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The environment: A vector of phenotypic disparity during the settlement phase of coral reef fishes

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ABSTRACT

In coral reef fish, the transition from pelagic larvae to reef-associated juveniles is a complete metamorphosis in which coordinated physiological, morphological, and behavioural changes occur, enabling the fish to settle and grow in coastal habitats and then recruit into the adult population. Environmental factors can modulate different aspects of metamorphosis such as the timing of its initiation, its duration, and the coordination of the morphological changes. Here, we raised the coral-reef-dwelling convict surgeonfish, *Acanthurus triostegus,* in different types of habitats during the post-settlement period. The selected habitats, whether natural (beach rock, mangrove, and sand beach habitats where *A. triostegus* settle naturally), or experimental (pelagic ocean and oxygen depleted 'dead' zone) were characterized by their substrate type, fish community composition, and physico-chemical profile. By using landmark-based geometric morphometric methods, we compared growth, body shape changes, and quantified phenotypic disparity levels among and within the different habitats. The results showed that fish raised in mangrove grew faster than in the other habitats and, most importantly that different habitats lead to variations in the rate and the nature of shape transformation. The ontogenetic trajectories defined in the shape space differed across habitats in terms of length and direction. A peak of shape disparity was observed for the natural habitats at three days post settlement when compared to fish reared in dead zone or oceanic environment. Overall, these results suggest that environmental diversity could generate developmental plasticity, ultimately producing phenotypic disparity that may allow the acclimation of fish to their local environment.

1. Introduction

The environment exerts a fundamental role in the life of organisms, especially during their development, and it can have profound effects on phenotypic expression (Lema, 2020). Different environmental conditions can generate various phenotypes from the same genotype, a process often referred to as phenotypic plasticity (Miner et al., 2005; Pigliucci et al., 2006; Pfennig et al., 2010), or, when it occurs during development, developmental plasticity (Smallegange, 2022). A classic example of developmental plasticity, which can result in adaptive changes in morphology, physiology, and behaviour during ontogeny, is the metamorphosis of the anuran tadpole (Denver, 2021). Tadpoles raised in decreasing water levels metamorphose earlier and at a smaller size compared to tadpoles developing in constant water levels (Székely et al., 2017). Similar effects have been observed in the presence of predators (Gomez-Mestre and Buchholz, 2006; Warkentin, 2011; Florencio et al., 2020). While this variation in development allows them to escape a stressful environment, it results in a plethora of consequences for juvenile survival. For example, increased developmental plasticity might be associated with metabolic alterations that compromise the health and lifespan of individuals which can ultimately have demographic consequences (Burraco et al., 2017).

Metamorphosis is one of the most extraordinary life history transitions. It occurs during the post-embryonic development of vertebrates,

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especially in amphibians and teleost fishes. This transition is generally associated with a shift in ecological niche including habitat change (*e.g.,* from aquatic to terrestrial, or oceanic to demersal habitats), and is accompanied by physiological, morphological, and behavioural transformations (Bishop et al., 2006; Laudet, 2011; Roux et al., 2022). In teleost fish, as in all chordates, metamorphosis is orchestrated by thyroid hormones (THs) that control and modulate physiological and morphological changes (*e.g.*, Paris et al., 2008; Laudet, 2011; reviewed in McMenamin and Parichy, 2013; Roux et al., 2022). Shifts of habitat and diet, as well as morphological changes associated with metamorphosis and settlement phase have been documented in various reef fish taxa (*e.g.*, Bosley et al., 2002; McCormick et al., 2002; Frédérich and Vandewalle, 2011; Frédérich et al., 2012).

During metamorphosis, THs act on most organs and are particularly important as major regulators of bone development and remodelling (Campinho, 2019; Keer et al., 2022; Nguyen et al., 2022). For instance, THs regulate shifts in allometric trajectories during the transition from zebrafish larvae to juveniles, notably by inhibiting the relative growth of the head (Hu et al., 2019). This critical function of THs in bone remodelling during metamorphosis, and therefore associated allometric variation, is particularly relevant given the fact that THs signalling is sensitive to environmental conditions (Deal and Volkoff, 2020). Many studies have shown that THs are involved in mechanisms that respond to changes in environmental conditions such as temperature, dissolved oxygen level, salinity, pH, or pollutants (Arjona et al., 2008; Little et al., 2013; Rossi et al., 2015; Potrokhov et al., 2019; Besson et al., 2020). With the very large number of TH-regulated changes occurring during metamorphosis (Buchholz et al., 2007; Heimeier et al., 2010; Pelayo et al., 2012; Ochsner and McKenna, 2020), environmentally induced alterations of THs status during this developmental period have the potential to affect the outcome of the metamorphosis, that is, the "quality" of the juvenile. Indeed, this has already been observed in the convict surgeonfish *Acanthurus triostegus*. Recent studies using this species as a model system (Holzer et al., 2017; Besson et al., 2020) have shown that changes in TH levels after treatment with the pesticide chlorpyrifos can result in delayed maturation of sensory organs, a decrease in the ability of juveniles to perform their ecological function (*i.e.*, grazing algal turf), and an impaired ability to escape predators. Similarly, relocation in the open ocean of young juveniles passing the reef crest delayed their metamorphosis and altered their TH levels (McCormick, 1999; Holzer et al., 2017; Besson et al., 2020). These studies not only highlight the role that the environment plays in the timing of fish metamorphosis but they also reveal a great degree of developmental plasticity. However, so far these effects have only been observed in artificial conditions (*e.g.*, pollution or extreme environmental changes), thus raising the question of how developmental plasticity of the metamorphosing fish responds to the local environment (Lowe et al., 2021).

In the present study, the surgeonfish *A. triostegus* was used as model to investigate the effect of habitat on metamorphosis and associated morphological changes. Coastal ecosystems house a unique mosaic of habitats with inherently different environmental condition (Anthony et al., 2009). These habitats range from algae or submersed vegetation (*i.e.*, seagrasses, mangroves, marshes) to coral reefs and other animal-derived structures (such as oysters, mussels, sponges) to abiotic substrates (*i.e.*, rock crevices, shell hash, cobble) (Lefcheck et al., 2019). Importantly, some of these habitats serve as nursery sites, *i.e.*, sites where the density, the growth, and the survival of juvenile fish and/or the movement to adult habitats are, on average, greater than in other habitats, for many fish species (Beck et al., 2001; Hamilton et al., 2017; Whitfield, 2017; Lefcheck et al., 2019). Given the link between environment and TH signalling, and the importance of THs in coordinating morphological transformations, we expect that the diversity of habitats available to settling larvae plays a crucial role in reef fish metamorphosis and the generation of phenotypes in juvenile fishes. This environmental diversity could indeed sustain developmental plasticity, producing phenotypic disparity at the population level. In our study, we selected and tested the effect of five types of habitats, from which three were habitats where *A. triostegus* juveniles are commonly found, on the pattern of form (*i.e.*, size and shape) variation during post-settlement ontogeny. These habitats were characterized by biotic (*e.g.*, fish abundance, alpha diversity) and abiotic parameters (*e.g.*, temperature, pH, and salinity). By using landmark-based geometric morphometrics, we investigated growth rates and body shape variation across habitats to determine whether different environmental conditions lead to plastic responses in the morphometry of *A. triostegus* and induce variation in the level of phenotypic diversity, or disparity, at the scale of a population.

2. Methods

2.1. Shoreline categories of Moorea and tested habitats

The study was conducted between September 2020 and June 2021 on Moorea Island (17″30′S, 149″5′W; French Polynesia). This island is surrounded by a 61 km long barrier reef which delimitates a lagoon ranging from 0.8 km to 1.3 km in width. Fringing reefs exhibit a range of environmental features that are dependent on the nature and composition of sediments, freshwater runoff, as well as presence of mangrove trees (*Rhizopora stylosa*), algae, or corals (Gasc et al., 2021). These coastal systems can be subdivided into different types of habitat and we focused on five of them: beach rock (BR), mangrove (MG), sand beach (SB), dead zone (DZ), and ocean (OC).

Beach rock (BR) habitats have been described as eroded beach material cemented by calcite or aragonite (Stoddart and Cann, 1965). We performed substrate identification (Point Intersection Transect method following Hill and Wilkinson, 2004) and observed that the substrate of this habitat was composed of 66.7% bare coral slab, 17% macroalgae, and 12% live coral. Mangrove (MG) habitats consisted mainly of mud (97%) and roots of the mangrove plant *Rhizophora stylosa* (Langer and Lipps, 2006). Sand beaches (SB) are lacking high vegetation (Madi Moussa et al., 2019) and they are made of high proportions of sand (46.7%) with 20.7% macroalgae, 16.7% live coral, and 14.7% dead coral. These three habitats are nursery areas for many fish species including *Acanthurus triostegus* (Lecchini and Galzin, 2005; Lecchini and Tsuchiya, 2008; Lecchini et al., 2009) and thus can be described as natural environments for this species at the juvenile stage. We selected these habitats to test and to compare their effect on size and shape changes that occur in *A. triostegus* during the settlement period.

Moreover, we also tested other habitats where *A. triostegus* does not usually settle – *i.e.*, dead zone and open ocean – to assess the importance of habitats on ontogenetic morphological changes in reef fishes. Dead zones (DZ) are locations where algae rafts stagnate and their degradation leads to turbidity, eutrophication, altered foodwebs, and oxygen depletion in the water column (Boesch, 2002; Howarth et al., 2011). Generally, high swells rip off macroalgae (mostly *Turbinaria ornate*) from their substratum and currents concentrate them into specific zones of the lagoon often close to the shoreline. These detached macroalgae form rafts of which size and occurrence vary depending on the season, the wind and the wave regime (Zubia et al., 2015). Lastly, the ocean (OC) or oceanic environment is not considered as a habitat for demersal fishes. However, the ocean environment was used as a positive control as it was previously shown to delay metamorphosis in reef fishes (McCormick, 1999; Holzer et al., 2017; Besson et al., 2020).

2.2. Biotic and abiotic parameters

Some major ecological characteristics of the selected habitats were assessed by fish surveys, physico-chemical measurements, nutrients quantification, and substrates identification. On each site, underwater fish census surveys of juvenile and adult fishes were conducted along three belt transects parallel to the shore. Each transect was 25 m long and two m wide (50 m^2). The first transect was located as close to the

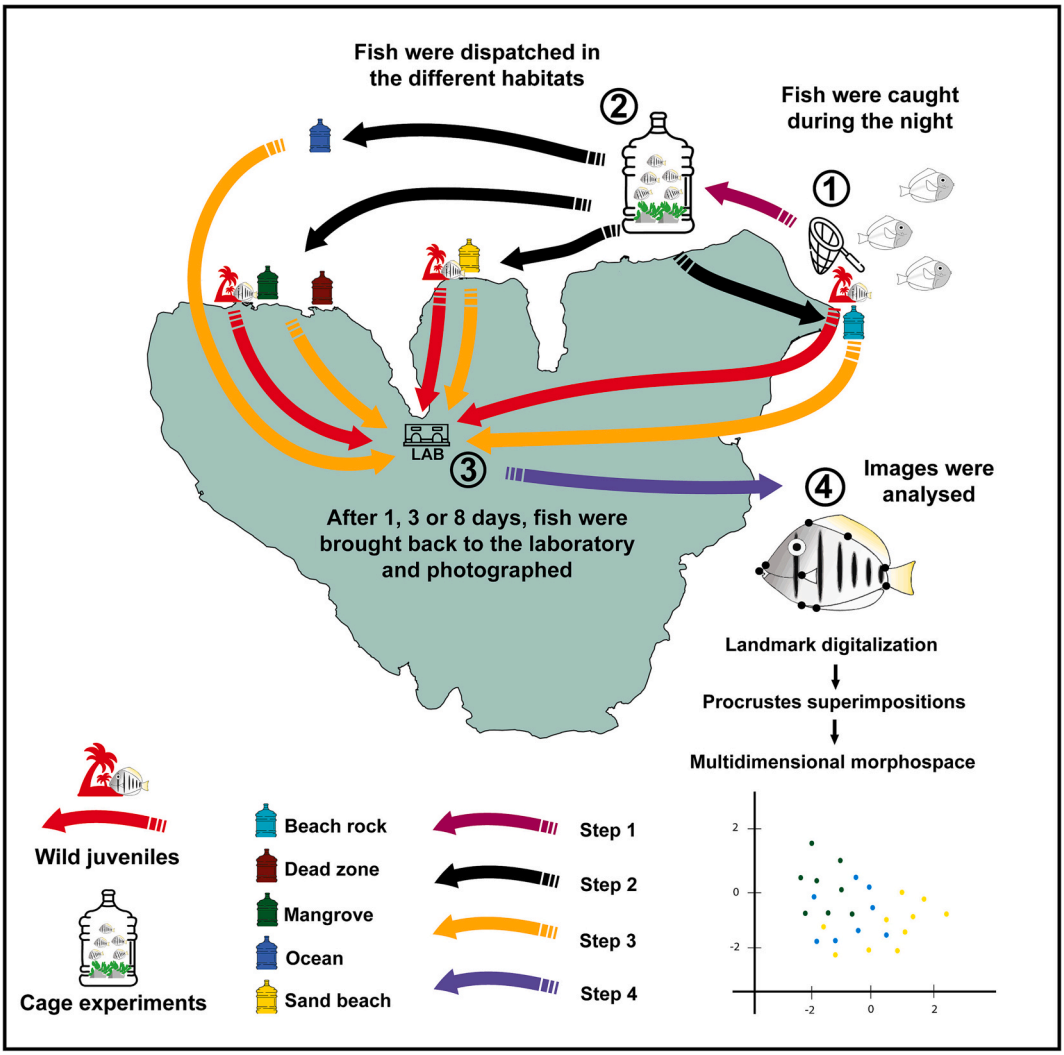

Fig. 1. Overview of the methodology showing the set-up cage experiments and the use of wild juveniles.
Step one (light purple arrow): fish (0 dpc) were captured during colonization at night. Step two (black arrow): fish are placed in cages to be set-up in different habitats for 1, 3, or 8 days. The number of fish per cage was six ($n = 6$) with three replicate cages per habitat. Step three (orange arrow): fish were removed and brought back to the laboratory, then photographed. Step four (dark purple arrow): images were analysed using landmark-based geometric morphometrics. The red arrow indicates wild juveniles sampling. The scatter plot on the bottom right corner is a schematic representation of shape space (morphospace) where one dot is one fish characterized by its shape. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shoreline as possible, generally one meter or two meters away, the second one 10 m from the shoreline, and the third one 30 m away. These visual censuses allowed us to estimate the total abundance and the diversity of fish species. For each habitat, we calculated the alpha diversity of fish (*i.e.,* species richness), the density of *A. triostegus* at juvenile and adult stages, and the density of piscivorous fish species (species that feed on fish or small fish as defined on FishBase; Pauly and Froese, 2021). Temperature (in °C), dissolved oxygen (in %), salinity, and pH were measured with a multi-parameter probe (YSI-Professional Plus Multiparameter Meter). Measurements were taken three times per month over the course of the study (7 months). Three water samplings were done (in November 2020, March 2021, and May 2021) to determine the nutrient concentration in each habitat (NH_4, NO_2, NO_3, PO_4, and $Si(OH)_4$). Water samples were preserved at −40 °C, then nutrients were analysed by colorimetry using a Technicon Autoanalyzer III system at the CRIOBE research station. Substrate identification was performed using the Point Intercept Transect (PIT) method along three 25 m belt transects (parallel to the shoreline) on each habitat (Hill and Wilkinson, 2004). The category of substrate was recorded every meter. The categories were: dead coral (DC), live coral (LC), macroalgae (MA), mud (Mud), coral rubble (Rubble), sand (Sand), coral slab (Slab), and volcanic rock (VR).

2.3. Fish capture, husbandry, and experiments

We compared the post-settlement development of *A. triostegus*, captured while entering the reef, and raised them in cages within different habitats. Additionally, we compared the fish raised in cages to juveniles naturally settled in the same habitats. The various steps of the experiment are depicted in Fig. 1. The cages consisted of large PVC water jugs with numerous holes (to allow a free flow of water) and were attached to a metal bar fixed into the substrate. This system has proven to be very convenient for *in situ* manipulation experiments.

In brief, post-larvae (settlement-stage – fully transparent individuals, Holzer et al., 2017, Fig. 1) were collected using hand nets at night while recruiting to the reef crest between September 2020 and June 2021 in the week of the new moon on the North-East coast of Moorea. Here, we defined the age of the juveniles based on the number of days spent in the reef environment: the number of days post-capture (dpc). These ages do not correspond to the absolute age because we do not know the age of the fish entering the reef (but see McCormick, 1999). Accordingly, the

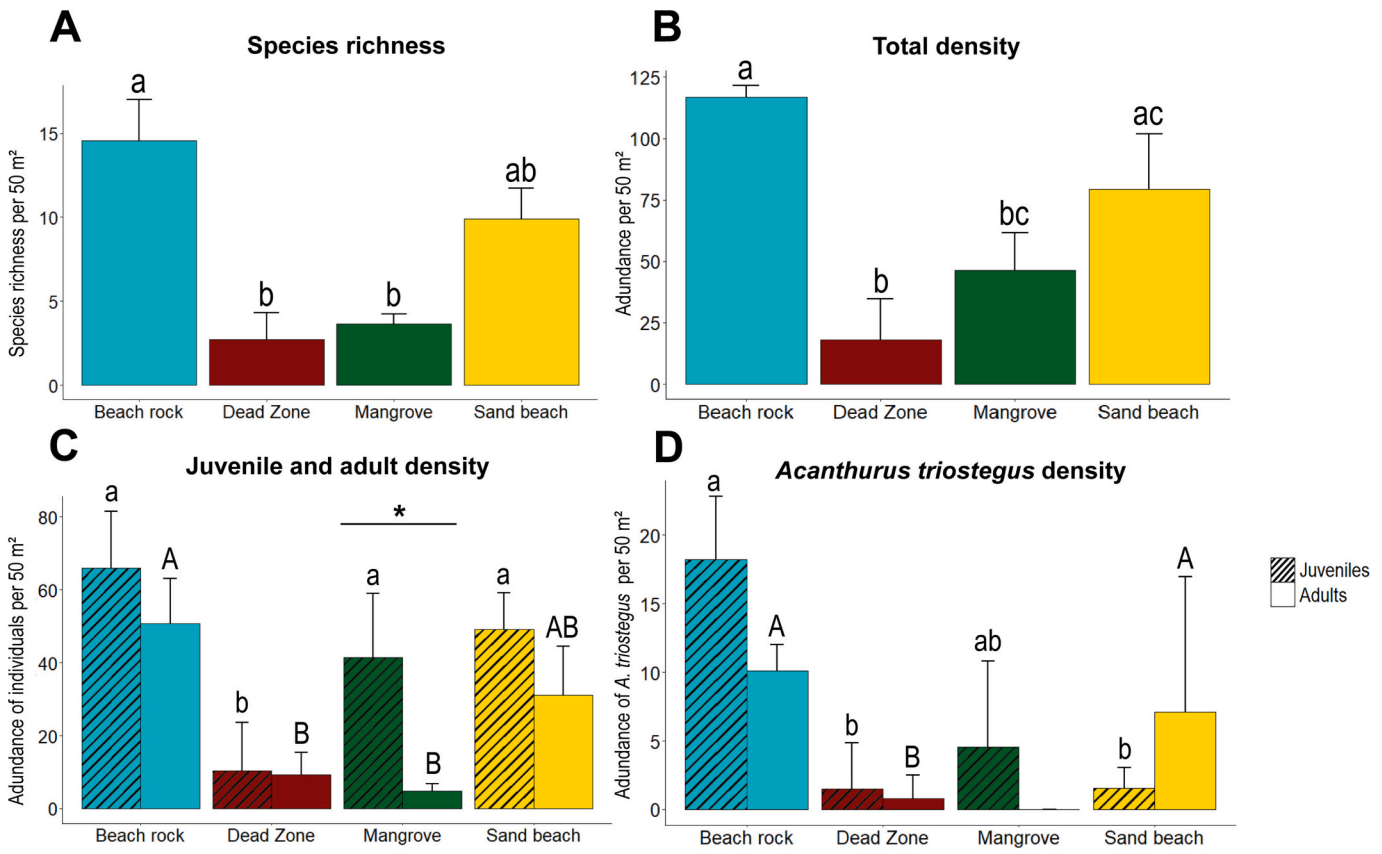

Fig. 2. Fish composition in each habitat.
(A) Mean of species richness per 50 m^2. (B) Mean total density (all species) expressed in number of individuals per 50 m^2. [A-B] Black letters refer to significant differences between habitats based on GLM with a quasi-Poisson distribution followed by a Tukey test. (C) Mean total density (all species) of juveniles and adults expressed in number of individuals per 50 m^2. Asterisks refers to the significant difference between juvenile and adult density in mangrove habitat. (D) density of *Acanthurus triostegus*, juveniles and adults expressed in number of individuals per 50 m^2. Error bars show the standard deviation (SD). [C—D] Capital letters and regular letters show significant differences among habitats (GLM with a quasi-Poisson distribution followed by a Tukey test) for adults and for juveniles, respectively.

settlement stage corresponds to zero dpc (D0). Fish at this stage were kept in *in situ* cages (five L) in each habitat for one dpc, three dpc, and eight dpc (Fig. 1). Six fish were placed in each cage and one cage was used for each sampling period (*e.g.,* six fish in one cage for one dpc, six fish in one cage for three dpc, and six fish in one cage for eight dpc). Each habitat-exposure time was repeated three times ($n = 18$ per time period and per habitat). Fish were fed by placing coral rubble with algal turf collected on each habitat – turf algae is the preferred food source of *A. triostegus* post-larvae (Frédérich et al., 2012). Finally, wild juveniles naturally settled on the three nursery habitats – beach rock, mangrove, and sand beach – were collected with hand nets at dusk (Wild juveniles, Fig. 1).

All fish were euthanized by an overdose of MS-222 (0.4 mg ml-1 by balneation) and each individual was then weighed and photographed in left lateral view with a Nikon 5300 (105 mm lens). Juveniles collected in the wild populations were conserved at −20 °C for otolithometry.

2.4. Otolithometry

Six fish per habitat were collected and used to estimate the age of the juveniles caught on each habitat by counting the daily growth increment on their lapilli otoliths (following Morat et al., 2018).

2.5. Body size and shape

The standard length (SL; mm) of each fish was measured with the software "ImageJ" based on fish photographs. The variation of body shape through post-settlement ontogeny was studied by using landmark-based geometric morphometrics (Rohlf and Marcus, 1993). The x, y coordinates of the same 15 homologous landmarks used by Frédérich et al. (2012) to study allometric shape changes in *A. triostegus* were digitized with the software TPSDIG2 v2.31 (© 2017, Rohlf). A Generalized Procrustes Analysis (GPA) was performed to align specimens by using the *gpagen* function from the R-package geomorph (v. 4.0.0; Adams and Otárola-Castillo, 2013), and a shape dataset was obtained.

2.6. Statistical analysis

2.6.1. Comparisons of habitats using biotic and abiotic parameters

To compare fish abundance (adults and juveniles) and fish diversity among habitats, generalized linear models (GLM) using a quasi-Poisson distribution to control for common over-dispersion in the ecological count data were performed. Tukey's tests were then applied to perform pairwise comparisons between habitats. Physico-chemical parameters did not follow a normal distribution. Thus, Kruskal-Wallis tests followed by a multiple comparison Dunn's test using the Holm method were used to test differences in temperature, pH, DO, salinity, and nutrient concentrations among habitats.

2.6.2. Effects of habitats on growth and body shape variation

Fish growth was estimated by linear regression models and associated slope parameters for every condition. We compared slopes of linear models among habitat experiments and between fish raised in cages and wild juveniles. To do so, we used the function *emtrends* implemented in the R-package emmeans (Lenth, 2019) to perform post-hoc tests for pairwise comparisons of the estimated slopes.

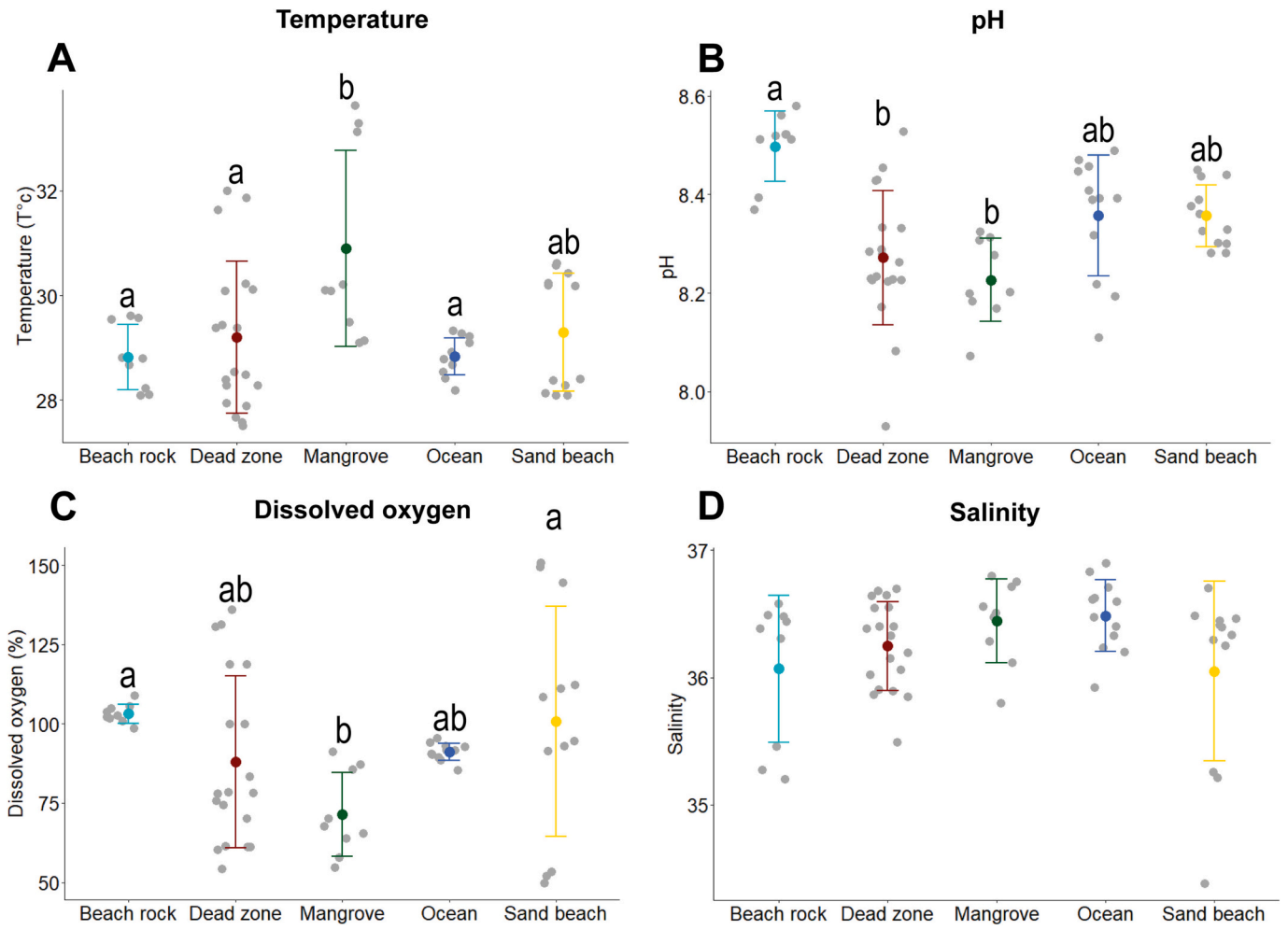

Fig. 3. Variation of the physico-chemical parameters for each habitat.
(A) temperature. (B) pH. (C) dissolved oxygen expressed in percentages. (D) salinity. Colored points represent the mean value and the error bars show the standard deviation. Grey points are every measurement illustrating the variability in each habitat. Letters show significant differences among habitats based on Dunn tests (Holm method, $p < 0.05$).

Differences in the pattern of body shape variation among conditions were tested by combining four comparative analyses. We first performed a principal component analysis (PCA) on shape variables to explore and visually compare the trajectory of body shape variation among and within habitats in a reduce shape space defined by the two first principal components (PC axes). Deformation grids and vectors (lollipop diagrams) were respectively produced by TPSRELW32 V1.70 (© 2017, Rohlf) and by the function *plotRefToTarget* from the R-package geomorph to illustrate and describe shape variation associated with PC axes. Then, we compared the rate of shape variation among habitats and between cage experiments and wild populations by regressing PC1 as well as PC2 against time. In addition to these univariate linear models, we tested such a variation in the rate of shape transformation among habitats by using the function *procD.lm* from the R-package geomorph fitting linear models including all shape variables. Comparisons between multivariate linear models were performed with the function *anova.lm.rrpp* from the R-package RRPP (Collyer and Adams, 2018). Lastly, ontogenetic trajectories defined by the four age stages (zero dpc, one dpc, three dpc and eight dpc) in the shape space were compared by using the function *trajectory.analysis* from the R-package geomorph. Pairwise comparisons were used to compare the length (the amount of shape changes), the curvature (the shapes of the trajectories), and the direction (the angles of the trajectories) of these trajectories in the morphospace (Adams and Collyer, 2009).

Plasticity produces phenotypic diversity (*i.e.*, disparity) between and within populations. Accordingly, we aimed to compare the level of disparity among habitats during the first week of post-settlement. Indeed, the heterogeneity of biotic and abiotic factors differ among habitats (see Results, section 3.1), and we thus expect that these environmental differences lead to variation in the level of disparity within and among populations. To test this hypothesis, we calculated and compared shape disparity levels across the four age stages for each habitat using the *morphol.disparity* function from the R-package geomorph. We then applied the same function to compare the level of shape disparity observed at eight dpc among habitats.

3. Results

3.1. Characterization and comparison of habitats with biotic and abiotic parameters

A total of 52 fish species were recorded with a maximum of 17 species per transect (Supplementary Table S1). Species richness significantly differed among habitats (GLM family "quasi-poisson", Chisq = 58.611, df = 3, *p*-value <0.001; Fig. 2A). The dead zone and the mangrove showed the lowest species richness while the beach rock had the highest one (Tukey's test: p-value <0.001, Supplementary Table S2). Sand beach habitat had an intermediate level of species diversity as no significant difference was observed between this habitat and the three others (Fig. 2A, Supplementary Table S2).

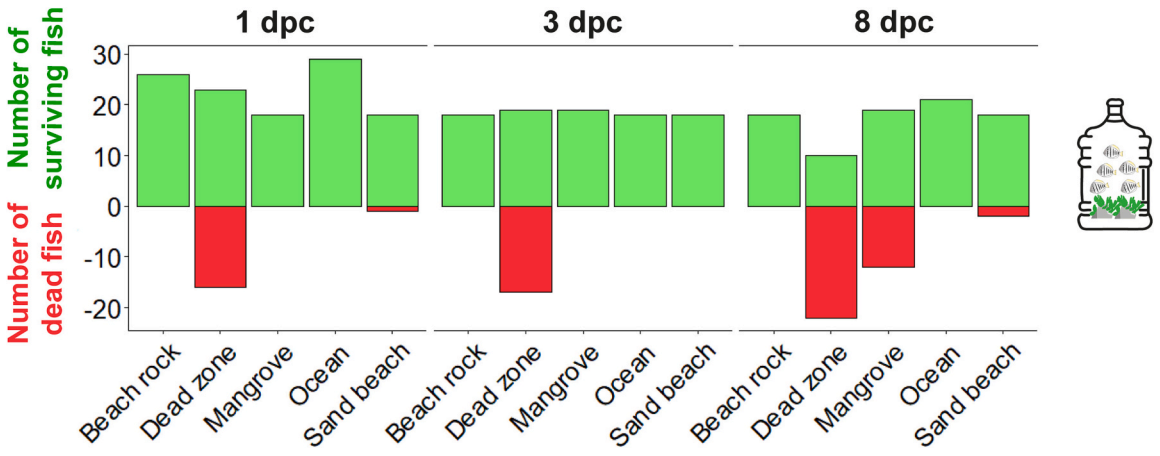

Fig. 4. Survival and mortality of fish during the cage experiment after one, three and eight days (dpc) in each habitat.
Green bars represent the number of fish that survived, and the red bars correspond to the number of dead fish. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Habitats also differed in terms of fish abundance (GLM family "quasi-poisson", Chisq = 46.357, df = 3, p-value <0.001; Fig. 2B). With a mean total abundance of 116.7 ± 4.9 individuals per 50 m^2, the beach rock showed a higher abundance of fish (adults and juveniles) than mangrove and dead zone habitats (Tukey's test: *p*-value <0.001, Supplementary Table S2). Sand beach (79.3 ± 38.9 fish per 50 m^2) hosted significantly more individuals than the dead zone, which showed the lowest abundance of fish (17.9 ± 16.8 individuals per 50 m^2, Fig. 2B, Table S2). No significant differences were observed among the other habitats (Supplementary Table S2).

Beyond a comparison about total fish abundance, we also separately compared the number of juveniles and adults among habitats to determine a potential nursery function. Generally speaking, we observed more juveniles than adult fishes on the studied habitats (Fig. 2C) even if this difference was only significant for mangrove (GLM family "quasi-poisson", p-value = 0.01). Among habitats, dead zones supported lower proportions of juveniles (10.3 ± 13.3% juveniles per transect) in comparison with beach rock (65.9 ± 15.7%), mangrove (41.4 ± 17.5%) and sand beach (49.2 ± 10%, Fig. 2C).

Adults and juveniles of *A. triostegus* were observed across all the studied habitats. However, the abundance of juveniles varied among habitats (GLM family "quasi-poisson", Chisq = 16.384, df = 3, *p*-value <0.001). The abundance of juveniles was the highest in beach rock (18.2 ± 4.6 individuals per 50 m^2) and mangrove (4.6 ± 6.2 individuals per 50 m^2, Fig. 2D, Table S2) habitats. Conversely, the dead zone (1.5 ± 3.3 individuals per 50 m^2) and sand beach habitats (1.6 ± 1.5 individuals per 50 m^2) were characterized by the lowest abundance of *A. triostegus* juveniles (Supplementary Table S2). The beach rock, dead zone, and mangrove habitats hosted higher proportions of juveniles than adults (Fig. 2D).

Among encountered fish species, the piscivorous *Caranx sexfasciatus*, *Lutjanus bohar*, *L. fulvus*, *L. kasmira*, *Rhinecanthus aculeatus*, and *Synodus binotatus* may be considered as predators of the juveniles of *A. triostegus*. However, their abundance was relatively low in all habitats with a mean of 0.7 predators per 50 m^2 in the mangrove, 0.6 per 50 m^2 in beach rock, 0.1 per 50 m^2 in sand beach habitats, and none in the dead zone.

Generally speaking, habitats differed in their physico-chemical parameters during our study. Oceanic environment and beach rock habitats showed less variability in abiotic parameters across time compared to the other habitats.

The mangrove habitat had a significantly higher mean temperature than the beach rock, dead zone, or ocean habitats (Kruskal-Wallis test: $X^2 = 9.75$, df = 4, *p*-value = 0.04; Supplementary Table S3, Fig. 3A). The dead zone, mangrove, and sand beach habitats were characterized by larger variation in temperature compared to the ocean or beach rock habitat. Indeed, the standard deviation of the temperature was 1.45 °C in the dead zone, 1.64 °C in the mangrove, 1.23 °C in sand beach, 0.62 °C in the beach rock, and 0.35 °C in the ocean. This difference may be linked to the fact that dead zones and mangroves are shallower habitats with relatively stagnant water in contrast to the beach rock and the oceanic environment that are exposed to deeper waters and continuous water renewal.

The highest mean pH value was recorded on the beach rock habitat with 8.5 ± 0.07 (± mean standard deviation). The dead zone and mangrove habitats had the lowest pH mean value with 8.27 ± 0.14 and 8.23 ± 0.08, respectively (Fig. 3B). The dead zone habitat exhibited the highest variability in pH.

Dissolved oxygen (O_2) varied greatly in the dead zone and sand beach habitats (50% to 150%; Fig. 3C). The mangrove was characterized by lower concentration of O_2 than the beach rock and sand beach (Fig. 3; Supplementary Table S3). No differences of salinity were observed among habitats (Kruskal-Wallis test, Chi-square = 6.7835, df = 4 *p*-value = 0.15; Fig. 3D).

Overall, nutrient measurements (NH4; NO2; NO3; PO4; and Si(OH) 4) varied greatly across replicates for all habitats (Fig. S1 A-E). As a result, no significant difference was observed among habitats in terms of mean values of the different nutrients (Kruskal-Wallis test, NH4: chi-squared = 4.4625, df = 4, p-value = 0.35; NO_2: chi-squared = 8.2375, df = 4, p-value = 0.15; NO_3: chi-squared = 5.825, df = 4, p-value = 0.21; PO_4: chi-squared = 1.0101, df = 4, p-value = 0.91; $Si(OH)_4$: chi-squared = 8.4375, df = 4, p-value = 0.08). However, the dead zone habitat was characterized by recurrent peak values of NO_2, PO_4, and $Si(OH)_4$ (Fig. S1B, S1D, S1E).

3.2. Mortality

Settlement-stage fish were raised in cages in each habitat over a period of eight days, and the number of survivors was recorded in each habitat and for each time period (Fig. 4). Overall, mortality was low across habitats except for the dead zone. There, the mortality across replicates (six fish per replicate) was 41%, 47% and 69% in fish exposed for one, three and eight dpc, respectively. This level of mortality explained the low numbers of individuals sampled at eight dpc for the dead zone habitat ($n = 10$ *vs* $n = 18$ for the other habitats). We also quantified that mortality was higher in the mangrove habitat after eight dpc (39%, Fig. 4), which was possibly linked to high temperature and low dissolved oxygen periods (Supplementary Fig. S1).

Table 1
Habitat effect on the growth of *Acanthurus triostegus* raised in cages, assessed by linear multiple regression analyses.

Model	Estimate	Std. Error	T-value	P-value
Time	−0.00921	0.04093	−0.225	0.82207
Time x DZ	0.111443	0.064765	1.721	0.08597
Time x MG	0.167627	0.057884	2.896	**0.00396**
Time x OC	0.001515	0.057884	0.026	0.97913
Time x SB	0.03933	0.057884	0.679	0.49719

Bold *p*-values are significant at the 0.05 level. Habitats are abbreviated as follow: beach rock (BR); dead zone (DZ); mangrove (MG); ocean (OC); sand beach (SB).

3.3. Effects of the habitat on growth

As growth is a crucial parameter for the survival of new settlers, we investigated differences in growth rates across habitats. Only fish raised in the mangrove habitat showed a significant linear relationship between size and age ($N = 18$/habitat/time, p-value = 0.004; Table 1). For the other habitats, linear models were not significant and growth rates seemed slower. Indeed, if a positive fish growth is observed between zero dpc and three dpc, growth was null between three dpc and eight dpc on the beach rock, dead zone, ocean, and sand beach habitats (Fig. 5A).

To validate our cage results, we collected individuals from natural populations in each type of habitat, except for the dead zone where no juvenile could be collected (Fig. 1). The analysis of fish otoliths allowed us to estimate the time spent in the reef environment since their settlement and to obtain a size-age relationship. The distribution of juveniles collected in the wild fall within the size-age range of fish from cage experiments (Fig. 5B), which was validated by linear models including juveniles and fish raised in cages (Table 2). These linear models revealed a significant size-age relationship with a significant effect of habitats on growth ($F = 6.434$, $R^2 = 0.1$, p-value = $1.08E^{-05}$; Table 2). Fish individuals living in mangroves had higher growth rates during the

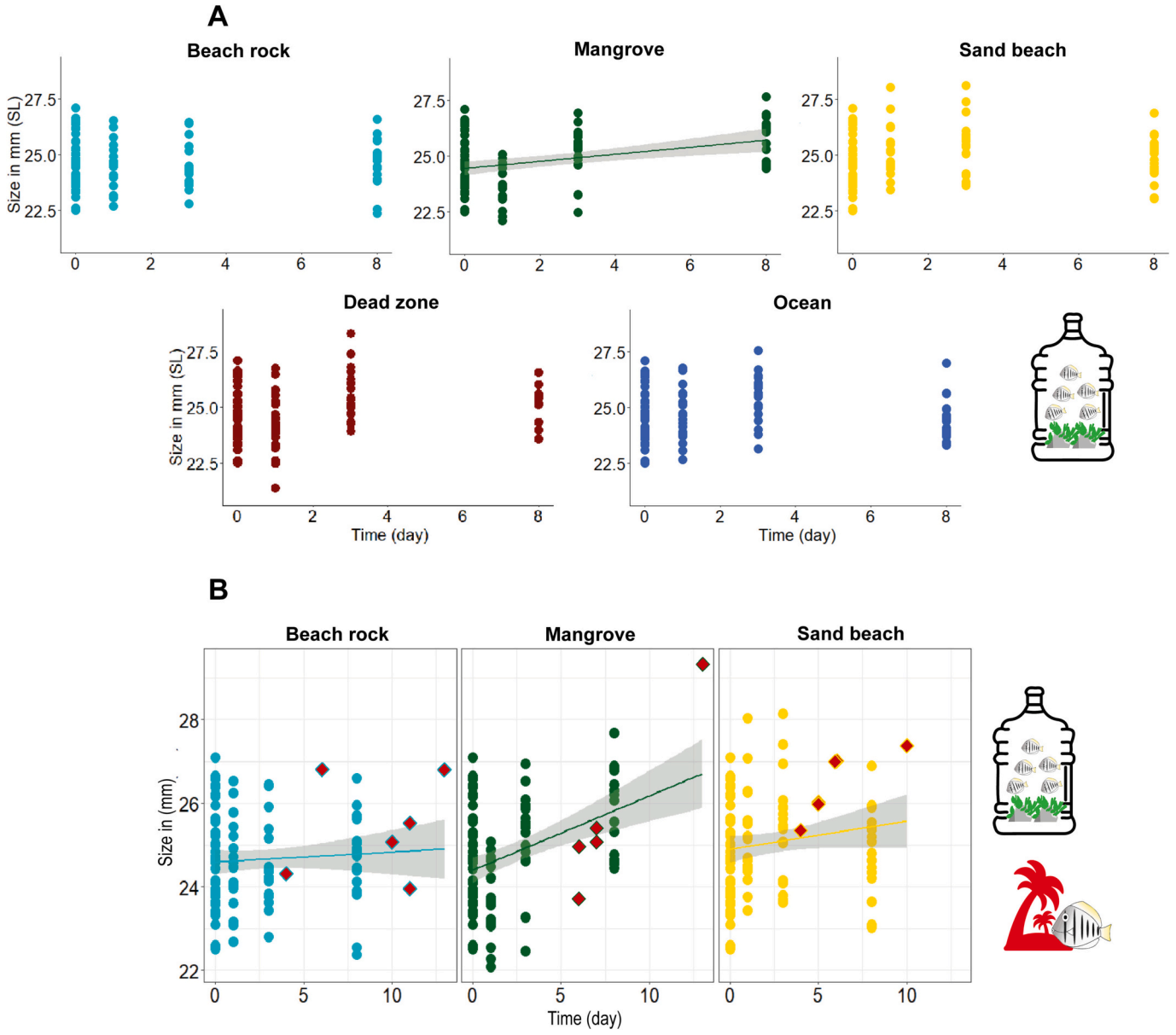

Fig. 5. Habitat effect on the growth of *Acanthurus triostegus*.
(A) size variation during the eight days of the cage experiment in every habitat. (B) size variation including both fish raised in cages (colour points) and wild juveniles (red dots). The age of wild juveniles was estimated by otolithometry (n = 6 per habitat). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Habitat effect on the growth of *Acanthurus triostegus* when fish raised in cages and wild juveniles are combined, assessed by linear multiple regression analyses. Pairwise comparisons were performed by testing signification variation of slope parameters.

Multiple linear model				
Model	F	R^2	AIC	P-value
Size ~ Time x Habitat	6.434	0.09894	108.0636	**1.08E-05**

Slope comparison				
Habitat	Estimate	SE	T ratio	P-value
MG *vs* BR	−0.1536	0.051	−3.013	**0.0079**
SB *vs* BR	−0.0434	0.0521	−0.833	0.6826
SB *vs* MG	0.1102	0.0538	2.049	0.1026

Bold p-values are significant at the 0.05 level. Habitats are abbreviated as follow: beach rock (BR); dead zone (DZ); mangrove (MG); ocean (OC); sand beach (SB).

studied period of post-settlement ontogeny than fish living in other habitats (Fig. 5B; Table 2).

3.4. Habitat affects body shape variation during settlement

To assess the effect of the habitats on shape changes, we first explored body shape variation during post-settlement ontogeny in the shape space defined by the two first axes of a PCA performed on shape variables. The first two PCs captured >51% of the total shape variation (Fig. 6A). PC1 (38.6%) primarily captured variation associated to the relative body depth and head shape (Fig. 6B) and PC2, which explained 12.8% of the total shape variation, expressed changes associated to the dorsal, the ventral, and the anal fin regions (Fig. 6C). At reef settlement (zero dpc), *A. triostegus* had an elliptic body shape (Fig. 6D) which became more streamlined, with a mouth more ventrally oriented at eight dpc (Fig. 6E-F). Variation along PC2 was observed at zero, one, three and eight dpc for every habitat. At eight dpc, fish from the mangrove showed higher values along PC2 than in other habitats (Fig. 6A).

The visual comparison of ontogenetic trajectories suggested that the pattern of shape variation differed across habitats (Fig. 6A), which was confirmed by linear regression models. Indeed, even if the relationship between the shape expressed by PC1 and the age (*i.e.*, dpc) of fish did not differ among conditions (Fig. 7A; Supplementary data Table S4; *p*-value >0.05), those associated with PC2 varied significantly across habitats (Fig. 7B, Table Supplementary S5). Shape changes observed in fish living in mangrove differed from those of fish raised in other habitats (Supplementary Table S5). Notably, at eight dpc, fish from mangrove habitat showed more streamlined body shapes than those from the other habitats (Fig. 7B).

Multivariate linear models confirm that body shape varied across time and habitats (Table 3). The settlement habitat induced significant variation in the rate of shape changes in *A. triostegus* (F = 2.32, Z = 3.16, p-value = 0.001; Table 4). Body shape of fish raised in mangrove and ocean habitats were significantly different from those living in beach rock and sand beach habitats (Table 4).

Ontogenetic trajectories can be defined in the shape space by connecting the three linear segments linking the four age stages (zero dpc, one dpc, three dpc and eight dpc). Comparisons of these time-delimited ontogenetic trajectories revealed differences in terms of magnitude and direction, but not in their curvature (Table 5). Fish raised in the oceanic environment showed the shortest trajectory (0.073), revealing that fish body shape transformation after eight dpc was the most limited in this habitat. Conversely, the longest trajectories were observed for dead zone (0.090) and beach rock (0.087); (OC *vs* DZ, d = 0.016, p-value = 0.007; OC *vs* BR, d = 0.014, p-value = 0.013; Table 5; Fig. 8A). The direction of ontogenetic trajectories was similar for beach rock and sand beach habitats while these trajectories were divergent in the shape space for the other habitats (Table 5). The combination of the results from linear models and characterisations of ontogenetic trajectories demonstrated that the amount, the nature, and the rates of body shape transformation during post-settlement are impacted by the habitat.

The levels of body shape disparity within habitats were maximum at three dpc across the natural habitats, *i.e.,* beach rock, mangrove, sand beach, and then decreased at eight dpc (Fig. 8B). Shape disparity levels increased over ontogeny in the dead zone habitat when they were relatively constant over ontogeny for fish raised in the oceanic environment (Fig. 8B). At eight dpc, fish from dead zone were significantly more variable in their phenotype than fish from ocean or sand beach (Supplementary Table S6).

3.5. Body shape comparison between caged and wild juveniles

In order to estimate the effect of cage rearing on fish development, we collected fish from the natural environment (wild juveniles) and compared their morphological variation along the first two PC axes with fish reared in cages. No variation in the slope of the univariate linear models (PC1 or PC2 *vs* time) was observed between the wild and caged fish for the beach rock and sand beach habitats (Fig. 9 A & C, Supplementary Tables S7 & S8). The only significant difference was highlighted in the relation of PC2 *vs* time for fish living in mangrove (Fig. 9B; Estimate = 0.29, t.ratio = 3.526, p-value = 0.0006; Supplementary Table S8). Fish raised in cages in the mangrove habitat had more elongated body shape than wild fish. Despite this difference, the overall body changes of fish raised in cages and wild juveniles were similar.

4. Discussion

Within the framework of developmental plasticity (Lema, 2008; Denver, 2021; Smallegange, 2022), our main hypothesis was that the growth rate, ontogenetic shape changes, and generated phenotypic disparity in post-settlement reef fishes might vary among habitats in the coastal environment. We experimentally showed that the coastal habitats and associated biotic and abiotic factors play a role in modulating the growth of fish, with the highest growth rates in mangroves (Fig. 5). In addition, shape changes and ontogenetic trajectories varied across habitats both in magnitude and direction. The longest trajectories were detected in fish raised on beach rocks and dead zones, stating that *A. triostegus* settled in these habitats undergo a larger amount of shape changes after eight dpc in comparison with other habitats (Fig. 8). A peak in shape disparity level at three dpc was measured in *A. triostegus* juveniles settled in their natural habitats (*i.e.*, beach rock, sand beach, and mangrove) compared to the others. In the dead zone habitat, the disparity tended to increase over the eight days of experimentation while it was stable for fish raised in the oceanic environment. Taken together our results suggest that differences in habitats are translated into differences in ontogenetic trajectories culminating into producing different levels of phenotypic disparity in reef fishes.

4.1. Experimental set-up for future studies devoted to reef fish metamorphosis

We observed low mortality rates in our experiments across most studied habitats. Only the dead zone habitat was characterized by significant mortality. The identification of the main factors leading to this mortality are not obvious, but we hypothesize eutrophication processes highlighted by recurrent peak values of NO_2 and PO_4 as well as depletion of O_2 could be one of them (Fig. 3C; Supplementary Fig. S1). By comparing the caged fish to wild juvenile fish, we generally obtained similar growth and shape change rates, except for wild juvenile fish for the mangrove habitat (Table 2, Fig. 5B). We cannot reject the hypothesis that our experimental set-up did not capture the extent of environmental niches naturally provided by mangroves, and this may have led to the minor differences in shape variation. Except for the case of the mangrove

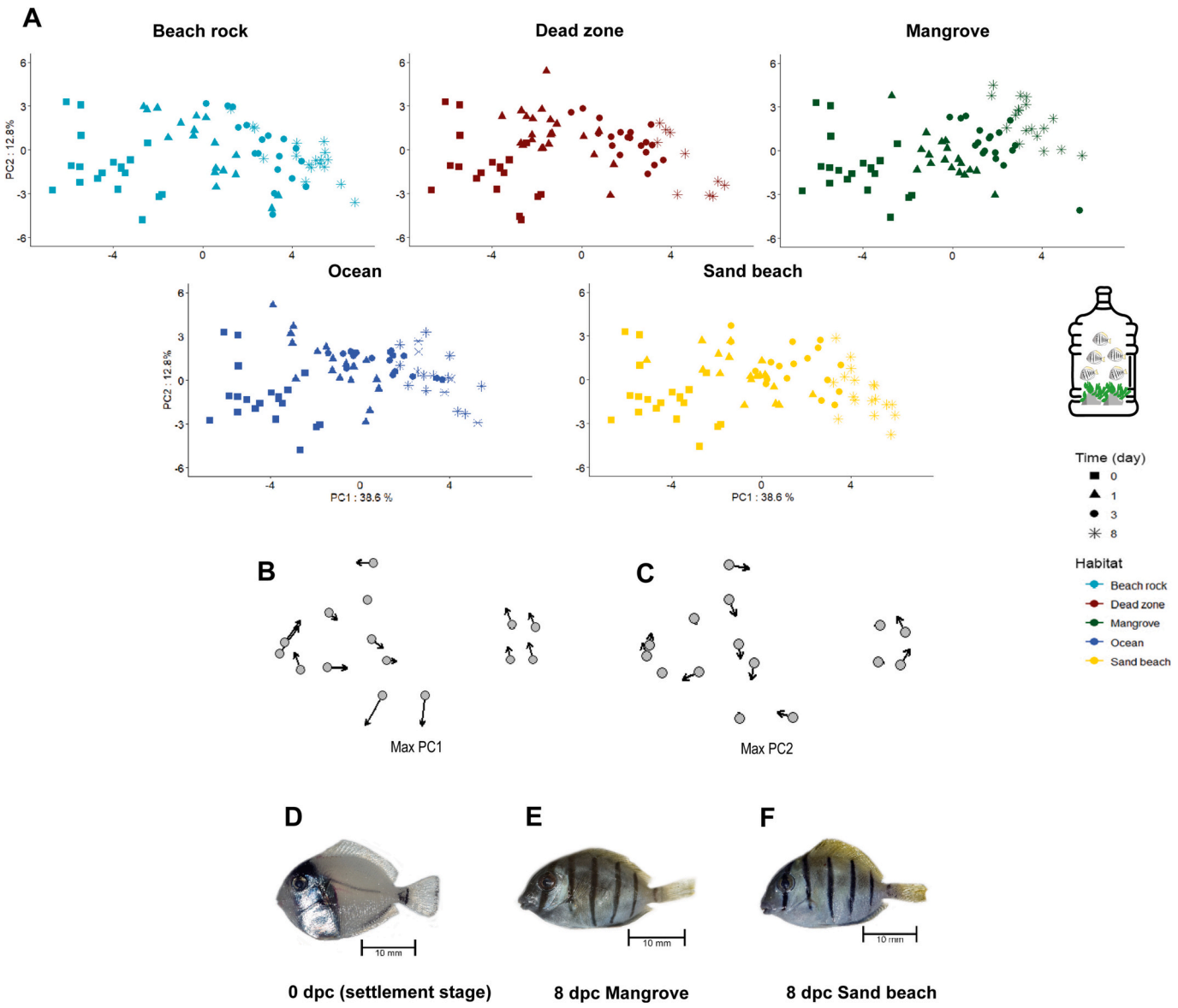

Fig. 6. Illustration of shape variation in *Acanthurus triostegus* during the first eight days of post settlement ontogeny.
(A) plots of the first two principal components (PC1 and PC2) defining the shape space; for a better visualization, fish specimens associated with a habitat are separated in different scatter plots; the percentage of shape variance summarized by each PC is provided in brackets. (B) vector displacements illustrate maximum shape changes associated with PC1. (C) vector displacements illustrate maximum shape changes associated with PC2. (D) picture of a settling larvae (zero dpc). (E) picture of an eight-days post-settlement stage fish from the mangrove habitat (*i.e.*, maximum value along PC2). (F) picture of an eight-days post-settlement stage fish from sand beach habitat (minimum value along PC2).

habitat, we did not observe any particular phenotype that could have been an effect of the captivity in cages itself when comparing them to those of wild individuals. Accordingly, we believe that our results can be interpreted without an obvious bias related to the experimental set-up itself and we are confident that all the observed morphometric differences can be interpreted in the light of differing habitats.

Several studies demonstrated the effects of the environment on intraspecific shape variation in vertebrate species including birds, amphibians, or fishes (Lema, 2008; Boyle et al., 2016; Denver, 2021). In fishes, most studies were devoted to freshwater fishes while similar studies on marine fishes are rare. This is probably due to the difficulty of rearing marine fishes for experimentation (O'Dea et al., 2019). The present work with its *in situ* set-up highlights the ability to study environmental factors acting on the development of coastal fishes, offering thus new perspectives in the study of metamorphosis and post-settlement ontogeny in reef fishes.

Through an experimental set-up with cages, our work strengthens previous studies revealing that variation in abiotic factors may modify ontogenetic shape variation in marine fishes (Day and McPhail, 1996; Marcil et al., 2006; Lema, 2008; Georga and Koumoundouros, 2010; Eagderi et al., 2019; O'Dea et al., 2019). It is also known that shape variations can also be induced by biotic factors, such as predation or competition (Svanbäck and Eklöv, 2002; Peres-Neto, 2004), which was not directly tested by our experimental design with cages. However, some differences observed between fish raised in cages and those captured in the wild, especially in mangrove habitats, may be attributed to the potential lack of exposure of caged fish to certain environmental factors.

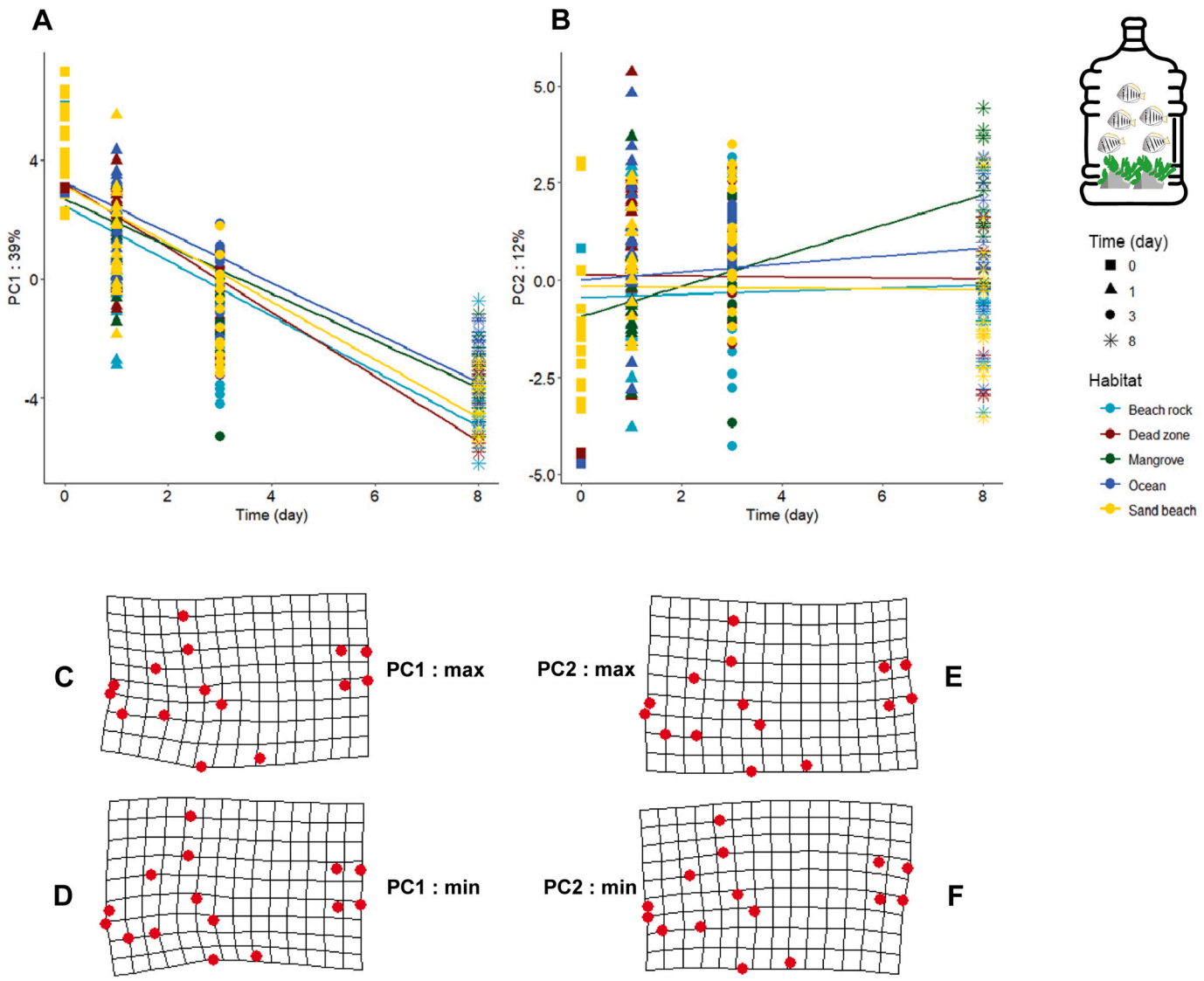

Fig. 7. Rate and nature of shape changes in *Acanthurus triostegus* reared in experimental cages.
The rate of shape changes is expressed as a variation of PC scores (PC1 (A) and PC2 (B)) across time (in days). Percentage of shape variation explained by each PC axis is provided on the y-axis of the plot (A-B). (C—F) TPS-deformation grids illustrate shape changes associated with each PC: (C) PC1 max, (D) PC1 min, (E) PC2 max, (F) PC2 min.

Table 3
Habitat effect on shape variation in *Acanthurus triostegus* during the eight-days post-settlement period, assessed by multivariate linear models.

Predictors	Df	SS	MS	Rsq	F	Z	P-value
Time	1	0.33648	0.33648	0.42803	282.3081	5.3898	0.001
Habitat	4	0.01187	0.00297	0.0151	2.49	3.4169	0.001
Time x Habitat	4	0.01107	0.00277	0.01409	2.3226	3.1628	0.001
Residuals	358	0.42669	0.00119	0.54279			
Total	367	0.78611					

Bold p-values are significant at the 0.05 level.

4.2. Ecomorphology of ontogenetic body shape changes in Acanthurus triostegus

During the first eight days post settlement, the main shape changes observed in *A. triostegus* concerned an overall body elongation as well as head shortening, with the mouth becoming more ventrally oriented. These results are similar to what has been reported in previous studies describing allometric variation in *A. triostegus* (McCormick, 1999; Frédérich et al., 2012). During their pelagic larval phase, *A. triostegus* feeds on plankton in the water column (Sampey et al., 2007). After their metamorphosis, the reef juveniles adopt an algivorous regime: filamentous benthic algae can represent >75% of the gut content of juveniles (Frédérich et al., 2012; Holzer et al., 2017). The ventral orientation of the mouth is implemented simultaneously to the diet change from a planktivorous (mobile resources) to an herbivorous regime (sessile resources) and is particularly suited for grazing activities. The orientation of the mouth could be crucial for *A. triostegus* to shift to herbivory and survive in their new habitat. In addition, the body of *A. triostegus* became

Table 4
Pairwise comparison of multivariate linear models (shape *vs.* time) among habitats.

Comparison	d	ULC	Z	P-value
BR vs DZ	0.00868589	0.01075354	0.56218172	0.291
BR vs MG	0.00745996	0.00549628	2.85427063	**0.003**
BR vs OC	0.00874809	0.00538289	3.63208531	**0.001**
BR vs SB	0.00466837	0.00550057	1.01540618	0.165
DZ vs MG	0.00752827	0.01079647	−0.07684126	0.53
DZ vs OC	0.00615843	0.01066485	−0.92354127	0.831
DZ vs SB	0.00835274	0.01058012	0.3964727	0.349
MG vs OC	0.00534031	0.00535522	1.60267234	0.053
MG vs SB	0.00852421	0.00540407	3.52189892	**0.001**
OC vs SB	0.00986481	0.00549873	4.35952035	**0.001**

Bold p-values are significant at the 0.05 level.

Table 5
Comparison of the ontogenetic trajectories of *Acanthurus triostegus* among habitats.

Comparison	Magnitude	Curvature	Direction
BR vs DZ	0.633	1	**0.024**
BR vs MG	0.157	0.957	**0.001**
BR vs OC	**0.013**	0.273	**0.001**
BR vs SB	0.227	0.988	0.211
DZ vs MG	0.089	0.957	**0.001**
DZ vs OC	**0.007**	0.478	**0.002**
DZ vs SB	0.116	0.998	**0.001**
MG vs OC	0.264	1	**0.17**
MG vs SB	0.871	1	**0.001**
OC vs SB	0.202	1	**0.001**

P-values are provided for comparison on each parameter of the ontogenetic trajectory, *i.e.*, the magnitude (distance), the curvature (form) and the direction (angle). Significant results are in bold.

more streamlined, which may improve their swimming and manoeuvring abilities in the structurally complex reef habitats (Lauder and Drucker, 2004; Fisher and Hogan, 2007). Swimming speed can be directly correlated to survival, and this change in body shape could provide a great advantage during the settlement period, when the settlers are extremely vulnerable to predation (Almany and Webster, 2006). The streamlined body shape is probably a response to predator avoidance (Scharnweber et al., 2013; Arnett and Kinnison, 2016) which is put in place in all studied habitats, and, in particular, in the mangrove after eight days when compared to the other locations.

4.3. Factors driving the variation of growth and the pattern of body shape changes

Our data showed that the habitat and associated ecological factors can induce different mechanisms of developmental plasticity in reef fishes such as ontogenetic repatterning (*i.e.*, variation of the direction of the trajectory in the shape space) and change of the rate of shape variation. Beyond these results, we question the possible underlying mechanistic underpinnings these modifications. Among the mechanisms that may play a role in developmental plasticity, hormone-mediated plasticity cannot be ignored. The neuroendocrine system is an important modulator of phenotypes, directing cellular genetic mechanisms to respond to external cues such as temperature, dissolved oxygen level, salinity, pH, or pollutants (Besson et al., 2020; Lema, 2020; Salis et al., 2021). Growth hormones, the stress hormone cortisol, or thyroid hormones are known to have the potential to modulate shape changes, especially during ontogeny (Arjona et al., 2008; Lema, 2008; Lõhmus et al., 2010; Moreau et al., 2014; Keer et al., 2022). A striking clue is provided when placing post-settlement individuals back in the oceanic environment. The amount of shape transformation – the length of the ontogenetic trajectory in the shape space – was the lowest in fish raised in the ocean in comparison with the ones raised in lagoonal habitats. This is new evidence that placing *A. triostegus* back in the open ocean interrupts its metamorphosis. Other studies highlighted delays in changes of thyroid status, intestinal lengthening, and feeding behaviour (McCormick, 1999; Holzer et al., 2017). The thyroid hormone system is well known to be sensitive to environmental variations (temperature, dissolved oxygen level, salinity, pH, or pollutants; Lema, 2020), highlighted in the studied habitats, and may play a major role in the developmental plasticity observed in this study.

In the natural environment, many biotic or abiotic factors, such as predation, competition, food availability, diet composition, temperature, salinity, water quality, or dissolved oxygen level, induce variation in growth rate in fish (Tupper and Boutilier, 1995; Bœuf and Payan, 2001; Lorenzen and Enberg, 2002; Eby et al., 2005; Sponaugle et al., 2006; McLeod et al., 2015; Bertucci et al., 2019). In our experimental study, biotic factors (*e.g.,* the presence of predators or competitors for food) were mostly avoided by cage culture, and therefore we consider only abiotic factors that may have influenced growth rate. Interestingly, only fish raised in mangroves showed a significant linear relationship between size and age and their growth rate was the highest. The mean temperature was higher in mangroves than in beach rock, dead zones, and oceans, and probably played a role in the differences in growth rates. Temperature influences growth-related traits, including daily growth, size-at-age, and length of development, in demersal fishes (Grorud-Colvert and Sponaugle, 2006; Rankin and Sponaugle, 2011; McLeod et al., 2015). It is well known that warmer temperatures without thermal stress increase the growth rate in many fish species, including Northeast Arctic cod (*Gadus morhua*), Indo-Pacific sergeant (*Abudefduf vaigiensis*), white-ear scalyfin (*Parma microlepis*), or bluehead wrasse (*Thalassoma bifasciatum*) (McCormick and Molony, 1992; Figueira et al., 2009; Denechaud et al., 2020). The higher mean temperatures observed in the mangrove are possibly the main reason for the higher growth rates recorded. Diet composition could be seen as an additional factor explaining differences in growth rates. During our experiments, fish were fed by providing coral rubbles with algal turf coming directly from the tested habitat. However, there is great heterogeneity in the composition of turf algae from one habitat to another (Harris et al., 2015), and changes in diet composition with different nutritive characteristics may affect growth (Bertucci et al., 2019). Finally, the rate of growth and development is often related to the availability of energy. Thus, changes in TH-mediated metabolic regulation can influence phenotypic expression both directly, by changing gene expression in pathways associated with growth and development (Very and Sheridan, 2002), and indirectly, by affecting energy availability through its effects on metabolism (Lema, 2014).

The potential drivers of the difference in development highlighted in this study remain up to now a matter of speculation. These drivers can be internal, such as the physiological or endocrinological status of the fish in the various habitats. For example, thyroid hormones whose secretion are known to be under environmental control (Laudet, 2011) are important regulators of skeletogenesis and bone remodelling in fish (Galindo et al., 2019; Keer et al., 2019, 2022) and could therefore play an important role here as previously discussed (Besson et al., 2020). Another, non-mutually exclusive driver could be differential selection by predation or other factors in different habitats. Greater body elongation is often associated with better predator escape, and this could indicate that in the context of Moorea there is high level of predations in mangroves. Work is under way in our laboratories to better understand the nature of the drivers that are at play.

4.4. First days post-settlement: a crucial period generating phenotypic diversity

Phenotypic variability and plasticity are the core factors for natural selection to occur: the phenotypes of individuals determine their performance in different environmental contexts. Since environmental

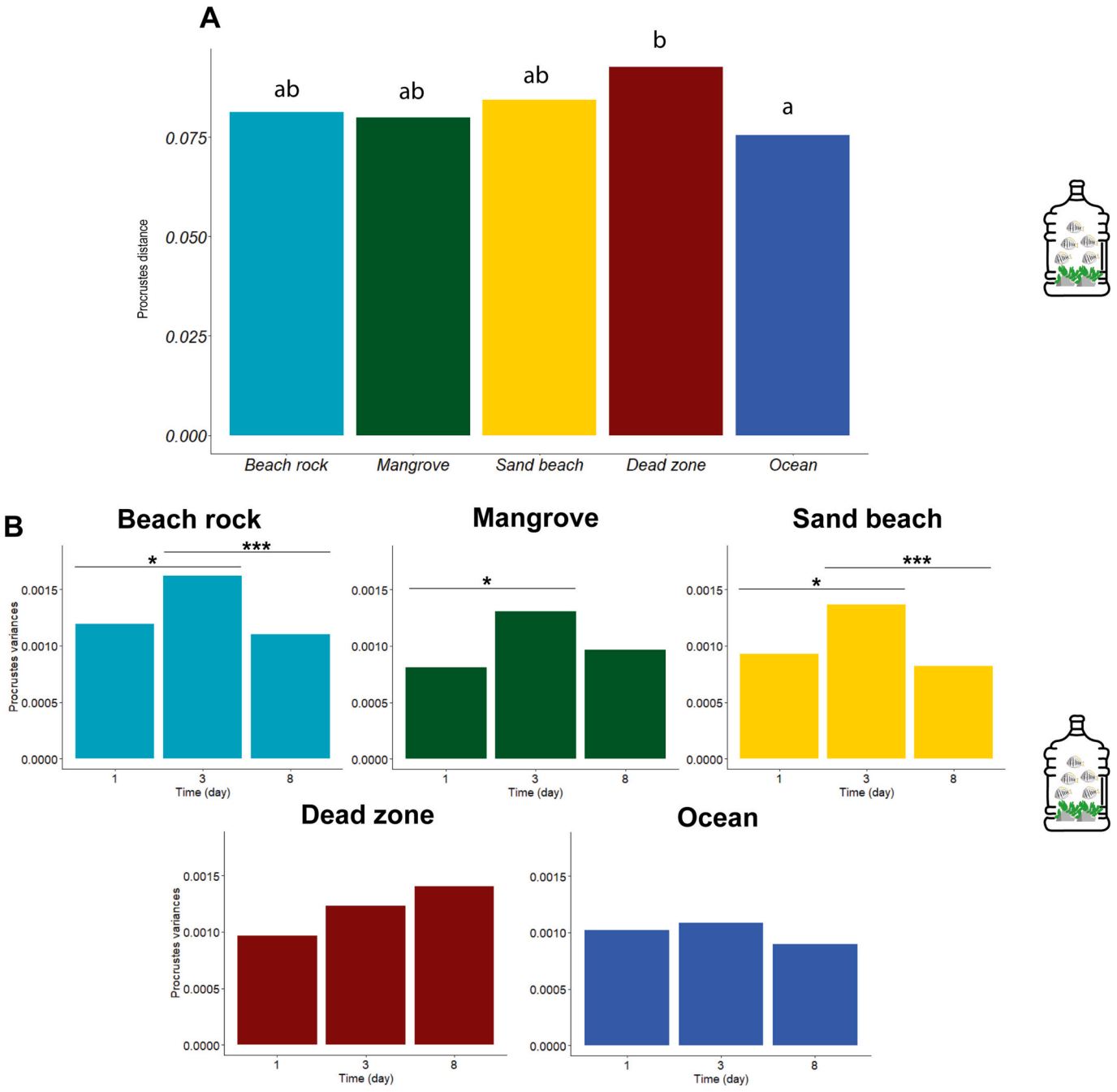

Fig. 8. Length of ontogenetic trajectories and variation of the levels of shape disparity in *Acanthurus triostegus* during post-settlement ontogeny.
(A) Length of the ontogenetic trajectories translating the amount of shape variation observed after eight-days of post-settlement, expressed as Procrustes distance. Letters show significant differences among habitats. (B) for each habitat, levels of shape disparity, expressed as Procrustes variance, at one, three and eight days of post-settlement. Significant differences are highlighted with asterisks (*: *p*-value <0.05; **: p-value <0.01).

conditions are largely heterogeneously distributed, phenotypes are generally found to be spatially and/or temporally structured across habitats (Jacob and Legrand, 2021). When environmental conditions fluctuate over time, populations with a diverse set of phenotypes have a higher probability of persisting and maintaining themselves (Bolnick et al., 2011). In this study, in association with variation in ontogenetic trajectories, the emergence of shape disparity within a given habitat also varies across habitats and time. Interestingly, peaks in the level of shape disparity were observed after three days on the natural habitats (*e.g.*, beach rock, mangrove, and sand beach). This peak of disparity at three days could reflect heterogeneous physiological status within the population, with individuals early or delayed in terms of their morphological changes. These first three days of settlement seem to promote the most significant morphological changes, which are then more discrete between three and eight days – a period during which the advance or the delay of certain individuals could be compensated to obtain more homogeneous morphologies.

5. Conclusion

Our study unveiled developmental plasticity in *A. triostegus* during post-settlement ontogeny, as observed in individuals reared in different habitats. We demonstrate that the habitat and associated ecological factors play a crucial function in producing phenotypic disparity at the

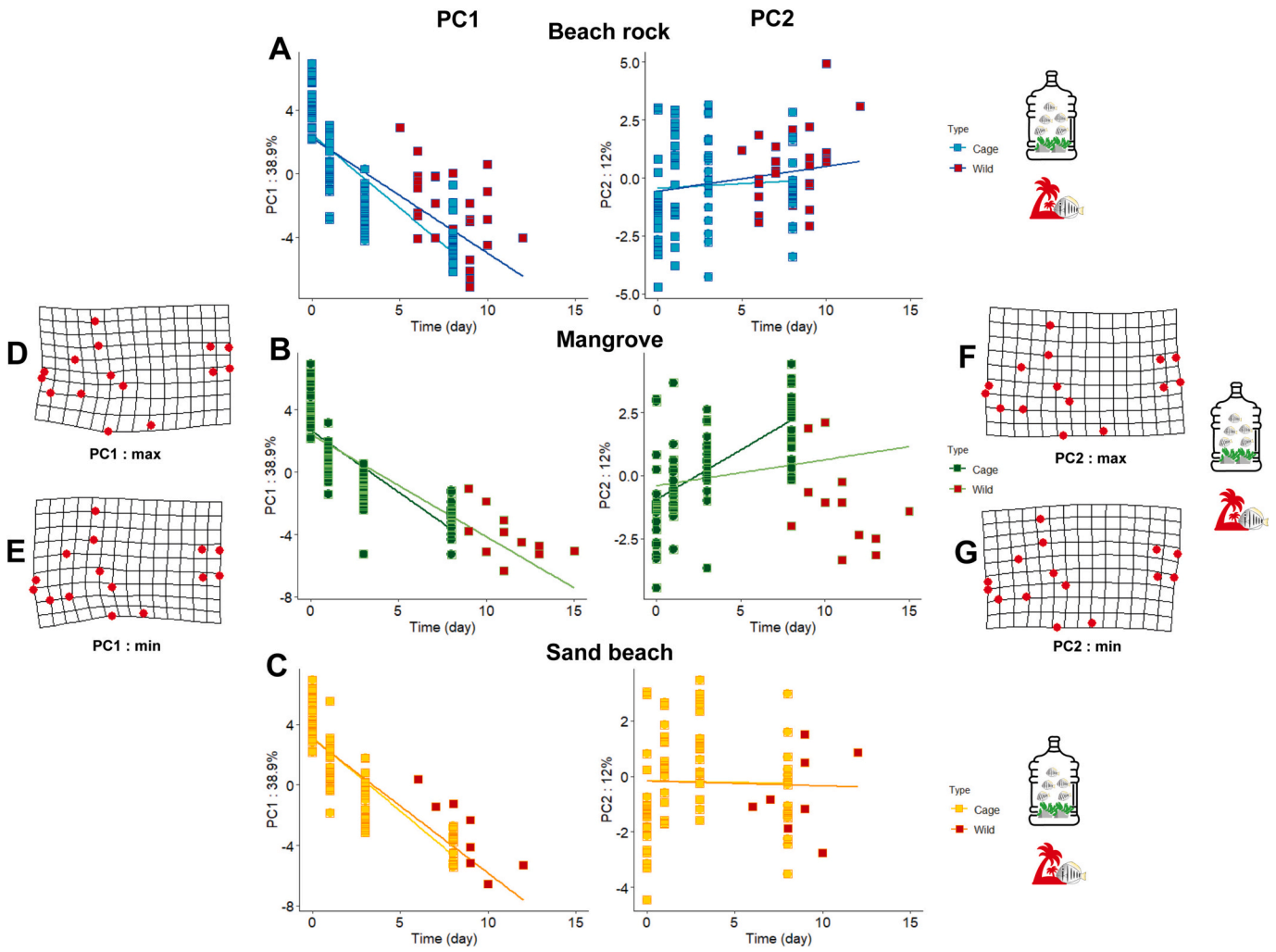

Fig. 9. Comparison of the rate and the nature of shape changes in *Acanthurus triostegus* between wild fish and fish raised in cages.
The rate of shape changes is expressed as a variation of PC scores (PC1 and PC2) across time (in days). Percentage of shape variation explained by each PC axis is provided on the y-axis of the plot (A-C). (D-G) TPS-deformation grids illustrate shape changes associated with each PC: (D) PC1 max, (E) PC1 min, (F) PC2 max, (G) PC2 min.

population level in a reef fish species during its metamorphosis, which may be linked to possible habitat-specific adaptations.

Adult populations are dependent upon the recruitment of juveniles following their successful metamorphosis and settlement. Improving our understanding of the endocrine, molecular, and ecological mechanisms during this critical transition period is a major challenge to better understand how teleost fish populations are maintained sustainably. Our results are new arguments for the conservation of the diversity of natural habitat in coastal environments. Indeed, there is a positive link between the diversity of habitats and the diversity of generated phenotypes during post-settlement ontogeny which may ultimately promote species adaptation.

Author contributions

M.R., V.L., D.L. and B.F. designed the study. D.L. and V.L. managed and funded the work. M.R. performed all the field experiments with the help of E.G. and D.L. M.R. and B.F. performed the morphometric analyses. M.R., D.L., V.L. and B.F. wrote the manuscript. All the authors have read and approved the manuscript.

Ethical statement

Animal experimentation: This study was performed in strict accordance with the guidelines of the French Polynesia committee for publication and animal ethics. All the animals were handled in accordance with the guidelines CRIOBE-IRCP animal ethics committee, and every effort was made to minimize suffering.

Declaration of Competing Interest

The authors have no conflict of interest to report.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2023.151937.

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