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Evolutionary diversification of pelagic larval duration in three reef fish families

Emmanuelle Huet [1,*], Amandine Gillet [2,3], Claire Philippart [1], David Lecchini [4,5] & Bruno Frédérich [1,*]

[1] Laboratory of Evolutionary Ecology, FOCUS, University of Liège, Liège, Belgium.

[2] Bristol Palaeobiology Research Group, School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK.

[3] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.

[4] PSL Research University: EPHE-UPVD-CNRS, UAR 3278 CRIOBE BP 1013, 98729 Papetoai, Moorea, French Polynesia.

[5] Laboratoire d'Excellence "CORAIL", 66100 Perpignan, France.

[*] Corresponding authors: emmanuelle.huet@uliege.be, bruno.frederich@uliege.be

Abstract. In many animal taxa, studies of trait diversification have mainly focused on adult phenotypes, while early life traits have been poorly studied from a macroevolutionary perspective. Reef fishes provide a good system for studying the evolution of animals with complex life cycles. Their biphasic life cycle – a pelagic larval stage and reef-associated juvenile/adult stages – and the fact that they are among the most diversified groups of vertebrates make them ideal candidates. This study aims to describe the patterns of diversification of an important larval trait, the pelagic larval duration (PLD), responsible for the dispersal ability of reef fishes in the ocean. Leveraging data available in the literature, we explored the diversification of PLD in three diverse families (Labridae, Pomacanthidae, and Pomacentridae). Our results show significant variation in PLD across the three fish families and across biogeographic regions, and reveal a strong phylogenetic signal in PLD. Our macroevolutionary analyses support that the tempo of PLD evolution is tightly associated with speciation events in Labridae and Pomacanthidae, sustaining the role of the pelagic larval phase in reef fish diversification. The hypothesis of a single optimal PLD value for all fishes – representing a trade-off between genetic mixing, colonisation of isolated reefs and mortality during the pelagic phase – was rejected by our comparisons of trait evolution models. Instead, we highlight multiple evolutionary shifts towards both short and long PLD durations. Finally, we reveal that PLD is linked to some adult ecological traits in Pomacanthidae but the same relationship is absent for Pomacentridae and Labridae. Our results strengthen the idea that PLD diversity is structured by phylogenetic relationships, and that the evolutionary dynamics of PLD are lineage-specific.

Keywords. Macroevolution, complex life-cycle, larval trait, trait evolution, coral reef fishes.

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Introduction

Most organisms possess complex life cycles comprising two or more stages that are temporally and spatially distinct (Wilbur 1980). In marine systems, most bottom-associated animals, including fishes, spend part of their early development as larvae in open pelagic waters before transitioning to a demersal lifestyle (Leis 1991; Marcus & Boero 1998). Consequently, most coastal teleosts exhibit a biphasic life cycle, consisting of (1) a pelagic larval phase and (2) a sedentary juvenile and adult phase associated with coastal habitats (Leis & McCormick 2002). The ontogenetic shift from larva to juvenile involves a thyroid hormone-regulated metamorphosis that typically coincides with settlement from the pelagic zone into demersal coastal environments (Holzer *et al.* 2017; Roux *et al.* 2023). Both juvenile and adult stages depend strongly on reef substrates (Leis & McCormick 2002) and generally display limited home ranges (Nash *et al.* 2015).

Several ecological benefits of a pelagic lifestyle for larvae have been proposed. The pelagic larval phase enhances dispersal and connectivity among spatially fragmented reef habitats, reducing the risk of local population loss. It also allows larvae to exploit plankton-rich offshore environments, promoting rapid early growth while avoiding competition with demersal adults (Doherty *et al.* 1985; Leis 1991; Leis & McCormick 2002). Since the 1980s, the duration of this pelagic larval phase has been extensively studied in reef-associated fishes, i.e., fishes living in broadly defined reef habitats from coastal areas including corals, rocks, seagrass beds, mangroves or even soft-bottom zones adjacent to reef (Robertson 1998; Siqueira *et al.* 2023). The discovery of daily incremental growth marks and settlement marks on the otoliths of numerous reef fish species (Victor 1982; Brothers *et al.* 1983; Wilson & McCormick 1997) has provided a robust method for ageing individuals on a daily scale. This methodological advancement enables precise estimation of the duration that larvae spend in the pelagic environment prior to their settlement on the reef.

The analysis of daily otolith increments has subsequently been widely used to document pelagic larval duration in many reef fishes, revealing substantial variation in larval duration among species (e.g., Brothers *et al.* 1983; Victor 1986; Wellington & Victor 1989; Victor & Wellington 2000). Indeed, the pelagic larval duration (PLD) – defined as the interval between hatching and settlement – varies generally across reef fish species from a few days to a few months (Thresher *et al.* 1989; Leis & McCormick 2002). For example, the saddleback clownfish *Amphiprion polymnus* has a very short PLD of 9 to 12 days (Jones *et al.* 2005) whereas the larvae of the convict surgeonfish *Acanthurus triostegus* spend between 42 and 53 days in the pelagic environment (McCormick 1999; Juncker *et al.* 2006). In some reef fish clades, a few lineages even acquired an apelagic state, i.e., species that lack a pelagic larval stage (Doherty *et al.* 1985; Leis 1991). The number of apelagic species is, however, very limited, with the damselfish *Acanthochromis polyacanthus*, the banggai cardinalfish *Pterapogon kauderni* and the surfperch *Embiotoca jacksoni* being common examples.

Factors underlying the diversity of PLD are diverse. Temperature exerts a major influence on developmental rates from the embryonic stage onward, with elevated temperatures generally accelerating developmental processes (Johnston 2006; Green & Fisher 2004; Raventos *et al.* 2021). As a result, the PLD of a given species is typically shorter in equatorial regions, where seawater temperatures are higher, than at higher latitudes characterized by cooler waters (Bay *et al.* 2006; Sponaugle *et al.* 2006; McLeod *et al.* 2015). Temperature thus represents a key abiotic driver of intra-specific PLD variation. However, its explanatory power for inter-specific variation appears less straightforward. For instance, in the Mediterranean Sea, the sparid *Diplodus vulgaris*, which settles in winter, exhibits a slightly longer PLD than congeners settling in warmer months (e.g., *Diplodus sargus*), supporting the temperature dependence of PLD (Vigliola *et al.* 2000). Conversely, the PLDs of the Mediterranean damselfish *Chromis chromis* (17–19 days) are similar to those reported for *Chromis alta*, *C. insolata* and *C. retrofasciata* (18–19 days) inhabiting the tropical waters of the Caribbean Sea and the central

Pacific, whereas other tropical and subtropical species, such as *Chromis lineata* and *C. punctipinnis*, display substantially longer PLDs (35–37 days; Wellington & Victor 1989; Victor & Wellington 2000; Raventos & Macpherson 2001). Similarly, cardinalfish species (Apogonidae) from varied regions in terms of latitudes and climatic conditions, such as the Great Barrier Reef (Brothers *et al.* 1983), the Mediterranean Sea (Raventos & Macpherson 2001) and the Lagoon of Okinawa Island (Ishihara & Tachihara 2011) display comparable PLDs, also rejecting a direct link between PLD and temperature at the inter-specific level. Oceanographic features, including hydrodynamic structure or inshore/offshore flow regimes, represent other abiotic factors modulating PLD in reef fishes. These oceanographic variables act through physical mechanisms such as larval retention and transport barriers, ultimately determining how long larvae remain in the pelagic environment. The influence of oceanographic features on connectivity among reef fish populations has been highlighted in various regions (Sponaugle *et al.* 2002; Galarza *et al.* 2009) and they certainly affect variation of PLD within and among species at both ecological and evolutionary scales. Other abiotic factors, such as along-shore winds and solar radiation, have also been documented to induce intra-specific variation of PLD in reef fishes (Bergenius *et al.* 2005).

In addition to these extrinsic factors, numerous studies have demonstrated that intrinsic factors also influence the PLD of fish species. Initially considered as passive drifters, it was demonstrated that fish larvae, even at early stage, show good locomotor abilities (e.g., Leis 1991, 2006; Stobutzki & Bellwood 1997; Leis & Carson-Ewart 1997, 1998). Based on developmental data, it has been estimated that reef fish are capable of actively shaping their dispersal trajectories during more than 50% of their larval phase (Fisher *et al.* 2000; Fisher 2005). More importantly, they can orient themselves in the pelagic environment (e.g., Stobutzki & Bellwood 1998; Leis & Carson-Ewart 1999), swimming directionally (Leis & Carson-Ewart 2003), and actively select their vertical position within the water column (e.g., Irisson *et al.* 2010; Huebert *et al.* 2011), with vertical distribution also varying throughout ontogeny (Hernández *et al.* 2023). These findings strongly suggest that most species can influence their spatial and temporal settlement patterns, and consequently the duration of the pelagic phase through taxon-specific phenotypic traits that vary both among and within fish families (e.g., Stobutzki & Bellwood 1997; Leis & Carson-Ewart 1997; Fisher *et al.* 2005; Irisson *et al.* 2010; Hernández *et al.* 2023). From an ecomorphological perspective, such variation in larval behaviour and functional performance is likely supported by morphological diversity among reef fish larvae (Leis 1991, 2002; Lecchini *et al.* 2014), itself shaped by differences in developmental trajectories, environmental conditions, and underlying genotypes. Recently, Schalm *et al*. (2025) have provided evidence for an association between interspecific genetic variation and PLD differences within a reef fish clade, the damselfishes. Their findings showed that glutamine-rich regions of the *clock* gene are significantly correlated with PLD, supporting the hypothesis that some genetic markers are associated with PLD and settlement timing at a broad phylogenetic scale. Consequently, the well-documented diversity of PLD within and among reef fish clades (e.g., Brothers *et al.* 1983; Victor 1986; Wellington & Victor 1989; Victor & Wellington 2000; Soeparno *et al* 2012) appears to be shaped by a combination of factors, including ecological, environmental, and phylogenetic components. However, the variability of PLD has rarely been investigated in a broad comparative and evolutionary context, limiting our understanding of how PLD diversified across lineages.

Well-resolved phylogenies are now available for many reef fish clades; however, no study to date has examined the association between evolutionary history and PLD, nor the patterns of PLD diversification by using modern phylogenetic comparative methods. As observed in other taxa with complex life cycles (e.g., Bossuyt & Milinkovitch 2000; Rühr *et al.* 2021), a relevant question is whether traits expressed during early life stages, including PLD, are correlated with adult traits in reef fishes. For instance, comparative analyses have shown that larvae of demersal spawners typically settle after a short PLD, whereas the larval duration of species hatching from pelagic eggs can be much longer (Leis 1991; Sponaugle & Cowen 1994; Soeparno *et al.* 2012). However, this pattern has not been formally tested

using statistical analyses that account for phylogenetic information. Conversely, differences in selective pressures across life stages (Wilbur 1980; Gagliano *et al.* 2007) together with evidence of variation in patterns of phenotypic diversification between stages (Sherratt *et al.* 2017) could support the hypothesis of ontogenetic decoupling of traits, especially between pelagic-adapted larvae and adult specialized for a demersal lifestyle in reef habitats (Moser 1981; Dornburg *et al.* 2024). These contrasting perspectives therefore raise the question of whether larval and adult life-history traits in reef fishes coevolve or instead evolve largely independently (Peniston & Burgess 2024).

Here, our general objective is to study the diversity of PLD in reef fishes through a comprehensive macroevolutionary analysis. Using data compiled from the literature, we examine the evolutionary diversification of PLD in three diverse reef fish families: the wrasses (Labridae), the angelfishes (Pomacanthidae), and the damselfishes (Pomacentridae). Specifically, we address three main questions. (1) How does PLD vary across families and geographical regions? (2) Is there phylogenetic conservatism in PLD and what are its evolutionary patterns? (3) Is PLD associated with some adult traits like body size and trophic ecology?

Material and methods

Studied reef fish families

Three families of reef fishes were targeted in this study: Labridae, Pomacanthidae and Pomacentridae. The wrasses (Labridae) include 689 species grouped in 83 genera, comprising parrotfishes and the eight odacids (Baliga & Law 2016; Burress & Wainwright 2019; Fricke *et al*. 2025). Most wrasses spawn pelagic eggs while some North Atlantic and Mediterranean species deposit benthic ones (e.g., species of *Symphodus* and *Labrus*; Lejeune 1985; Finn *et al.* 2002). They inhabit nearly all warm temperate and tropical oceans, with the highest abundance in the Western Pacific and Indian Ocean (Westneat & Alfaro 2005). Wrasses are morphologically and ecologically diverse (Wainwright *et al.* 2004), ranging in size from 5 cm (*Wetmorella tanakai*) to 230 cm (*Cheilinus undulatus*) (Burress & Wainwright 2019). Beyond their cleaning behaviour (Baliga & Law 2016), their trophic ecology can be classified into four main categories: benthic feeders, generalist carnivores, pelagic feeders, and tiny biters (Gajdzik *et al.* 2019). Angelfishes (Pomacanthidae) occur on tropical and subtropical reefs and include 90 species in seven genera (Baraf *et al.* 2019). Their size ranges from 7 to 60 cm, a major axis of morphological diversification leading to the recognition of pygmy forms (Frédérich *et al.* 2017). Pomacanthids are pelagic spawners (Moyer *et al.* 1983) and fall into three feeding guilds: planktivorous, herbivores, and omnivores (Konow & Bellwood 2011). Damselfishes (Pomacentridae) comprise 436 species across 29 genera, and are widely distributed in temperate and tropical reefs, with sizes from 5 to 35 cm (Frédérich & Parmentier 2016; Tang *et al.* 2021; Fricke *et al*. 2025). Three feeding guilds are recognized: pelagic feeders, benthic feeders, and a mixed group feeding on both zooplankton and benthic prey (Frédérich *et al.* 2009, 2016). They deposit benthic eggs in nests on the substrate, where they hatch before the larvae enter the pelagic environment. A monophyletic group (*Acanthochromis polyacanthus* and *Altrichthys* spp.) evolved brood care and hence lost the pelagic larval phase (Bernardi 2011). The ecological diversity of the three families, combined with the availability of large datasets about PLD in the literature and the availability of comprehensive and strongly supported phylogenies, make them ideal candidates for the present study.

Data collection and time-calibrated phylogenies

PLD data collection

An extensive literature review of scientific articles published since 1982 allowed assembling a database about PLD for 315 species: 145 wrasses, 37 angelfishes and 133 damselfishes (details and references in Suppl. file 1: Table S1), respectively. This taxon sampling represents ~30% of the extant diversity

TABLE 1

Number of species and genera for each of the three fish families, along with the number of species for which PLD data were available in the literature.

	Nb Sp Study	Nb Gn Study	Nb Sp Tot	Nb Gn Tot	% Sp	% Gn	Nb Sp after pruning
Labridae	147	42	689	83	21%	50.60%	127
Pomacanthidae	37	7	90	7	41%	100%	35
Pomacentridae	133	24	436	29	30%	82.70%	110

Chronograms were pruned to match available PLD data using the treedata function from the GEIGER R-package (ver. 2.0.11; Pennel *et al*. 2014). This pruning step also excluded species without PLD data. The final column shows the number of species retained for analysis after pruning. Nb Sp = number of species; Nb Gn = number of genera; Tot = total found in the literature; % Sp = percentage of species diversity included in this study; % Gn = percentage of genera included.

of each fish family and includes ~78% of genera (Table 1). Previous studies revealed intra-specific variation of PLD (Wellington & Robertson 2001; Bay *et al.* 2006), and several species in our database have different PLD values according to the study location. When several values of PLD were found for one species, we calculated and used mean values for all comparative analyses.

Biogeographic data

The geographical distribution of fish species was extracted from FishBase (Froese & Pauly 2025) and then they were assigned to the regions defined by Kulbicki *et al.* (2013). Here, we used five regions which mainly align with major ocean basins: the Atlantic Ocean (including the Mediterranean Sea - A), the Western Indian Ocean (including the Red Sea - WI), the Central Indo-Pacific (extending from the edge of India to the northern edge of New-Zealand - CIP), the Central Pacific (CP) and the Tropical Eastern Pacific (TEP).

Ecological data

In addition to PLD, we collected two major biological traits from the adult stage: maximum body size and trophic ecology (Suppl. file 1: Table S1). Maximum body size was retrieved from FishBase (Froese & Pauly 2025). Feeding guilds were defined following the classification used by Gajdzik *et al.* (2019) for Labridae and Pomacentridae, and from Konow & Bellwood (2011) for Pomacanthidae.

Time-calibrated phylogenies

We explored the diversification of PLD in Labridae, Pomacanthidae and Pomacentridae using published, strongly supported multi-gene, time-calibrated phylogenies. Details regarding the computation of phylogenetic analyses and time calibration are provided in these works: Baliga & Law (2016) for Labridae, Baraf *et al.* (2019) for Pomacanthidae and McCord *et al.* (2021) for Pomacentridae.

Comparative analyses and statistics

All statistical analyses were performed with R software (version 4.3.0, R Core Team) and processed in the RStudio interface.

PLD variation among families and biogeographic areas

The statistical assumptions of normality and homoscedasticity of the PLD values were not respected (Shapiro test & Levene test, $P<0.05$) across families and regions. We thus performed a distance-based Procrustes ANOVA using the *procD.lm* function from the R-package GEOMORPH (ver. 4.0.6; Adams

et al. 2013) to test for differences in PLD among families and regions. This function allows the use of non-parametric univariate dependent variable and directly performs an ANOVA on the regression parameters. Whenever significant differences were detected, the *pairwise* function from the same R-package was used to perform pairwise comparisons. Results from Levene tests, used to assess homoscedasticity of PLD data, were also used to examine differences in the variance of PLD among families and regions.

Pattern of PLD diversification across phylogenies

We applied a suite of phylogenetic comparative methods to investigate the evolutionary patterns of PLD diversification. Since the models we used are designed for continuous traits, PLD was log-transformed for subsequent analyses. However, three damselfish species (*Acanthochromis polyacanthus*, *Altrichthys azurelineatus* and *Altrichthys curatus*) lack a pelagic larval stage, i.e., their PLD equals zero. Thus, their PLD values were converted to 0.9 (instead of 0) before log-transformation.

We first assessed whether PLD is conserved across phylogenies by testing for phylogenetic signal, which is defined as the statistical dependence among species trait values due to their phylogenetic relatedness (Revell *et al.* 2008). We used Pagel's lambda (λ) method for estimating the phylogenetic signal (Pagel 1999). It is commonly expected that closely related species should have phenotypic similarities. Pagel's lambda measures how the trait depends on the phylogeny with $\lambda = 0$ meaning there is no relation with phylogeny whereas $\lambda = 1$ suggests that trait evolution highly depends on phylogeny. The calculation of the phylogenetic signal λ was performed using the *phylosig* function from PHYTOOLS (ver. 2.4-4; Revell 2024). We then mapped the evolution of PLD on phylogenies by using the *contMap* function from the PHYTOOLS R-package. This function, using a maximum likelihood approach, allows to visualize and reconstruct the evolution of trait values along a time-calibrated phylogeny, under a Brownian motion model. This is particularly useful to estimate ancestral states at the root and each node, and to visualize PLD similarities across related lineages. However, given that Pagel's λ is based on a Brownian Motion model, which was not the best fitting model for PLD evolution (see Results section), we also compared this test of phylogenetic signal with another non-model-dependent statistic. The M statistic, recently developed by Yao & Yuan (2025), offers a method to quantify phylogenetic signals of both continuous and discrete traits by directly computing the phylogenetic signal based on the concept that related species resemble each other more than random species (Blomberg & Garland 2002), rather than relying on specific evolutionary models. The M statistic tests whether trait distances reflect phylogenetic distances by comparing the observed pattern to a null distribution generated through permutations. A higher M statistic indicates a stronger correspondence between phylogenetic distances and trait distances, but its absolute value is not interpreted. M statistics and associated permutations were produced with the R-package phylosignalDB (ver. 0.2.2).

To determine the tempo and mode of PLD diversification, we compared the fit of five candidate models of trait evolution. (1) We fitted the gradual time-dependent model called Brownian motion (BM). (2) As PLD might be stabilized around a PLD-optimum balancing constrains and benefits from genetic mixing, colonisation of isolated reefs and mortality during the pelagic phase, we fitted an Ornstein-Uhlenbeck (OU) model with a single optimal PLD for all species. The OU model is a BM model supplemented with a stabilizing force α that attract all lineages towards an optimal theoretical value. The strength of the stabilisation force determines how fast lineages are attracted towards the optimum (Hansen 1997). (3 & 4) ACDC models correspond to an evolutionary scenario in which the tempo of trait evolution can accelerate (AC) or decelerate (DC) exponentially over time (Blomberg *et al.* 2003; Harmon *et al.* 2010). These two models differed in their parameters: we set an upper bound for the estimation of the exponential rate to zero for the DC model while the upper bound was not constrained in the AC model, allowing a positive exponential rate (Puttick *et al.* 2020). (5) Finally, as PLD might be directly related to processes of speciation, we fitted the ψ model which examines the proportion of the evolutionary

rate (σ) attributable to a speciation rate parameter ψ (Ingram 2011). All these models were fitted using the function *transformPhylo.ML* from MOTMOT (ver. 2.1.3; Puttick *et al.* 2022). We used scores and weights of Akaike's information criterion corrected (AICc) to compare the fit of the models. An absolute difference in AICc values (ΔAICc) of four or more was interpreted as an indication of support for one model over the others following Burnham & Anderson (2004).

We further investigated the pattern of PLD diversification by testing whether lineages have evolved toward different PLD optima. We ran an exploratory analysis of PLD evolution within each family by using the function *estimate.shift.configuration* from L1OU (ver. 1.4.3; Khabbazian *et al.* 2016). Detecting shifts using the lasso method provides a rapid and suitable solution to estimate the number of potential shifts in our three families. This method may be less precise in localizing shifts than the Bayesian method implemented by Uyeda & Harmon (2014), but it is less dependent on priors and has much faster computation times. As our aim was to explore the existence of shifts in PLD evolution rather than to precisely determine their location, we chose the lasso method implemented by Khabbazian *et al*. (2016) in the R-package L1OU. Following their recommendations, we used both "pBIC" and "BIC" criteria and compared our results. The shifts detected were then represented on the phylogeny using the *plot* function of the L1OU R-package.

Relationship between PLD and traits of adults

To test whether PLD is linked to some biological characteristics of the species at the adult stage, we performed Phylogenetic Generalized Least Squares (PGLS) analyses. We used the *gls* function from NLME R-package (ver. 3.1-162; Pinheiro *et al.* 1999) to test the effect of diet and maximum body size on PLD in separate analyses. For each explanatory variable and each fish family, we compared three models: (1) a linear model with no phylogenetic correction, (2) a linear model with a Brownian correlation that corrects the regression with the phylogenetic covariance expected under a Brownian motion model, and (3) a linear model with the Martins correlation that corrects the regression with the phylogenetic covariance expected under a Ornstein-Uhlenbeck model. The two correlation structures were produced with the NLME R-package (*corBrownian* and *corMartins* function). Based on AIC and BIC values of each model, we then selected the best model for each family to assess the relationship of diet and maximum body size with PLD.

Results

PLD variation among families and biogeographic entities

Inter-familial variation

Levene's test and the Procrustes ANOVA revealed that both the variance and the mean PLD differed significantly among the three fish families (Levene: $F=27$, p-value$=1.5\times10^{-11}$; Procrustes ANOVA: $F=45.15$, Z-score$=6.73$, p-value$=0.001$). Pairwise comparisons showed that PLD values in wrasses (Labridae) significantly differ from those of angelfishes (Pomacanthidae) (Z-score$=2.91$; p-value$=0.002$) and damselfishes (Pomacentridae) (Z-score$=4.98$; p-value$=0.001$), while means PLDs of angelfishes and damselfishes were comparable (Z-score$=1.38$; p-value$=0.086$; Fig. 1). Labridae exhibited a higher mean PLD than Pomacanthidae and Pomacentridae (37, 27 and 22 days, respectively) and the highest disparity of PLD (SD$=18$). The variability within Pomacanthidae and Pomacentridae was low in comparison with Labridae (SD$=6.04$ and SD$=7.01$, respectively; Suppl. file 2: Table S2).

Geographic variation of PLD

The amount of PLD values recorded per region largely varied for each family (Fig. 2). There were no PLD data recorded in the TEP region for Pomacanthidae in our database.

In Labridae, the mean PLD varied significantly among regions (Procrustes-ANOVA: F=2.51; Z-score=1.73; p-value=0.04), while no difference in PLD variance was found (Levene's test: F=0.26; p-value=0.9). The mean PLD of the Atlantic region was significantly different from all other regions (p-values ≤ 0.05), except the CIP region (Fig. 2, Table 2). Mean PLD was the lowest in the Atlantic region (30.5 days) and the highest in the TEP region (42.5 days). Labridae with outlier PLD means were found in the Atlantic region: *Symphodus ocellatus* with the lowest PLD (9.9 days) and *Xyrichtys splendens* with the highest one (103.9 days) (Suppl. file 2: Table S3).

Mean PLD did not vary significantly across regions in the Pomacanthidae (Procrustes-ANOVA: F=1.1; Z-score=0.37; p-value=0.35), nor did the PLD variance (Levene's test: F=0.12; p-value=0.95). Notably, the Atlantic region had the lowest mean PLD value in Pomacanthidae (25.1 days), similar to the pattern observed in Labridae. The CP region showed the highest mean PLD (30 days). Extreme values of PLD were also found in the Atlantic region (min=17.7 and max=36.8 days in *Pomacanthus paru* and *Centropyge argi*, respectively).

Finally, the mean PLD differed significantly among regions in Pomacentridae (Procrustes-ANOVA: F=5.63; Z-score=3.43; p-value=0.001). Pairwise comparisons showed significant variation of mean PLD values between CIP and all other regions (p-values<0.01), except the WI region (Fig. 2, Table 2). The Pomacentridae did not follow a pattern comparable to the two other families since the lowest mean PLD (20.4 days) was found in the CIP region. However, as for Labridae, the mean PLD was the highest

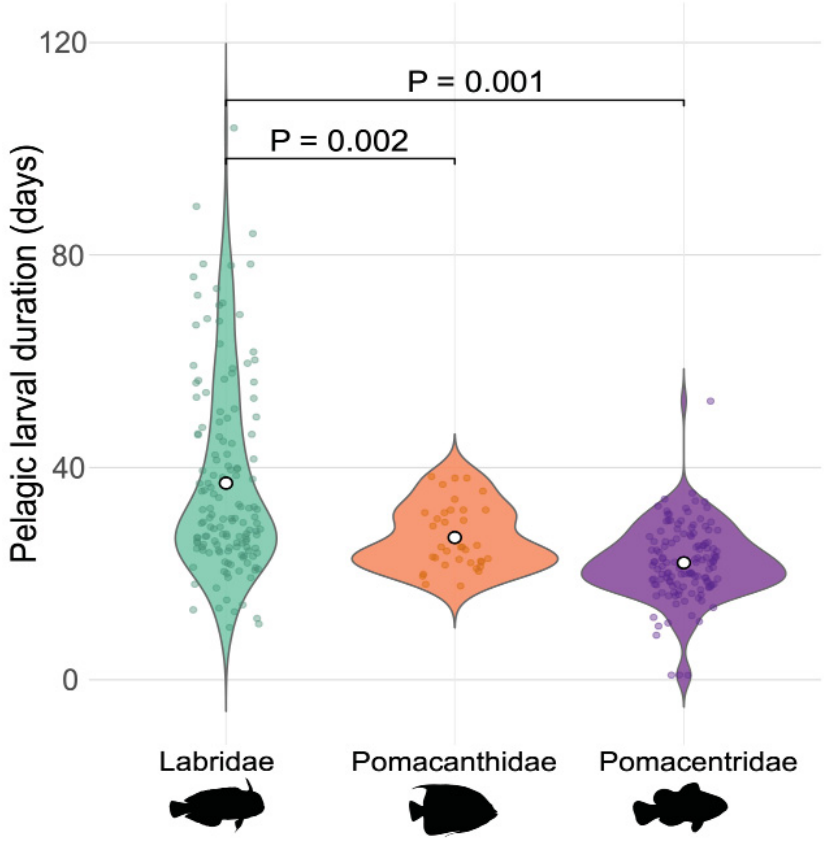

Figure 1 – Distribution of PLD values in the three studied reef fish families. Pairs of families that differ significantly in PLD means are indicated by horizontal bars and associated p-values.

TABLE 2

Pairwise comparisons of PLD among regions.

	A-CIP	A-CP	A-TEP	A-WI	CIP-CP	CIP-TEP	CIP-WI	CP-TEP	CP-WI	TEP-WI
Labridae										
Z-score	1.32	**2.09**	**2.24**	**1.76**	0.79	1.29	0.28	0.21	-0.86	0.43
P-value	0.095	**0.01**	**0.005**	**0.03**	0.22	0.09	0.39	0.45	0.79	0.34
Pomacentridae										
Z-score	**2.21**	0.22	-0.5	0.84	**2.22**	**2.65**	1.45	0.98	-0.06	1.44
P-value	**0.009**	0.43	0.69	0.21	**0.003**	**0.001**	0.07	0.17	0.54	0.07

No pairwise comparison was performed for the Pomacanthidae since no effect of the regions on the PLD were detected for this family. Abbreviations: A =Atlantic region; CIP = Central Indo-Pacific region; CP = Central Pacific region; TEP = Tropical Eastern Pacific region; WI = Western Indian region.

in the TEP region (26.3 days). Even if extreme values of PLD were found in the CIP region for three species with no pelagic larval phase (*Altrichthys azurelineatus*, *Altrichthys curatus* and *Acanthochromis polyacanthus*) and *Pomacentrus australis* with the highest PLD (52.5 days) (Suppl. file 2: Table S3), the Levene test did not reveal any difference in PLD variance among regions (F = 1.41; p-value = 0.23).

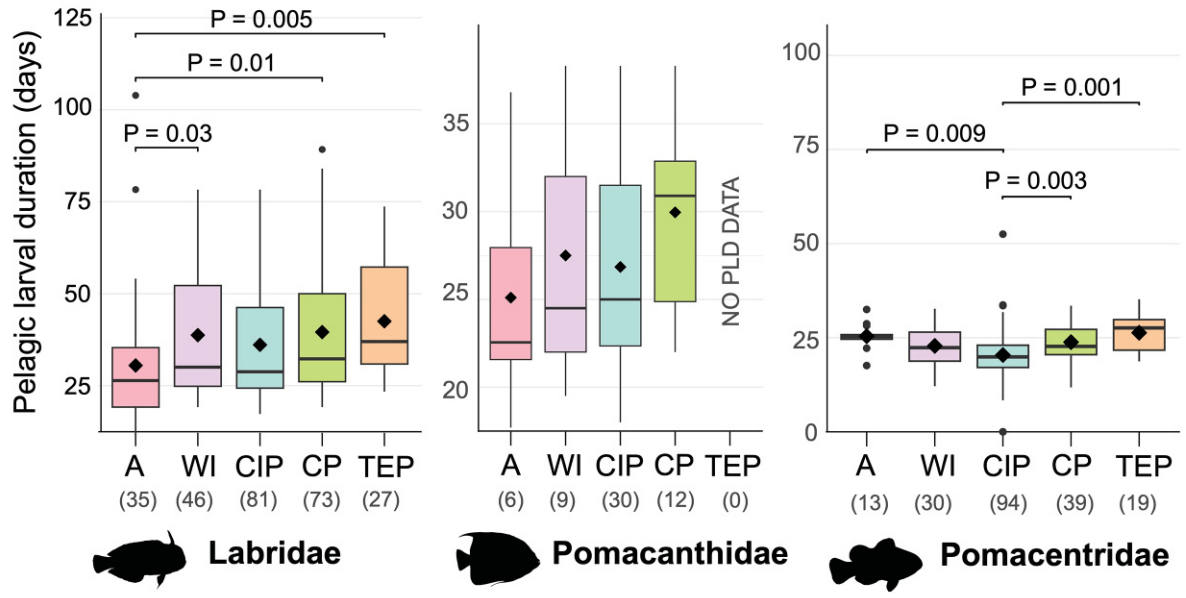

Figure 2 – Variation of the PLD among the five geographical regions for each family. Pairs of regions that differ significantly in PLD means are indicated by horizontal bars and associated p-values. The number of species with PLD data present in each region is indicated under the associated abbreviation. Abbreviaitons: A = Atlantic region; WI = Western Indian region; CIP = Central Indo-Pacific region; CP = Central Pacific region; TEP = Tropical Eastern Pacific region. PLD data were not available for Pomacanthidae in the Tropical Eastern Pacific region.

Pattern of PLD diversification

Both tests of phylogenetic signal consistently revealed that the PLD was tightly associated with the phylogenetic relationships within each fish family. Pagel's λ suggested a strong and statistically significant phylogenetic signal of PLD ($\lambda_{Pomacentridae} = 1.01$; $\lambda_{Labridae} = 0.94$; $\lambda_{Pomacanthidae} = 0.86$; p-values < 0.001) and the M statistic showed a pronounced phylogenetic structuring of PLD variation ($M_{Pomancanthidae} = 0.77$, $M_{Labridae} = 0.69$, $M_{Pomacentridae} = 0.69$; all p-values = 0.001). This phylogenetic dependence was well illustrated when PLD was mapped on phylogenies (Fig. 3). Globally, the evolutionary divergences for PLD occurred in subclades of closely related species in the three families. In Labridae, the estimated PLD value at the root was approximately 35 days. At least three major events of strong divergence from the root state were visible: PLD was longer in the genera *Xyrichtys* and *Thalassoma* (up to 104 days), and shorter in the genus *Symphodus* (10–15 days). In Pomacanthidae, the evolutionary pattern of PLD seemed to follow the divergence of major lineages. The most derived taxa, mainly including pygmy angelfishes of the genus *Centropyge*, evolved with longer or similar PLD values compared to the ancestral state (24 days). Conversely, all large angelfishes (*Pomacanthus* spp.) had a shorter PLD than the ancestral state. Finally, trait mapping on the phylogeny of Pomacentridae revealed that PLD was conserved across this family. Globally, PLD values diverged only slightly from the ancestral state of 23 days. However, it appeared that the subfamily Pomacentrinae (node D on Fig. 3) grouped species with shorter PLD than the three other subfamilies. Within Pomacentrinae, two major events of divergence were clearly visible. The first occurred in the monophyletic group of 'larval brooders' (*Acanthochromis* and the two species of *Altrichthys*) where the pelagic stage was absent. The second divergence occurred in the genus *Amphiprion* (clownfishes), which developed a shorter PLD (10–14 days) compared to the ancestral state.

Comparisons of evolutionary models revealed that neither the Brownian Motion (BM) model – which assumes a constant, unconstrained divergence of PLD values over time – nor the Ornstein-Uhlenbeck (OU) model – which assumes evolution toward a single optimal PLD value shared by all species – were the best-supported models (Table 3). Conversely, the ψ model was the best supported one ($\Delta AIC \geq 4$) for both Labridae and Pomacanthidae, suggesting that PLD diversification is directly proportional to the number of speciation events. In Pomacanthidae, the large estimate of the ψ parameter ($\psi = 1$) indicated that most evolutionary change occurred at speciation events rather than gradually along branches, supporting a punctuational mode of PLD evolution. In contrast, a lower ψ estimate in Labridae ($\psi = 0.25$) was consistent with a predominantly gradual evolution. Support for the ACDC and DC models highlighted variation in the tempo of PLD diversification over time in Pomacentridae (Table 3). The "free ACDC model" and the DC model converged (same AICc values) and estimated the same negative rate parameter ($r = -0.07$), indicating a deceleration in the rate of PLD evolution.

The lasso-based methods for adaptive shifts detection indicated the presence of shifts towards varied optimal PLD values in the studied families. The l1OU + BIC approach suggested the presence of seven shifts in Labridae, three in Pomacanthidae and four in Pomacentridae, while the l1OU + pBIC approach was more conservative, detecting no shift in Labridae and two shifts in both Pomacanthidae and Pomacentridae (Table 4). Figure 4 illustrates the location and the magnitude of each shift detected with the BIC criterion. In Labridae (Fig. 4a), the number of PLD lengthening events (five events) exceeded the number of events of PLD shortening (two events). Nonetheless, the shift with the highest magnitude corresponded to a remarkable shortening event found in the genus *Symphodus* (magnitude = 0.9). A notable elongation event with high magnitude (magnitude = 0.77) occurred in the monophyletic tribe Novaculini (that groups the five genera *Novaculoides*, *Novaculichthys*, *Cymolutes*, *Iniistius*, *Xyrichtys*) and the sister species *Cheilio inermis*. This was followed by a shortening event in the Julidines tribe (magnitude = 0.88) and a major PLD elongation in the *Thalassoma/Gomphosus* group (magnitude = 0.82). In Pomacanthidae (Fig. 4b), there was one shift for a shortening event that occurred at the node supporting the genera *Pygoplites*, *Holacanthus*, *Centropyge*, and *Genicanthus*, followed by

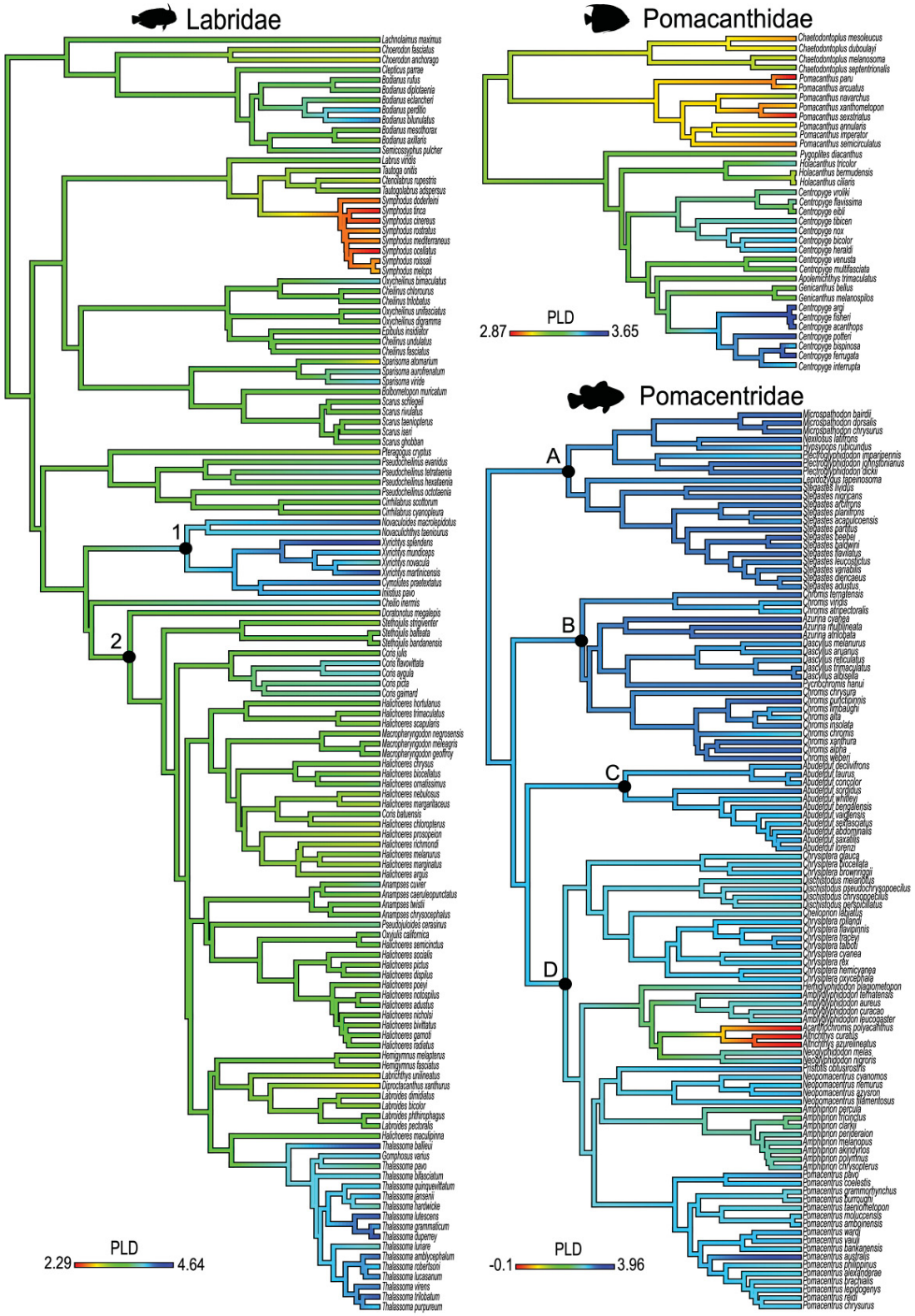

Figure 3 – PLD mapping and ancestral state reconstruction on the phylogeny of Labridae, Pomacanthidae and Pomacentridae. A colour gradient is adjusted for each phylogeny. For each family, cold colours show longer PLD values and warm colours show shorter PLD values (log-transformed). Digits and black points indicate two tribes in Labridae: 1 = Novaculini and 2 = Julidines. Letters and black points indicate the four subfamilies of Pomacentridae: A = Microspathodontinae; B = Chrominae; C = Glyphisodontinae; D = Pomacentrinae.

TABLE 3

Evolutionary model classification based on AICc. ΔAICc represents the absolute difference in AICc between the best model and remaining models. The best-fitting models are shown in bold.

Model	AICc	ΔAICc	Weight
Labridae			
ψ	51.39	/	0.75
OU	55.33	3.94	0.1
ACDC	55.33	3.94	0.1
BM	57.71	6.32	0.03
DC	59.81	8.42	0.01
Pomacanthidae			
ψ	-38.54	/	$9.99*10^{-1}$
OU	-22.67	15.87	$3.58*10^{-4}$
ACDC	-22.02	16.51	$2.59*10^{-4}$
BM	-16.39	22.15	$1.55*10^{-5}$
DC	-13.96	24.58	$4.6*10^{-6}$
Pomacentridae			
DC	63.6	/	0.5
ACDC	63.6	$1.14*10^{-13}$	0.5
BM	73.86	10.26	$2.94*10^{-3}$
ψ	75.98	12.38	$1.02*10^{-3}$
OU	75.98	12.38	$1.02*10^{-3}$

TABLE 4

Estimation of the number of adaptive shifts under an OU model with two different corrective criterions based on the method of Khabbazian *et al*. (2016).

	Number of shifts	Score	Alpha	Sigma²	logLik
Labridae					
pBIC	0	61.64	0.91	0.39	-24.56
BIC	**7**	**50.24**	**18.61**	**1.71**	**16.06**
Pomacanthidae					
pBIC	2	-25.53	50.24	0.96	30.43
BIC	**3**	**-42.78**	**76.83**	**0.96**	**37.12**
Pomacentridae					
pBIC	2	-36.28	0.84	0.1	42.1
BIC	**4**	**-65.64**	**5.1**	**0.22**	**58.62**

Figure 4a – Shifts in the PLD values of wrasses detected by l1OU+BIC. On the left, the shifts configuration is represented in the phylogeny: each estimated shift is indicated by a star and by its magnitude. On the right, the bar graphs show the value of PLD species by species. The scale of the bar graph indicates standardized PLD values: left tip and right tip of the scale are the minimum and maximum of standardized PLD values, respectively. The colours only function as a visualization aid.

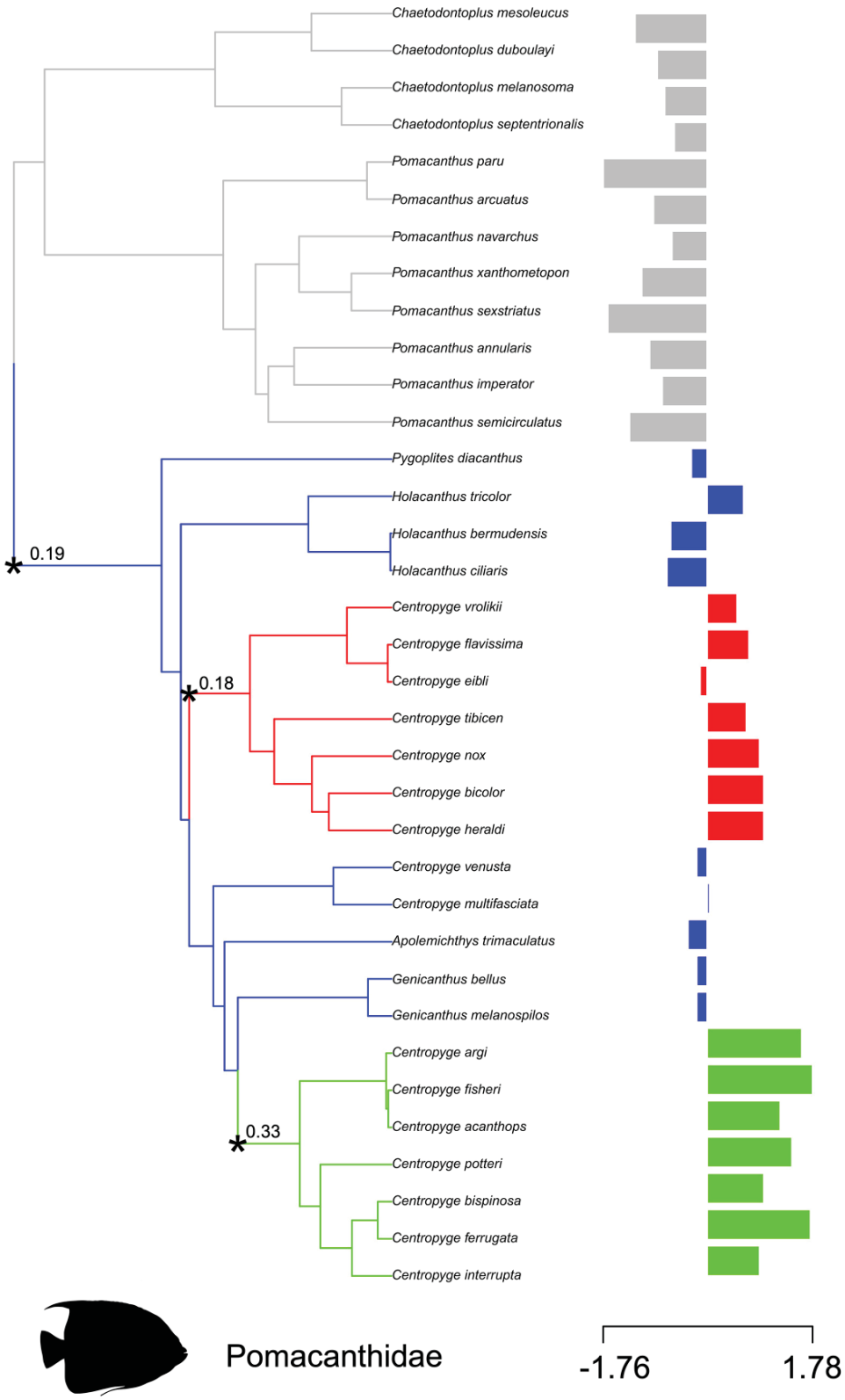

Figure 4b – Shifts in the PLD values of angelfishes detected by l1OU+BIC. On the left, the shifts configuration is represented in the phylogeny: each estimated shift is indicated by a star and by its magnitude. On the right, the bar graphs show the value of PLD species by species. The scale of the bar graph indicates standardized PLD values: left tip and right tip of the scale are the minimum and maximum of standardized PLD values, respectively. The colours only function as a visualization aid.

Figure 4c – Shifts in the PLD values of damselfishes detected by l1OU+BIC. On the left, the shifts configuration is represented in the phylogeny: each estimated shift is indicated by a star and by its magnitude. On the right, the bar graphs show the value of PLD species by species. The scale of the bar graph indicates standardized PLD values: left tip and right tip of the scale are the minimum and maximum of standardized PLD values, respectively. The colours only function as a visualization aid.

TABLE 5

Relationship between adult traits (diet and maximum size) and PLD in the three fish families.

DIET					
	AIC	BIC	logLik	F	P-value
Labridae					
/	187.98	202.04	-88.99	0.77	0.51
corBrownian	66.5	80.56	-28.25	**0.68**	**0.56**
corMartins	189.98	206.85	-88.99	0.77	0.51
Pomacanthidae					
/	**-14.15**	**-10.05**	10.08	**37.33**	**<.0001**
corBrownian	-13.9	-9.8	9.95	9.38	0.01
corMartins	-12.15	-6.68	10.08	37.33	<.0001
Pomacentridae					
/	197.05	207.67	-94.52	3.95	0.02
corBrownian	79.43	90.05	-35.72	**2.8**	**0.06**
corMartins	199.05	212.32	-94.52	3.95	0.02
ADULT MAX SIZE					
	AIC	BIC	logLik	F	P-value
Labridae					
/	190.3	198.78	-92.15	1.68	0.2
corBrownian	**71.85**	**80.33**	-32.92	**0.94**	**0.33**
corMartins	192.3	203.61	-92.15	1.68	0.2
Pomacanthidae					
/	-12.56	-8.26	9.28	**43.44**	**<.0001**
corBrownian	-4.35	-0.04	5.17	0.35	0.56
corMartins	-10.56	-4.82	9.28	43.44	<.0001
Pomacentridae					
/	204.01	212.03	-99.01	3.03	0.08
corBrownian	**82.99**	**91.01**	-38.5	**2.14**	**0.15**
corMartins	206.01	216.7	-99.01	3.03	0.08

AIC, BIC and loglikelihood are from the output of the gls function; F and P-values come from ANOVA performed on the models' parameters. The bests models (based on the AIC) are in bold.

two shifts associated with elongation events concentrated in derived lineages, especially *Centropyge* spp. In Pomacentridae (Fig. 4c), the four shifts identified with l1OU + BIC occurred in the subfamilies Glyphisodontinae and Pomacentrinae. These shifts mainly reflected shortening events. The first shift occurred at the ancestor of Glyphisodontinae and Pomacentrinae (magnitude = 0.3), suggesting a general trend for shorter PLD in both subfamilies in comparison with other lineages. The second occurred on the branch leading to *Amphiprion* (magnitude = 0.48). The most important shift (magnitude = 3.41) was found in the monophyletic group formed by *Acanthochromis polyacanthus* and the two *Altrichthys*, which lack a larval pelagic phase. In contrast, *Pomacentrus australis* showed a high-magnitude elongation event (magnitude = 1.33), opposing the general shortening trend.

Relationships between PLD and adult traits

We selected the best-fitting model to describe relationships between PLD and adult traits for each family using AIC and BIC criteria (models in bold, Table 5). For Pomacanthidae, the best-fitting models were

GLS without any phylogenetic correction, for both diet and body size. For Labridae and Pomacentridae, PGLS models assuming Brownian motion (BM) covariation were the best supported ones for each of the adult traits. For Labridae and Pomacentridae, the selected linear models revealed that adult traits had no significant relationship with PLD. Conversely, in Pomacanthidae, we found that both adult diet and maximum body size had a significant association with PLD (ANOVA: $F > 35$; p-values < 0.0001).

Discussion

Our study is one of the first to analyse the diversification of pelagic larval duration (PLD) in reef fishes using modern phylogenetic comparative analyses. First, by assembling the largest dataset about PLD in Labridae, Pomacanthidae and Pomacentridae, we confirmed variation of PLD diversity among these three families, and we revealed how this diversity of PLD varied across geographic regions. Then, using tests of phylogenetic signal, we demonstrated that PLD is strongly associated with phylogenetic relationships in the studied reef fish families. Furthermore, models of trait evolution revealed that the tempo of PLD evolution was associated with lineage diversification (Labridae and Pomacanthidae) or varied over time (Pomacentridae), and that a significant proportion of the PLD diversity in reef fish families resulted from multiple adaptive evolutionary shifts towards different PLD optima. Finally, we showed that variation in PLD was associated to adult body size and diet in Pomacanthidae but not in Labridae and Pomacentridae.

Our results documenting variation in PLD diversity among reef fish families align with some previous works (e.g., Leis 1991; Victor & Wellington 2000; Leis *et al.* 2013), and such a variation across demersal reef fish families is the first evidence that some part of the PLD diversity is linked to intrinsic characteristics of lineages. Because elevated temperatures accelerate physiological rates, tropical fish larvae are expected to develop more rapidly, resulting in shorter pelagic larval durations compared to their temperate counterparts (O'Connor *et al.* 2007; Munday *et al.* 2009). This hypothesis could sustain variation in PLD diversity among families because the geographic and the latitudinal distribution of wrasses, angelfishes and damselfishes differs. Both angelfishes and damselfishes, mainly restricted to tropical and subtropical regions, displayed broadly comparable mean PLD values and these durations were consistently shorter than those observed in many labrid species, highlighting a clear divergence in larval developmental strategies among the three families. Labridae include species distributed across a broad latitudinal range, from tropical to temperate environments (e.g., Mediterranean Sea, Norway; Floeter *et al.* 2008; Skiftesvik *et al.* 2015), where temperature differences could potentially influence larval duration. However, our geographic comparisons of PLD diversity did not entirely support the idea that latitude and associated water temperature act as the major driving force of the level of interspecific variation among reef fish families. Contrary to the simple prediction that the regions spanning the largest range of latitudes would support a pool of species showing the largest PLD variance, our analyses revealed no significant variation in the level of PLD disparity across regions in the three studied fish families. Extreme PLDs were encountered in the Atlantic region for wrasses and angelfishes whereas the shortest and the longest PLD values were observed in the mainly tropical Central-Indo Pacific for damselfishes. Overall, our comparative analyses strengthened the idea that PLD is not tightly linked to temperature at the inter-specific level. In line with Leis *et al.* (2013), regional differences in PLD diversity were more likely rooted in lineage-specific characteristics than in thermal and latitudinal variation.

Our macroevolutionary analysis revealed a clear relationship between phylogenetic relationships and PLD variation at the intra-family level. Both indices (i.e., Pagel's λ and model-independent M statistic) consistently indicated a strong phylogenetic signal in PLD across the three families, in line with the visual distribution of PLD values on the phylogenies (Fig. 3), where closely related species tended to exhibit similar PLD and large intra-generic variation was rare. These convergent results highlighted a strong correspondence between phylogeny and trait variation, indicating that PLD was not randomly

distributed across the phylogeny but showed a clear hierarchical structure. This pattern thus supports a significant role of evolutionary history in shaping PLD variation and is consistent with phylogenetic conservatism.

The phylogenetic structuring of PLD variation across the three families supported a potential link between PLD variation and lineage diversification. This hypothesis is further strengthened by the strong support for the ψ model in wrasses and angelfishes, as these speciation models of trait evolution (Ingram 2011; Ingram *et al.* 2016) suggest that shifts in PLD accompany speciation events, including lineage splitting, in these two families. While this interpretation is likely relevant to damselfishes as well, the evolutionary tempo of PLD variation in this family appeared to be influenced by additional factors. Pomacentrinae and Glyphisodontinae, which diverged during the Eocene (McCord *et al.* 2021), are among the clades in which PLD shortening first evolved. Two Pomacentrinae subclades (*Amphiprion* and *Acanthochromis*/*Altrychthys*) showed further reduction in PLD (Figs 3–4). Aside from these shifts, PLD appeared to have remained relatively stable across most extant lineages since the Eocene, a pattern consistent with a model indicating a slowdown in the rate of PLD evolution in Pomacentridae. Taken together, these patterns suggest that PLD variation may play a role in shaping species diversification. Future studies could build on this by exploring the relationship between PLD variation and speciation rates, to assess whether shifts in PLD are associated with differences in diversification dynamics across lineages.

From an eco-evolutionary perspective, we might hypothesize that PLD evolves toward a single selective regime reflecting a balance between constrains and benefits from genetic mixing, colonisation of isolated reefs and mortality during the pelagic phase. By contrasting the single-optimum OU model with a range of alternative evolutionary scenarios, our results made it clear that PLD did not converge toward a universal optimum across species as we instead found support for multiple adaptive shifts (multiple optima) in each family (Figs 3–4), emphasizing the lineage-specific nature of its evolutionary dynamics. Hansen (1997) proposed the Ornstein-Uhlenbeck process as an appropriate model for traits evolving under stabilizing selection toward one or more optima. Here, we used the automated shift-detection approach developed by Khabbazian *et al.* (2016), which identifies the presence and location of multiple optima without requiring *a priori* hypotheses. This framework compares shift configurations using several information criteria, including BIC and pBIC – the latter being an adaptation of BIC corrected for phylogenetic correlation. Khabbazian *et al.* (2016) showed that pBIC is more conservative and should be prioritized for locating shifts, whereas BIC is more reliable for estimating the total number of shifts across the phylogeny. They concluded that BIC provides a good balance to "reach a reasonable precision with a reasonable recall rate" (Khabbazian *et al.* 2016). Following their recommendations, we considered the number of shifts detected by the BIC method to provide a reasonable estimate. In Pomacanthidae, most shifts corresponded to PLD elongation events, whereas in Pomacentridae they were predominantly associated with PLD shortening. In angelfishes, PLD lengthening occurred independently within the monophyletic subgenus *Xiphypops* and among the most derived *Centropyge* species. In damselfishes, PLD shortening was observed in the monophyletic clade comprising *Altrichthys* spp. and *Acanthochromis polyacanthus*, and within *Amphiprion* spp. In wrasses, we observed multiple events of PLD lengthening (e.g., *Thalassoma* and Novaculini) and shortening (e.g., *Symphodus*). The diversification of PLD did not follow a consistent evolutionary trend of shortening or lengthening in reef fish families.

One lineage characteristic often evoked to be associated with PLD variation is the spawning strategy. The PLD of demersal spawners has been proposed to be shorter than that of pelagic spawners (Leis 1991; Sponaugle & Cowen 1994; Soeparno *et al.* 2012), but this trend seems to be only partially supported when comparing the three families studied here. Although wrasses, most of which produce pelagic eggs, displayed significantly longer PLD than the other two families, pelagic-spawning angelfishes

and benthic-guarding damselfishes had similar PLD means. Nonetheless, some of the evolutionary shifts in PLD identified at the intra-family level supported the hypothesis that benthic egg guarding was associated with shorter PLDs (Fig. 4). For instance, temperate *Symphodus* labrids evolved to produce demersal eggs with parental care (Lejeune 1985), and we showed that a major PLD shortening event was associated with this change in reproductive strategy. Similarly, true brood care *sensu stricto* (i.e., post-hatching care), which evolved once in damselfishes (*Altrichthys* spp. and *Acanthochromis polyacanthus*; Bernardi 2011), was associated with the complete loss of a pelagic larval phase. Although future studies should formally test this hypothesis within a robust phylogenetic comparative framework (but see Riginos *et al.* 2014), our observations certainly strengthen the idea that reproductive strategies (including spawning mode and parental care) are important explanatory factors of PLD variation across reef fish clades (Leis *et al.* 2013).

Here, we also investigated the covariation of PLD with diet and maximum body size at adult stage to refine the expectations that PLD evolves independently from adult traits. In Labridae and Pomacentridae, there was no relationship between PLD and adult diet or maximum body size. However, in Pomacanthidae, we found an effect of both adult diet and body size on PLD. Small body size in pygmy angelfishes (*Centropyge*), which represent more than half of angelfish species (Fricke *et al*. 2025), has been shown to drive morphological convergence, leading to a certain degree of trophic niche specialization (Frédérich *et al.* 2017). This means that diet and adult body size covary in this family, explaining why both traits influence PLD. However, even though all *Centropyge* are small bodied, not all of them had a long PLD in our study. Overall, these analyses showed that a larval trait such as PLD can be associated to an adult trait, but not in a deterministic manner. These results also confirmed that the benefits for species to develop larval traits adapted to the specific requirements associated with this ontogenetic stage may outweigh the benefits of developing traits directly linked to the final adult stage (Dornburg *et al.* 2024).

Our macroevolutionary analysis demonstrated the presence of evolutionary transitions in PLD regime across three reef fish families and identified the position of these shifts on their phylogeny. Now, to better understand the origin and the mechanisms underlying these shifts, it would be beneficial to analyze genes being functionally associated with PLD variation. It was recently shown that mutations within the *Clock* gene may be at the origin of those shifts, since variability in PLD seems to be determined by genetics at the interspecific scale (Schalm *et al.* 2025). However, this genetic determinism appears to be less important at the population scale, at least in the damselfish *Pomacentrus coelestis* (Schalm *et al.* 2025). The phylogenetic conservatism of PLD certainly supports the hypothesis of a genetic mechanism underlying PLD variation. In addition to molecular markers, there is also some evidence for a correlation between PLD and cytogenetic features in Labridae (de Sena & Molina 2007) and Pomacentridae (Molina & Galetti 2004). Our analyses revealing multiple, independent events of shortening and lengthening of PLD across reef fish families offer a promising avenue for future investigations about the intrinsic factors associated with PLD evolution.

While our analyses provided valuable insights into PLD evolution across reef fish families, acknowledging the data-related limitations of our approach is essential for a balanced interpretation of our findings. Several works have demonstrated that incorporating within-species variation around mean values improves the accuracy of comparative models of continuous trait evolution (e.g., Ives *et al.* 2007; Garamszegi 2014; Silvestro *et al.* 2015), such as the models we used to explore the tempo and the mode of PLD evolution. To date, PLD measurements reported across the literature are heterogeneous, with some species represented by several independent estimates and others by a single value. Measures of within-species variation (e.g., SD or SE) are inconsistently reported and therefore cannot be systematically included without greatly reducing taxonomic coverage. Moreover, the range of PLD varies across taxa (Bay *et al.* 2006), which limited our ability to infer an approximate variance of PLD across all species included in our study. In this context, species-level mean PLD values represent the

most consistent metric available for large-scale comparative analyses (e.g., Lester & Ruttenberg 2005; Luiz *et al.* 2013). Furthermore, Victor & Wellington (2000) demonstrated that mean and maximum PLD are strongly correlated, supporting the biological relevance of using mean PLD values for our macroevolutionary analyses.

Conclusion

Our study of evolutionary trends of the pelagic larval duration (PLD) demonstrated that this larval trait is not a stationary trait, but it has evolved to different optima and under different scenarios across families of reef fishes. Although our conclusions would undoubtedly be strengthened by analyses including additional families with broader taxon sampling and by incorporating within-species variation into model fitting, the present study provided the first insight into a macroevolutionary trend for a larval trait in reef fishes. We revealed phylogenetic dependency of PLD, and multiple shifts to short and long adaptive values of PLD. We also provided additional support for the possibility of independent evolution of larval and adult traits in reef fishes. The combination of our geographic and phylogenetic comparative analyses supported that the diversity of PLD is rooted in lineage-specific characteristics.

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Author Contributions

BF and EH conceived of the study. EH, CP, AG, DL and BF collected data. EH, AG and BF performed analyses. EH and BF wrote the initial draft of the manuscript. All other authors contributed to the writing and subsequent development of the manuscript.

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Supplementary files

Suppl. file 1. Table S1: PLD data and references, adult biological traits, and species occurrences in the five regions. https://doi.org/10.26496/bjz.2026.205.312

Suppl. file 2. Tables S2–S3. https://doi.org/10.26496/bjz.2026.205.313