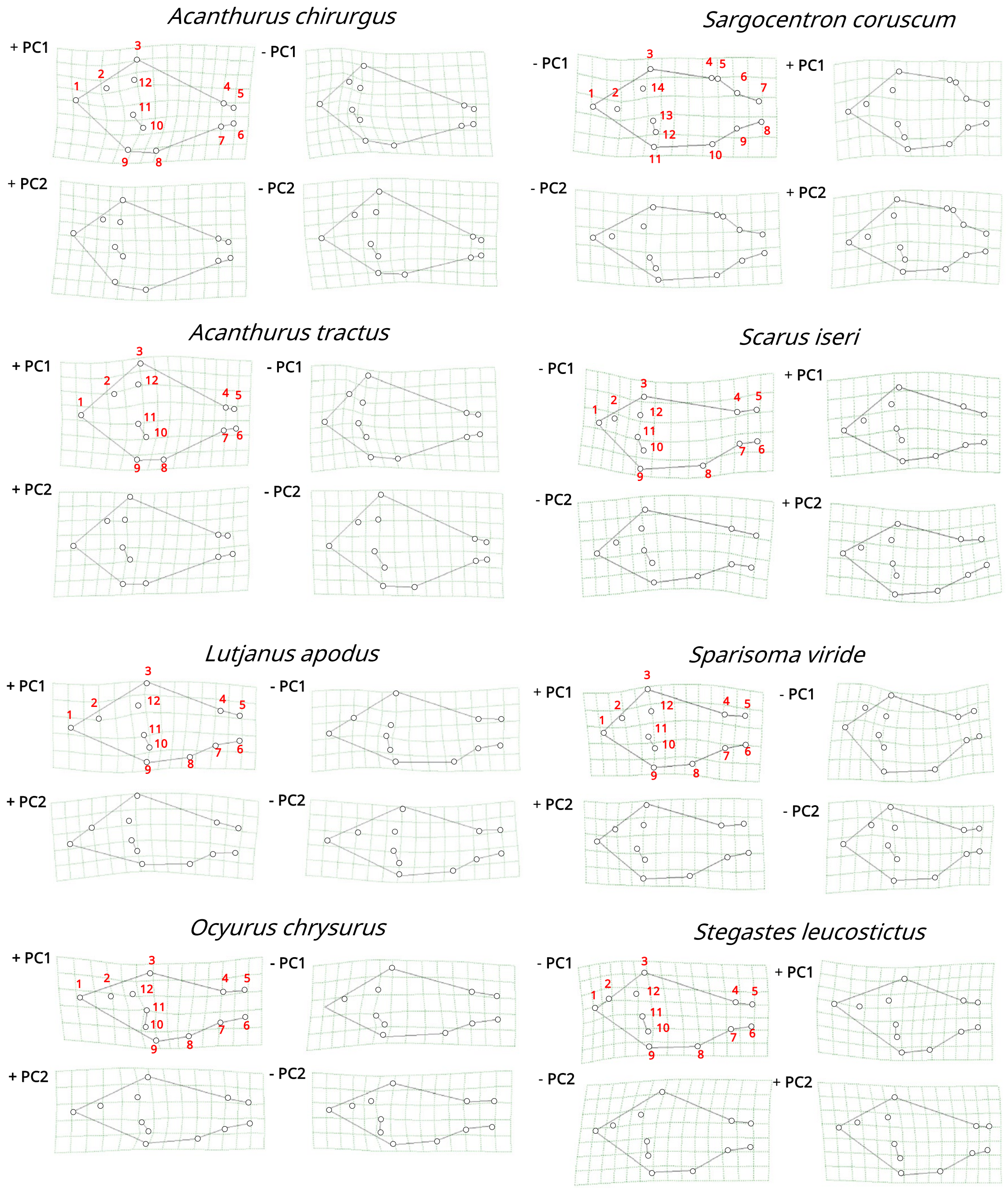


Fig. 5 TPS Deformation grids indicate shape variation represented by PC1 and PC2 axes (minimal (-PC) and maximal (+ PC) values) for each species. For each axis, the post-larval stage is represented on the left and adult on the right.

shorter jaws and cheeks, or a differently positioned mouth, enables adaptation to new feeding strategies and/or to a different diet. In surgeonfish, for example, a small, ventrally oriented mouth is particularly suited to grazing (Purcell and Bellwood 1993; Bellwood et al. 2014). Similarly, in damselfish, the morphological changes undergone are particularly beneficial to an increase in suction feeding (Frédérich et al. 2008; Frédérich and Vandewalle 2011).

Except for *S. leucostictus* and *S. coruscum*, the body shape of juveniles differs from that of adults. Such changes in body shape between the juvenile and adult stages are observed only in species showing ontogenetic ecological shift, which is not the case for *S. leucostictus* and *S. coruscum*. These two species use similar types of habitat and have the same diet at both stages (Wellington 1992). Both juvenile and adult *S. leucostictus* occupy a wide range of

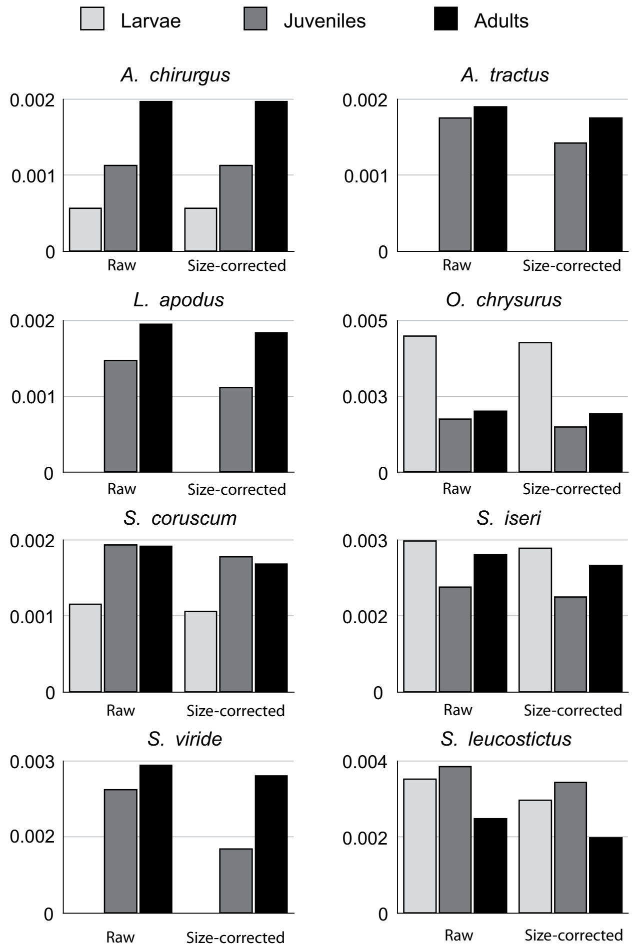


Fig. 6 Levels of body shape disparity for each studied ontogenetic stage in the eight species. The calculation of Procrustes variance was performed when using raw shape data and size-corrected shape data. Significance in the differences shape disparity between stages are provided in Table 5.

Table 5 Pairwise comparisons of the level of body shape disparity between the ontogenetic stages for the eight studied species, by using raw shape data (above diagonal) and size-corrected data (below diagonal). Significant differences (P-values) are indicated in bold. See Table 1 for the abbreviations of species.

		Post-larvae	Juvenile	Adult
A. chirurgus	Post-larvae		**0.007**	**0.022**
	Juvenile	0.222		0.448
	Adult	**0.002**	**0.008**	
A. tractus	Juvenile			0.645
	Adult		0.211	
L. apodus	Juvenile			0.175
	Adult		**0.022**	
O. chrysurus	Post-larvae		**< 0.001**	**< 0.001**
	Juvenile	**< 0.001**		0.643
	Adult	**< 0.001**	0.422	
S. coruscum	Post-larvae		**0.014**	**0.028**
	Juvenile	**0.009**		0.969
	Adult	**0.041**	0.772	
S. iseri	Post-larvae		**0.020**	0.4892
	Juvenile	**0.013**		0.113
	Adult	0.394	0.110	
S. viride	Juvenile			0.610
	Adult		0.063	
S. leucostictus	Post-larvae		0.546	0.075
	Juvenile	0.387		**0.018**
	Adult	0.081	**0.010**	

benthic microhabitats, including living and dead corals, coral rubble, sponges, mangrove roots and empty mollusk shells (Itzkowitz 1977; Wellington 1992). The species is omnivorous, feeding mainly on benthic invertebrates, turf algae and seagrasses at both stages (Wellington 1992; Vaslet et al. 2015). The soldierfish *S. coruscum* is nocturnal and demersal, living mainly in shallow waters, on rocky bottoms, and on coral reefs. During the day they hide in hollows and under massive corals. No studies have reported the transition of this species through nursery areas, and our morphological data agree with the assumption that this species recruits directly into the adult habitats.

Studied surgeonfishes (*A. chirurgus* and *A. tractus*), parrotfishes (*S. iseri* and *S. viride*) and snappers (*L. apodus* and *O. chrysurus*) have a complex ontogeny comprising shifts in habitat use, feeding habits, and behaviors. After their larval phase, the juveniles of *A. chirurgus* and *A. tractus* are associated with shallow, refuge-rich habitats in restricted reef areas, and more rarely in mangroves or seagrass beds (Nagelkerken et al. 2000; Robertson 1988). However, at the adult stage, these fishes exploit large territories, generally consisting of reefs and seagrass beds. This habitat use implies a nomadic lifestyle that juveniles do not possess, as they generally remain hidden on the reef to avoid predation (Valdes-Muñoz and Mochek 1994). In adults, pectoral fin attachment is more anterior and vertical, with a larger base than that found in juveniles. This difference in fin position may have implications for swimming performance, maneuverability, and turning ability. The morphology of adult fins enables powerful pectoral swimming without compromising the capabilities of maneuverability, which is of particular importance in structurally complex and turbulent environments such as coral reefs (Fulton 2007). Juveniles of both surgeonfish species are herbivorous, but the diversity of their food sources increases with the extension of their territories at the adult stage (Duran et al. 2019). Morphological variation between juvenile and adult surgeonfishes could thus be associated with changes in swimming performance allowing the exploitation of larger territories. In addition, juveniles of *S. viride* and *S. iseri* use seagrass beds or mangroves as nursery areas, while adults live in reef environments (Nagelkerken and Van Der Velde 2003). The passage of juveniles through nursery areas is associated with changes in morphology between the juvenile and adult stages, such as pectoral fin position and size (Fulton and Bellwood 2002). These species are herbivorous during both stages, but their ontogenetic habitat shift is associated with changes in algal resources (Overholtzer and Motta 1999). These changes in food resources are notably linked to morphological modifications of the jaws. For example, in *Scarus trispinosus* and *Sparisoma amplum*, adults have previously been classified as excavators and juveniles as scrapers (Lellys et al. 2019). Similarly, while juveniles of *L. apodus* and *O. chrysurus* pass through the mangrove during their ontogeny before reaching the reef to avoid predation (Kimirei et al. 2013), adults are known to live in the water column in different reef zones (Garcia et al. 2014). An ontogenetic trophic shift is present in both species and is associated with the capture of larger prey (Cocheret de la Morinière et al. 2003; Nagelkerken and Van der Velde 2004). Juveniles consume small, soft prey items, while adults eat larger, harder prey (Case et al. 2008). At the adult stage, *L. apodus* and *O. chrysurus* are both carnivores with lengthened body shape, probably linked to hunting and ram feeding strategies (Webb 1984a, 1984b). The body shape of adults, comprising a triangular head and fins that are evenly distributed along the body, may help these predators with stability and maneuverability in reef waters (Fulton 2007).

The dynamic of body shape disparity over ontogeny varies among species. While *O. chrysurus* and *S. leucostictus* exhibit the highest level of body shape disparity at the post-larval stage, *L. apodus*, *A. chirurgus* and *S. coruscum* show the highest shape disparity level at the adult stage. In juvenile *S. iseri* we detected a decrease in body shape disparity followed by an increase in disparity at the adult stage. Yet *A. tractus* and *S. viride* showed no significant differences in body shape disparity between stages. Despite our limited taxon sampling, we evidence the absence of any general trend of ontogenetic dynamic concerning phenotypic disparity for all the 8 studied reef fish species. However, we observed some different patterns according to the species. *L. apodus*, *A. chirurgus, S. coruscum* and *S. iseri* appear to validate our first hypothesized pattern, in which we predicted that the heterogeneous reef environment should sustain higher phenotypic disparity during the adult life stage than that of the structurally homogenous oceanic environment. Conversely, the ontogenetic dynamic of disparity in *O. chrysurus* and *S. leucostictus* agrees with our second hypothesized pattern, in which the greatest level of disparity is to be expected at the larval stage. Indeed, we hypothesized that selective pressure in play during the major habitat transition (reef colonization) may reduce the level of disparity during the growth of reef fish (Doherty 2002; Gagliano et al. 2007; Grol et al. 2014). The absence of variation in the levels of disparity throughout the ontogeny of *A. tractus* and *S. viride* may be related to a process whereby ecological factors counter-balance each other, leading to a constant level of phenotypic disparity throughout ontogeny. As observed in *S. leucostictus* and *S. coruscum*, the juvenile stage can show high levels of body shape disparity, similar to or higher than those of the adult stage. On the one hand, the ecology of the species may explain such a nonlinear variation in the level of shape disparity over ontogeny; indeed, as has recently been demonstrated by Reynaud et al. (2023), environments and associated ecological factors drive phenotypic variation in the surgeonfish *Acanthurus triostegus* during the first days of reef settlement. We might thus expect that the diversity of habitat used by both species could sustain a great diversity of phenotypes at the juvenile stage. On the other hand, internal factors such as a varied physiological status between individuals can also explain a higher level of disparity in juveniles. For example, the metamorphosis which enables the transition from post-larvae to juvenile has already been shown as a source of disparity (Keer et al. 2022; Nguyen et al. 2022). Accordingly, Reynaud et al. (2023) demonstrated the presence of a peak disparity level at three days of post-settlement in *A. triostegus*, *i.e.,* some days after the metamorphosis driven by thyroid hormones (Holzer et al. 2017). Globally, we hypothesized that the diversity of habitats used by juveniles might drive an increase of disparity level during the first days of settlement through a process involving both external and internal factors.

Finally, despite our limited species sample size, it is striking that the patterns of disparity levels differ between the two surgeonfishes (*A. chirurgus* and *A. tractus*) and the two snappers (*L. apodus* and *O. chrysurus*), even if both species pairs appear to undergo similar ecological transitions from one life stage to the next. This result suggests an absence of phylogenetic pattern in the dynamic of ontogenetic disparity level, a statement which should, however, be addressed via a more exhaustive taxon sampling of different reef fish families.

Conclusions

Body shape and associated levels of disparity were observed to vary during the ontogeny of fishes living on the reefs of Guadeloupe. We associate body shape variation between ontogenetic stages with shifts in habitat, diet, and behavior. The highest level of body shape disparity was observed at the post-larval or adult stage when some species showed no variation in the level of disparity. In a comparison of disparity across stages, our study opposes two contrasting scenarios: (1) either post-larvae exhibit reduced morphological disparity due to the homogeneity of pelagic habitats, or (2) life stages associated with the reef environment are less disparate because they experience stronger selective pressures.

As no consistent patterns were found among the eight species studied, additional factors are likely missing from our model. These might be other ecological external factors beyond the ones highlighted in our study, or possibly intrinsic factors specific to some of the species examined (external factors such as habitat diversity or food availability; internal factors such as the physiological status of metamorphosis). Therefore, although our study design and our species sample size preclude testing multiple individual explanatory variables, a more likely explanation is that one or multiple potential causal factors may have been overlooked, and that the patterns of body shape and associated levels of disparity during the ontogeny of fishes may be random across different species. The sampling of eight species remains restricted and we recommend further studies involving several species of the same family as well as several species having similar ecology in order to assess whether phylogeny or ecology is the major driver of the ontogenetic dynamic of phenotypic disparity in coral reef fishes.

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Author's contributions: Bruno Frédérich, Léa Vignaud, David Lecchini and Charlotte Dromard conceived the ideas and designed methodology as well as analyses. All authors collected the data. Léa Vignaud, Bruno Frédérich and Mehdi Boudault performed morphometric analyses and analysed the data. Bruno Frédérich and Léa Vignaud led the writing of the manuscript. All authors read critically the drafts and approved the final version.

Data Availability The data used during the current study is made available on figshare (https://doi.org/10.6084/m9.figshare.26310469), where you can access to the TPS files (landmark configurations for shape analyses) for every studied fish species.

Declarations

Conflict of interest: The authors declare no conflicts of interest.

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