Received: 29 May 2022 | Accepted: 29 September 2022

DOI: 10.1111/1365-2435.14202

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Adaptive effects of parental and developmental environments on offspring survival, growth and phenotype

Daphne Cortese[1,2] | Amélie Crespel[2,3] | Suzanne C. Mills[1,4] | Tommy Norin[2,5] | Shaun S. Killen[2] | Ricardo Beldade[1,6]

[1]PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, Moorea, Papetoai, French Polynesia; [2]School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK; [3]Department of Biology, University of Turku, Turku, Finland; [4]Laboratoire d'Excellence "CORAIL", France; [5]DTU Aqua: National Institute of Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark and [6]Estación Costera de Investigaciones Marinas and Center for Advanced Studies in Ecology and Biodiversity, Las Cruces, Pontificia Universidad Católica de Chile, Santiago, Chile

Correspondence
Daphne Cortese
Email: daphne.cortese@glasgow.ac.uk

Ricardo Beldade
Email: rbeldade@bio.puc.cl

Funding information
Agence National de la Recherche, Grant/Award Number: ANR-14-CE02-0005-01/StayorGo and ANR-11-JSV7-012001/WhereDoWeGoNow; LABEX Corail, Grant/Award Number: LiveandLetDie; Natural Environment Research Council, Grant/Award Number: NE/J019100/1; Danish Council for Independent Research (now 'Independent Research Fund Denmark'), Grant/Award Number: DFF-4181-00297

Handling Editor: Ismael Galván

Abstract

1. Phenotypic adjustments to environmental variation are particularly relevant to cope with putative environmental mismatches often imposed by natal dispersal.
2. We used an intergenerational cross-transplant field-based experiment to evaluate the morphological and physiological effects of parental and postsettlement water flow environments on the orange-fin anemonefish *Amphiprion chrysopterus* through ontogeny (at pre- and postsettlement stages).
3. Offspring born from parents under high water flow had an 18% higher caudal fin aspect ratio (a compound measure of shape) at the presettlement stage, 10% slower growth after settlement, and 55% lower survival after settlement compared to offspring from low water flow parents. At the presettlement stage, caudal fin length was determined by parental caudal fin length. At the postsettlement stage, fish survived equally well with similar phenotypes in both high and low developmental flow environments. However, results suggest potential developmental phenotypic plasticity in caudal fin length, which increases more under low water flow during development. After settlement, growth was the only morphological or physiological trait that was associated with parental water flow, which was lower from parents under high flow, as was survival.
4. These results give important insights into the parental contribution, both genetic and nongenetic, in determining early offspring phenotype and subsequent growth and survival. Our results also suggest that offspring may possess flexibility to cope with a wide range of local environments including those different from their parents. Overall, the findings of this study show the fitness consequences of living in different environments and the likely trade-offs between parental and offspring fitness in a wild population.

KEYWORDS
morphology, parental–offspring fitness, phenotypic plasticity, physiology, survival, water flow

1 | INTRODUCTION

The way in which the environment, either the immediate, developmental or parental environment, influences an individual's phenotype is one of the core research areas in evolution and ecology. Environmental variation is common within a population and phenotypes have different optima across environments. The relative importance of the mechanism, direct or intergenerational, that shapes phenotypes may vary throughout ontogeny (Lindholm et al., 2006; Mousseau & Dingle, 1991). While the parental environment, translated through parental effects, is likely most important in the first stages after birth (Lindholm et al., 2006), the offspring developmental environment will predominantly drive phenotypic changes in subsequent stages, especially in species that develop far from their natal habitat (Warner, 2014). Limited natal dispersal—the movement from birth place to settlement place—in stable and predictable environments may mean that parental and developmental environments are similar, leading to local adaptation (Linhart & Grant, 1996; Marshall & Uller, 2007). On the other hand, nonrandom associations between the environment experienced by parents and offspring (environmental mismatch) are often prevalent in species whose offspring disperse further away from their natal environment and in those that disperse in heterogeneous environments where even small natal dispersal distances can result in very different settlement environments (Galloway & Etterson, 2007), as oftentimes observed in the oceans (Beldade et al., 2016; Burgess et al., 2012). While natal dispersal may dissociate parental and offspring phenotypes, developmental plasticity promotes the match between the offspring's phenotype–environment. However, the environmental cues that render parental or developmental effects adaptive in offspring and select for the evolution of intergenerational or developmental plasticity respectively, are not always evident, especially in variable environments where the potential for mismatch is increased.

Optimal phenotypes depend on variable biotic and abiotic factors such as predation risk (Lively, 1986), temperature or photoperiod (Beldade & Brakefield, 2002). In marine ecosystems, and coral reefs in particular, water flow is spatially and temporally variable (Hearn, 2011; Lenhardt, 1991; Monismith et al., 2006), and may influence phenotypic variation. Fishes' morphological and life-history traits are associated with the water flow regime and habitat of their environment and are correlated with swimming modes (Fulton et al., 2001; Langerhans et al., 2003; Webb, 1984). Fish body shape, particularly the shape and length of the caudal fin, is important for swimming, acceleration and manoeuvrability in different water flows, as well as for catching prey or escaping predators (Domenici & Blake, 1997; Langerhans, 2008; Videler, 1993). The pectoral fin is also important for generating movement or manoeuvrability, especially in coral reef fish (Fulton et al., 2005; Webb, 1984). Distinct purposes and energetic costs are associated with different swimming modes, and each of them can be advantageous under different situations encountered in a complex environment.

The water flow in an environment may also require different performance and physiological traits which support more or less metabolically expensive swimming modes (Boisclair & Tang, 1993). For example, tropical reef fish living in high-flow areas have higher maximum swimming speeds and aerobic scopes, and quicker fast-start escape responses (Binning et al., 2014; Nadler et al., 2018), while those in lower flow areas have lower metabolic rates, aerobic scopes and maximum swimming speeds (Binning et al., 2014; Binning et al., 2015). Such differences in physiological (metabolism) and performance (swimming) capacities have rarely been shown in juveniles, making it difficult to know if observed differences come from developmental or parental environments. While some studies have found that water flow affects fin morphology and body shape during development of freshwater species and salmonids (Fischer-Rousseau et al., 2010; Pakkasmaa & Piironen, 2001), little is known for coral reef fishes. In addition, the different energetic costs of activity under different water flow environments (Boisclair & Tang, 1993) may impose trade-offs with, for example, reproduction cascading onto offspring traits (Marshall & Uller, 2007; Weiner, 1992).

Here, we used an intergenerational cross-transplant experiment to understand the morphological, performance and physiological effects of parental and postsettlement developmental water flow environments on *Amphiprion chrysopterus*, the orange-fin anemonefish. *A. chrysopterus* is a territorial coral reef fish, mutualist with sea anemones (Fautin, 1991), which can be found at varying depths (Haguenauer et al., 2021), water flow (Fautin, 1992; Holbrook & Schmitt, 2005) and geographic range (Emms et al., 2020). Similar to many other coral reef fishes that develop in open water (Leis & McCormick, 2002), anemonefish larvae settle (onto anemones) in environments which are often different to those of their parents, especially in terms of water flow and depth (Beldade et al., 2016). We predict parental and developmental environments interact to affect offspring phenotype in response to varying flow conditions, specifically: (1) parents from different flow environments may produce different offspring phenotypes because of either different parental investment and/or parental genotype and phenotype; (2) parents living in high-flow sites may invest less (due to trade-offs) in their offspring leading to lower offspring survival; and (3) selection imposed by water flow may explain the distribution of phenotypes, or (4) offspring phenotype may be directly modulated through developmental plasticity to match the postsettlement habitat. We evaluated parental contribution and developmental plasticity to explain survival and offspring phenotypic variation across water flow environments, while accounting for parental genotypic legacy. These results will help to better understand whether intergenerational plasticity or developmental plasticity provide a flexible mechanism by which fish cope with heterogeneous flow environments.

2 | MATERIALS AND METHODS

Ethical approval for the study was granted from The Animal Ethics Committee, Centre National de la Recherche Scientifique (permit number 006725).

2.1 | Experimental overview

A field-based experiment with low and high water flow treatments was carried out on the offspring of free-living pairs of orange-fin anemonefish *Amphiprion chrysopterus*, from a range of water flows in Moorea lagoon, French Polynesia. The experiment linked three life stages: adult; presettlement and postsettlement offspring (grey panels in Figures 1 and 2). To establish different water flow categories, flow at the sites of 23 free-living pairs of orange-fin anemonefish was measured over 12 days using Marotte HS (High Sampling Rate) drag-tilt current metres. Measurements at every 10 min were converted to flow velocity by postprocessing with a tilt-to-speed calibration curve using the MarotteHSConfig Software Version 3.0 (Marine Geophysics laboratory, James Cook University; Figure S1C). Water flow velocity (mean, maximum and variation) were combined in a principal component analysis (PCA) to identify two categories

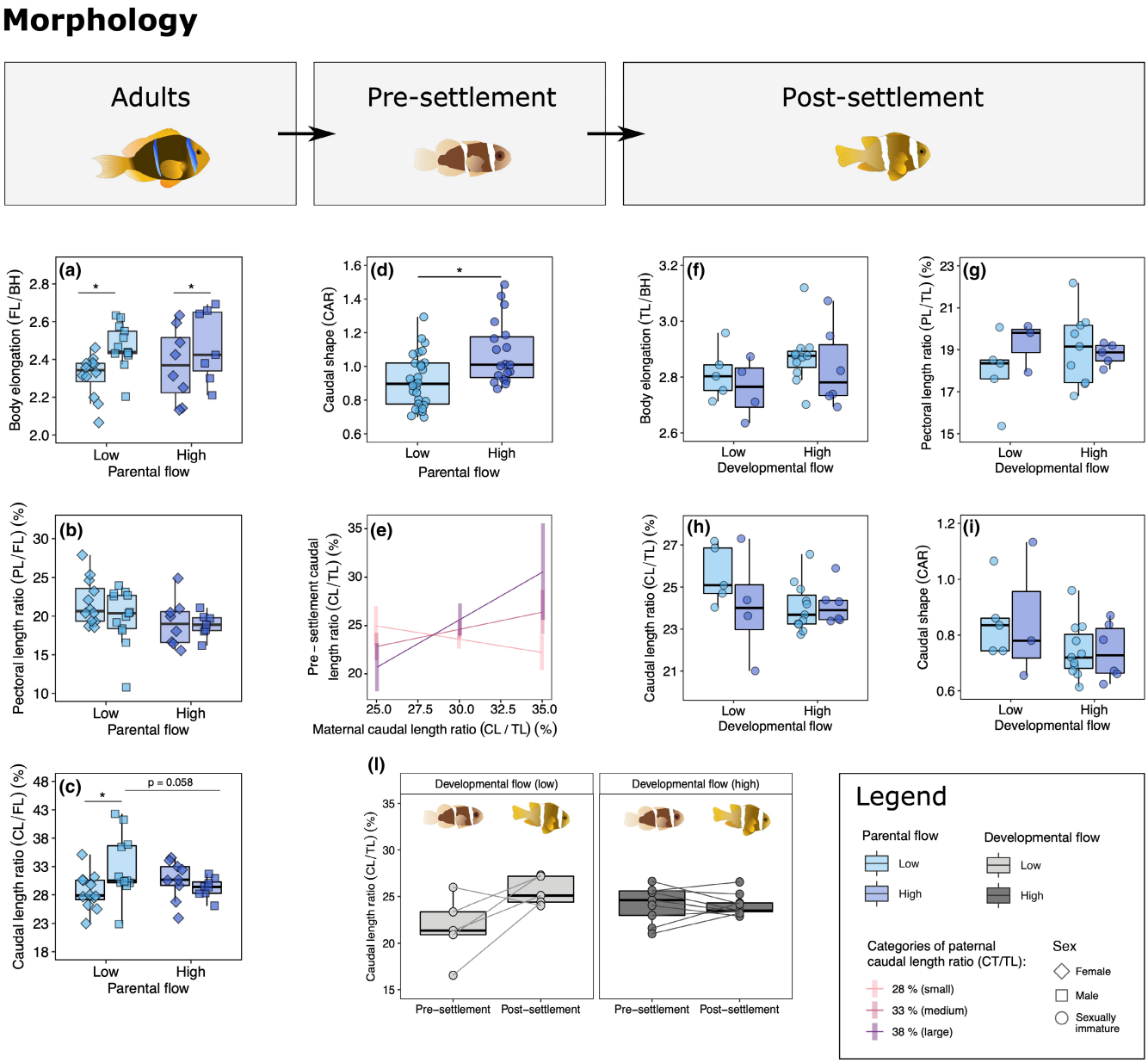

FIGURE 1 Morphological traits in adult, pre- and postsettlement fish. Body elongation (a), pectoral length ratio (b), and caudal length ratio (c) of adults (females and males) living in different water flows (low vs. high flow). Presettlement caudal length aspect ratio (CAR) of offspring produced by low- versus high-flow parents (d). Interaction of maternal and paternal caudal length ratio effect on offspring caudal length (e). Predicted lines from the model show the effect of maternal caudal length ratio for three categories of paternal caudal fin length ratio. Elongation (f), pectoral fin length ratio (g), caudal fin length ratio (h) and caudal fin shape (i) of postsettlers after 8–11 weeks in developmental water flow treatments (low vs. high flow). Caudal fin length ratio changes during development (l), from pre- to postsettlement, in low (left and light grey) and high developmental flow (right and dark grey). Symbols represent individual raw data points. In each panel, boxplots with medians, interquartile ranges (IQRs) and whiskers are shown (SI-4). Significant differences across water flow regimes or across sex are indicated with asterisks (*; refers to $p < 0.05$)

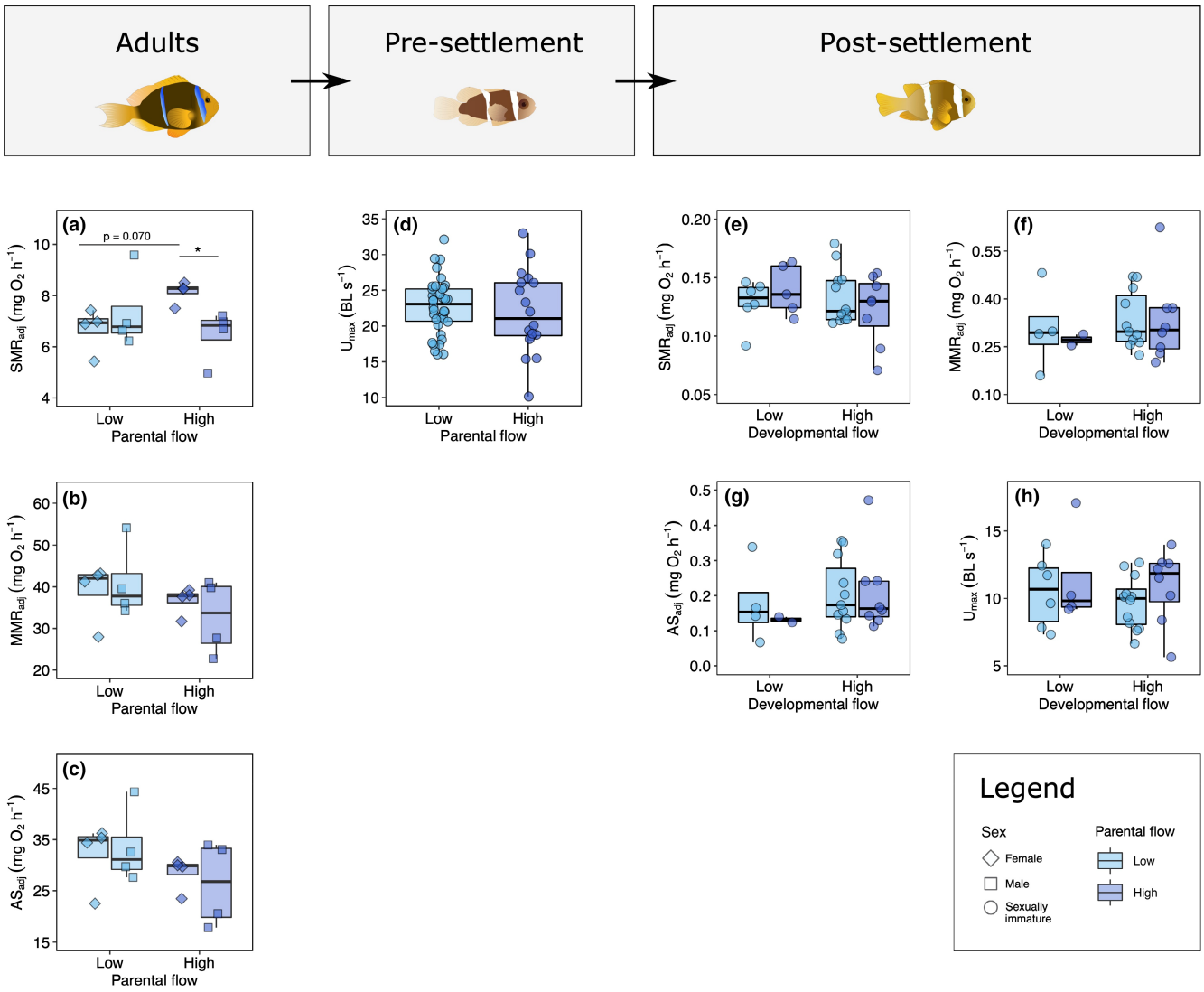

FIGURE 2 Physiological traits in adult, pre-and postsettlement fish. Standard metabolic rate (SMR, a), maximum metabolic rate (MMR, b) and aerobic scope (AS, c) of adults (females and males) living in different water flows (low vs. high flow). Presettlement swimming speed (U_{max}) of offspring produced by low- versus high-flow parents (d). Postsettlement SMR (e), MMR (f), AS (g) and U_{max} (h) after 6 weeks in developmental water flow treatments (low vs. high flow). Symbols represent individual values adjusted (using model residuals) to the overall mean body mass of measured fish (59.5 and 0.304 g in adults and juveniles respectively). Boxplots with medians, interquartile ranges (IQRs), and whiskers are shown (SI-4). Asterisks (*p < 0.05) indicate significant differences

of water flow based on their PCA scores: high and low flow (SI-1, Figure S2A–E; Table S1). Anemonefish breeding couples were monitored for over 5 years prior to this study (Beldade et al., 2017; Mills et al., 2020) and no differential parental mortality was found across flow regimes, which allowed us to disregard differential effects of parental selection on offspring phenotypic plasticity (Burgess & Marshall, 2014). Adult morphological and physiological (metabolic rate) traits were measured from 20 and 8 adult pairs (40 and 16 individuals) respectively. Second, 11 free-living pairs from the most practical sites and extreme water flows were selected and monitored until spawning, and eggs were collected from each clutch (one clutch per free-living pair). Eggs were hatched and reared until presettlement (after 18 days) under identical laboratory conditions, when performance (swimming) and morphological traits were measured on six randomly selected presettlers per clutch (n = 66). However, due to poor quality microscope photographs and a malfunction of the swim tunnel, not all performance and morphological traits could be measured (sample sizes on presettlers ranged from n = 48–58; Table S3). Using a full-sib split-brood design, the same six presettlers from each clutch were randomly assigned to six different developmental water flow sites in Moorea lagoon (two treatments; low and high flow, SI-1, Figure S3A–E; Table S4) and individually monitored. However, the six presettlers from only a subset of eight clutches were released into the developmental flow sites (n = 48) for practical reasons

(Table S3). Two presettlers died during performance measurements and could not be replaced, therefore only 46 presettlers were released in Moorea lagoon for the cross-transplant experiment. After release in the lagoon, 21 of the 46 postsettlers disappeared within a week of release. These missing fish were quickly replaced with a new, full-sib postsettler from the same clutch. However, presettler traits had not been measured on these replacement fish, nor were postsettler traits measured on the fish that disappeared. Fish disappearing after 1 week were not replaced as the remaining laboratory full siblings were too old for the purpose of the experiment (release at settlement). Therefore, a total of 46 + 21 = 67 individual fish were used for all or some part of the cross-transplant experiment. In the third part of the experiment, postsettler survival and water flow were measured at the developmental water flow sites over 60 days. Performance (swimming test), physiological (metabolic rate) and morphological traits were measured on surviving postsettlers after 6–8 weeks of developmental water flow treatment exposure (see 'Developmental water flow treatment, exposure and postsettler traits'). Natural morality accounted for the remaining reduced sample sizes of postsettler traits. Sample sizes of all traits along development are summarised in Table S3.

2.2 | Offspring traits at presettlement

The subset of 11 selected pairs (four high and seven low; SI-1, Table S2) were monitored every 2–3 days over 2 months for spawning. When egg clutches were found (Figure S1B), the day of hatching was predicted from their egg development stage (Beldade et al., 2017). On the day of hatching (6–7 days after fertilisation), approximately a fifth of the egg clutch (~200–300 eggs) was collected while SCUBA diving, brought to the laboratory and hatched overnight. All newly hatched larvae were maintained under common garden laboratory conditions minimising environmental variation during natal dispersal (SI-2). At the end of the larval (presettlement) stage, determined by the appearance of the first vertical white stripe after ~18 days posthatch (dph), performance (see 'Maximum swimming speed') and morphological (see 'Morphological measures') traits were determined for about six presettlers from each clutch (n = 48–58, sample sizes are summarised in 'Experimental overview' and Table S3). Over 3 days, the same six presettlers from the same clutch were kept in individual 5 L aquaria containing a small anemone (~5 cm diameter), to facilitate settlement for the postsettlement developmental water flow treatment.

2.3 | Developmental water flow treatment and postsettler traits

Developmental water flow sites (four high and two low, SI-1) were selected on lagoonal sandy flats (Figures S1A and S3; Table S4) in which eight plastic mesh cages, each containing a healthy anemone of approximately equal size (224 ± 83 cm^2 surface area), were placed 10 m apart. Cages were used to prevent anemone predation and once added, postsettlement anemonefish swam freely in and out of the cage mesh (3 × 3 cm squares). While the presence of cages slightly reduced the intensity and variation range in water flow velocities, average and variation in water flows were still different between water flow treatments (Table S4; Figure S4).

After 21 dph, six postsettlers from the same clutch (subset of eight clutches) were randomly added to caged anemones at each of the six developmental water flow sites (Figure S1A, n = 46 fish released, two fish were lost during measurements and therefore excluded from the analyses; Table S2). Postsettlers dying within a week of release (n = 21) were replaced with a new full-sib postsettler from the same clutch, but for which neither performance nor morphological traits had been measured at 18 dph. Total number of fish released: 46 + 21 = 67.

After 6 weeks of exposure to developmental water flow treatments, surviving postsettlers were captured and brought to the laboratory where performance and metabolic traits were measured. Postsettlers were then returned to their respective anemones and, after an additional 2–5 weeks, all surviving fish were re-caught and morphological traits were measured (i.e. after ~8–11 weeks total exposure with no difference in exposure time between the developmental flow treatments; ANOVA, all p > 0.05, Table S6; n = 22–26; Table S3).

2.4 | Maximum swimming speed (U_{max})

Fish swimming performance was measured for individual presettlers (18 dph, n = 56; Table S3) and surviving postsettlers (6 weeks exposure, n = 30; Table S3) using a constant acceleration test (Farrell, 2008) to estimate maximum swimming speed (U_{max}) following Brett, 1964 equation (SI-3). Measurements were carried out in a 170 ml Blazka-style swim tunnel (Loligo System, Viborg, Denmark) immersed in a larger aquarium kept at constant temperature (27.5 ± 1°C). The velocity of a one-way flow through the swim tunnel against which the fish swims was regulated by a voltmeter, which was calibrated for velocity in cm/s. After an acclimation period in the swim tunnel (presettlers: 10 min; postsettlers: 30 min) at a water velocity of ~0.5–1 body length s^{-1} (Plaut, 2001) water flow was gradually increased until the fish could no longer maintained its position in the flow (Killen et al., 2015).

2.5 | Metabolic rate measurements (SMR, MMR and aerobic scope)

Measurements of fish metabolic rates [standard metabolic rate (SMR) and maximum metabolic rate (MMR)], were carried out in respirometry chambers where fish oxygen uptake rate was recorded as a proxy for metabolic rate (Norin & Clark, 2016; Svendsen et al., 2016). Fish aerobic scope (AS) was calculated as the difference between MMR and SMR.

Eight of the 11 wild breeding anemonefish pairs and all surviving postsettlers after 6 weeks ($n = 31$) were caught and brought to the laboratory. Adults and postsettlers were transferred into 30 L individual tanks for 36 and ~24 h of fasting respectively. For MMR, adult fish were manually chased in a circular tub containing seawater for 2 min until exhaustion, then immediately transferred into the static intermittent-closed respirometry setup to measure oxygen consumption rate immediately postchase, which is a proxy of fish MMR (Norin & Clark, 2016). The SMR of adult fish and postsettlers was obtained by leaving the adults in or transferring the postsettlers to the respirometry chambers overnight (for ~20 and ~15 h, respectively, Table S7). The following day, the MMR of postsettlers was measured in the swim tunnel by recording fish oxygen uptake immediately after U_{max} measurements (Clark et al., 2013). After fish exhaustion, the velocity in the swim tunnel respirometer was reduced to 1 BL s^{-1} and three cycles of 10 min (6 min closed and 4 min flush) were used to estimate the maximum rate of oxygen uptake (MMR). Background microbial oxygen uptake was also recorded in an empty respirometry or swim chamber before and after SMR or U_{max} and MMR measurements respectively. Slopes of the decline in oxygen concentration over time during the closed phases of the intermittent respirometry cycles (Svendsen et al., 2016) were calculated using LabChart software (v.8.1.14; ADInstruments). Fish oxygen uptake rates were calculated by multiplying these slopes by the volume of the respirometry chamber after subtracting fish volume and background microbial respiration (additional details on metabolic rate measurements and calculations are listed in Table S7, following list from Killen et al., 2021). After all metabolic measurements, we weighed the adults (±0.1 g) and postsettlers (±0.001 g). Because the swim tunnel malfunctioned at one point, some measurements of postsettler MMR were excluded from the analyses ($n = 6$), so final $n = 25$ fish for MMR and AS, but $n = 31$ for SMR (Table S3).

2.6 | Morphological measures

After physiological measurements, adults were gently immobilised within hand nets and photographed using a Sony DSC-RX100 III camera. In addition, at 12 adult sites from which physiological measurements were not taken, adult anemonefish were captured, photographed for morphological measures and immediately released back onto their anemones. Presettlers were anesthetised (0.1 g of MS222 in 1 L of water) and, on losing equilibrium, transferred to a petri dish containing clean filtered water where lateral photographs were taken with a binocular microscope (LEICA EX4W) before regaining normal activity. Similarly to adults, postsettlers were photographed using a Sony DSC-RX100 III camera. All sample sizes are summarised in Table S3.

The following morphological traits were measured using ImageJ software (Figure S5; Table S3): body elongation, the ratio of either total length (TL; distance from head to end of tail) in pre- and postsettlers or fork length (FL; distance from head to the fork of the tail) in adults to body height (BH; distance from the pelvic fin and the start of the dorsal fin); pectoral fin length ratio, length of the pectoral fin from insertion to the longest tip of the leading edge (PL) divided by fish body length; caudal fin length ratio, the ratio of the length of the caudal fin from the end of the standard length to the longest tip (CL) and fish body length. Caudal fin shape was also measured in pre- and postsettlers as the caudal fin aspect ratio (CAR), the squared caudal fin height (CH) divided by the surface area of the caudal fin (CS).

2.7 | Specific growth rate

Specific growth rate (SGR) was determined as the percentage increase in individual body size per day between presettlers (18–29 dph; initial time, $n = 14$) and postsettlers aged ~70–96 dph (final time, $n = 14$; Hopkins, 1992) as: $SGR = \left(\ln\left(TL_{t2}\right) - \ln\left(TL_{t1}\right)\right)/n \times 100$; where TL is the body total length at t_2 (final time) and t_1 (initial time), and n is the number of days between the two consecutive measurements.

2.8 | Survival

Postsettlement survival (absence/presence) in each developmental water flow treatment was regularly monitored over the 11-week (76 days) experiment (every 1–2 days for the first week and every 4–5 days thereafter). Given the high predation risk outside anemone tentacles, especially for early life stages (Cortese et al., 2021), the chance of fish movement was highly reduced and the absence of a fish from its anemone was equated to mortality. Despite the use of cages, three anemones disappeared during the experiment, together with their anemonefish, which were excluded from the survival analyses. Nine additional fish were excluded due to nonnatural mortality (during transport or holding in the laboratory). Total sample size for survival was thus 55 (Table S3).

2.9 | Statistical analyses

All statistical analyses were carried out in R version 4.0.4 (R Core Team, 2019). To explore the effect of water flow regime on adult fish morphology and metabolism, we used LM with adult elongation, TL ratio, CL ratio and body mass-adjusted metabolic rate (MMR_{adj}, SMR_{adj} or AS_{adj}) as response variables (see SI-2 for details on body mass adjustments). Explanatory variables were fish sex, parental water flow and anemone surface area (Table S8). To find the best fit model, all covariates were initially included with interactions and subsequently removed if nonsignificant using the likelihood ratio test (LRT) in the LMTEST package (Zeileis & Hothorn, 2002). To reveal differences among groups on model results, we carried out a Tukey post-hoc test (EMMEANS package; Lenth, 2020).

We determined the effect of parental water flow on presettler phenotype using separate linear mixed-effects regression

models (LMERs) with presettler elongation, PL ratio, CL ratio, $\log_{10}$-transformed CAR or U_{max} as response variables. Parental water flow was used as an explanatory variable and parental ID as a random factor to account for nonindependence of full siblings (Table S9).

To determine the influence of parental phenotype on offspring phenotype, we fitted an LM that included presettler morphology as response variables (elongation, PL ratio, CL ratio or TL) and the same maternal and paternal morphological traits as explanatory variables. The interaction among parental traits was included to explore synergetic effects of both parents (Table S10).

To explore the effect of water flow on morphology, performance, metabolic rate and growth (SGR) postsettlement, we fitted LMERs with parental and developmental water flow as predictor variables, and parental ID and offspring sites as random effects. Response variables were elongation, PL ratio, CL ratio or CAR for morphological traits (Table S11A) and SMR_{adj}, MMR_{adj}, AS_{adj} or U_{max} for metabolic and performance traits (Table S12A). In the SGR model, the initial offspring length was also included as a covariate to account for their asymptotic growth (Table S14).

We also explored the effect of developmental water flow on each individual fish over time by fitting an LMER with developmental water flow treatment and fish stage (pre- vs. postsettlement) as explanatory variables. Response variables were elongation, PL ratio, CL ratio, CAR or U_{max}. Fish ID was also included as a random variable to account for repeated measures. Parental ID and offspring site were also included as random factors (Table S13).

The effect of parental and developmental water flow was also tested on offspring survival by fitting a mixed Cox proportional hazard model via the 'coxme' function in the COXME package (Therneau, 2020). Parental water flow and developmental water flow were used as explanatory variables, the hazard function (risk of death at time t, which refers to the end of the experiment) used as a response variable, and parental ID was used as a random effect (Table S15A).

3 | RESULTS

3.1 | Effect of water flow on adult phenotype

We observed no differences in body elongation among adults living between low and high water flow sites (LM, $flow_{high}$; $t = 0.688$, $p = 0.496$, $R^2 = 0.193$, $R^2_{adj} = 0.150$, Table S8B, Figure 1a), however, male bodies were 5.7% more elongated than females (LM, sex_{male}; $t = 2.928$, $p = 0.006$, Table S8B, Figure 1a). On the other hand, pectoral fin length ratio, despite showing a trend for a higher ratio in low flow for both sexes, did not vary across parental water flow sites nor with sex (LM—sex removed from the model according to LRT $p > 0.05$, $flow_{high}$; $t = -1.817$, $p = 0.077$, $R^2 = 0.080$, $R^2_{adj} = 0.056$, Table S8A, S8B, Figure 1b).

Water flow impacted adult caudal length ratio, but differently for each sex (LM, parental flow × sex; $t = -2.209$, $p = 0.034$, $R^2 = 0.238$, $R^2_{adj} = 0.151$, Table S8B, Figure 1c). The caudal fin to body length ratio of males at low water flow sites was 2.5% higher compared to that in males living at high flow (post-hoc test: $t = 1.957$, $p = 0.058$, Table S8C, Figure 1c), while no difference was observed in females. Within low parental water flow sites, the caudal fin length in relation to body length of females was 12.1% shorter than that in males (post-hoc test: $t = -2.585$, $p = 0.014$, Table S8C).

Fish body mass-adjusted standard metabolic rate (SMR_{adj}) was also affected by the interaction between parental water flow and sex (LM, parental flow × sex; $t = -2.254$, $p = 0.044$, $R^2 = 0.346$, $R^2_{adj} = 0.182$, Table S8B, Figure 2a). In females, there was a trend for a lower SMR_{adj} in low compared to high water flow (post-hoc test: $t = -1.988$, $p = 0.070$, Table S8C), whereas there was no difference in SMR_{adj} among sites in males (post-hoc test: $t = 1.201$, $p = 0.253$, Table S8C). Within high water flow sites, females had a 25.9% higher SMR_{adj} compared to males (post-hoc test: $t = 2.285$, $p = 0.041$, Table S8C). Neither parental water flow nor sex had any effect on fish MMR_{adj} or AS_{adj} (Table S8B, Figure 2b,c).

3.2 | Effect of parental water flow on presettler phenotype

Anemonefish breeding pairs at high water flow sites produced presettlement offspring whose caudal fin shape (CAR) was 18% greater than that of offspring from low water flow sites (LMER, $Flow_{high}$; $t = 3.389$, $p = 0.001$, $R^2_m = 0.196$, $R^2_c = 0.196$, Table S9, Figure 1d). No other presettler morphological trait or swimming capacity varied with parental water flow (LMER, $flow_{high}$; all $p > 0.005$, Table S9, Figure 2d).

3.3 | Effect of parental phenotype on presettler morphological phenotype

There was an interaction among maternal and paternal caudal length ratio on that of their offspring (LMER, $CLratio_{(maternal)} \times CLratio_{(paternal)}$; $t = 2.866$, $p = 0.007$, $R^2_m = 0.180$, $R^2_c = 0.115$, Table S10; Figure 1e). The caudal fin ratio of presettlers increased with maternal caudal fin ratio, but only if mothers were paired with fathers that also had a high caudal fin ratio. An opposite trend was observed if mothers were paired with a male that had a low caudal fin ratio (Figure 1e).

3.4 | Effects of water flow on postsettler morphology, metabolism and performance

After 8–11 weeks, with measures from up to 26 surviving postsettlers, we found neither an effect of parental nor developmental flow on any morphological trait (LMER, parental flow; all $p > 0.05$, developmental flow; all $p > 0.05$, Table S11A and S11B, Figure 1f–i). Similarly, neither parental flow nor developmental water flow

after 6 weeks had an effect on fish SMR_{adj}, MMR_{adj}, AS_{adj} or U_{max} (LMER, parental flow; all $p > 0.05$, developmental flow; all $p > 0.05$, Table S12A and S12B, Figure 2e–h).

3.5 | Offspring developmental plasticity due to water flow

Despite no difference in caudal length ratio of postsettlers between developmental flow treatments (post-hoc: $stage_{postsettlement}$: $flow_{low}$ vs. $flow_{high}$; $t = 1.098$, $p = 0.328$, Table S13C), there was variation in individual phenotype across early life stages. Regardless of parental water flow, the caudal length ratio of anemonefish developing in the low water flow treatment increased by 18.4% from the pre- to postsettlement stage (LMER: flow×stage; $t = -2.790$, $p = 0.016$, $R^2_m = 0.269$, $R^2_c = 0.396$; post-hoc: $flow_{low}$: $stage_{presettlement}$ vs. $stage_{postsettlement}$; $t = -3.397$, $p = 0.005$, Table S13B and S13C, Figure 1l), but not for fish developing in the high water flow (post-hoc: $t = 0.110$, $p = 0.914$, Table S13C, Figure 1l). Developmental flow category had no effect on any other measured morphological trait (Table S13B). However, there is some potential for type 2 errors because of to the low sample size (Table S3) due to limited number of surviving individuals that were repeatedly measured across life stages. Additionally, one outlier fish in a low water flow treatment may have been a driver of this difference between fish in high and low water flow treatments.

3.6 | Effect of water flow on postsettler growth and survival

Postsettlement fish from high-flow parents had a 10.3% lower specific growth rate (SGR) than the SGR of fish from low-flow parents (LMER, $flow_{high}$; $t = -2.392$, $p = 0.036$, $R^2_m = 0.728$, $R^2_c = 0.728$, Table S14; Figure 3a) but growth was not affected by developmental flow (LRT: $flow_D$; $p > 0.05$, Table S14A). In addition, only 32% of the offspring from high-flow parents survived over 76 days of water flow exposure compared to 71% of the offspring from low-flow parents, that is, the probability of survival was about 55% lower from high-flow parents (coxme, coef = 1.155, $z = 2.330$, $p = 0.020$, Table S15, Figure 3b) regardless of developmental water flow (LRT: $flow_P \times flow_D$; $p > 0.05$, Table S15A), which had no effect on survival (coxme: coef = 0.591, $z = 1.280$, $p = 0.200$, Table S15). Of those postsettlers that died, parental water flow treatments combined, approximately 82% of postsettlement mortality occurred within 3–4 days of release (i.e. at settlement).

4 | DISCUSSION

Our study highlights the importance of the environment and phenotypic variation on offspring phenotype and survival in a sex-changing coral reef fish, underlining the role of intergenerational environmental effects (nongenetic), genetic legacy and potential developmental phenotypic plasticity, in a system where the natal and settlement environments are often mismatched. The fitness implications of living in high and low water flow sites cascades across life stages, for example via a reduction in offspring survival after settlement, or through offspring morphological differences, which could have consequences for competition, foraging, reproduction and survival (Arendt, 1997; Sogard, 1997). Our field-based study reveals the importance of multiple mechanisms at play, including parental effects and adaptation but also the potential for phenotypic plasticity during development, allowing enough variability for species to survive, grow and persist under natural environmental conditions. Our study also raises other questions, such as morphological and physiological plasticity across male and female stages or the survival and dispersal implications of different larval fish morphotypes.

Over a period of about 8–11 weeks, offspring from high-flow parents had higher mortality and slower growth compared to those

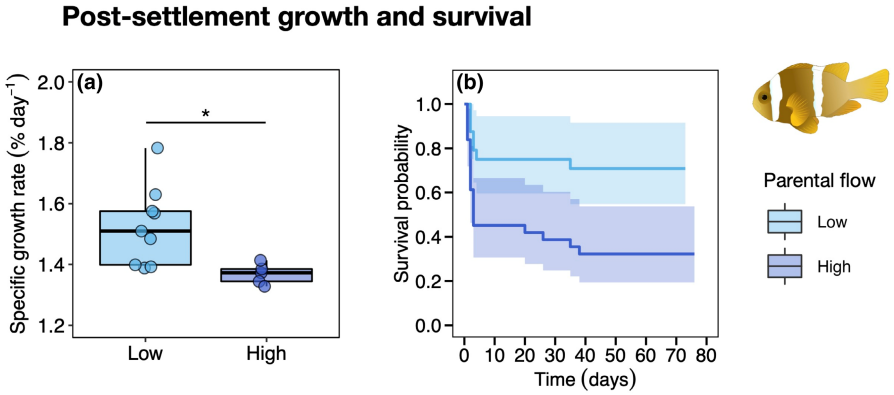

FIGURE 3 Postsettlement growth and survival. (a) specific growth rate measured from settlement (18 dph) to 8–11 weeks of flow exposure. Symbols represent individual data points adjusted to the initial body length (1.08 cm, size at settlement). The boxplot shows medians, IQRs and whiskers (SI-4). (b) Survival curve over 11 weeks (~75 days). Time 0 corresponds to the settlement stage, the time at which fish were released into the lagoon. Solid blue lines are survival probabilities curves, surrounded by 95% confidence bands. Colours refer to parental water flow sites (low vs. high flow). Asterisks (*$p < 0.05$) indicate significant differences

from low-flow parents, regardless of the flow conditions they settled into. Despite the majority of mortality occurring at settlement (~82% within 4 days after settlement), the overall mortality rate was comparable with another laboratory-reared field-based experiment on *A. chrysopterus*, which showed 50% survival on early life stages (Schligler et al., 2021). Adult fish may invest less into reproductive output to maximise their own growth and survival during unfavourable or more demanding environmental conditions (Green, 2008; Reznick et al., 2000). Anemonefish largely feed on plankton by swimming in the water column (Allen, 1972; Mariscal, 1970) and, despite the higher resource availability in high-flow environments, routine activity is likely to be more energetically demanding than in lower flow environments (Boisclair & Tang, 1993). If fish living in high-flow environments trade-off their energy budget between foraging activity and reproduction, offspring swimming performance could be impacted and explain the lower offspring growth and survival we found. While we only found a tendency for a higher standard metabolic rate in females in high-flow environments, and we did not find evidence for differences in adult maximum metabolic rates in response to water flow, there could still be differences in routine energy expenditure while swimming and performing daily activities between areas of high and low flow.

Parental environment and phenotype, as predicted, correlate with some presettlement offspring morphological traits associated with performance in high- and low-flow environments. Parents living in high-flow environments produce presettlement offspring with a higher caudal fin aspect ratio, a trait associated with steady swimming enabling fish to maintain their position in high water flow while minimising drag (Langerhans, 2008; Videler, 1993). While developmental plasticity of embryos exposed to parental flow (during egg development) may be involved in determining this trait, anemonefish eggs are often laid into rock cavities or protected by the anemone, potentially exposed to a different microflow compared to parental flow, making a direct effect of water flow on embryos unlikely and suggesting instead parental effects or genetic inheritance. While we cannot separate the effects of these two mechanisms, the genetic or epigenetic inheritance of caudal fin shape did not appear to provide any survival advantage after settlement. It is possible that having a higher caudal fin aspect ratio may be advantageous for survival at a different developmental stage, such as during the dispersal phase, to help maintain sustained swimming against water currents (Leis, 2006), suggesting context-dependent parental effects across life stages (Marshall, 2008). This result could explain why Beldade et al. (2016) found that anemonefish breeding pairs living in reef passes (gap in barrier reef created by fresh water runoff through which the dominant mechanism of water exchange with the open occurs), known to be high-flow environments, produce more self-recruits (i.e. larvae that return to their natal population) than pairs living in the lagoon or forereef. Our results also show that maternal and paternal caudal length have a synergistic effect on presettlement caudal length, suggesting that this morphological trait possesses some genetic inheritance. However, the lack of difference in presettlement caudal fin length with parental flow suggests that there may be no local adaptation to water flow for this trait. Indeed, a long caudal fin may not be particularly advantageous or disadvantageous in coping with a specific flow at the presettlement stage when larvae from different parental flow origin are dispersing in similar flow environments.

After settlement, despite some uncertainty due to the low sample size, results suggest an increase in the caudal fin length ratio through development in low-flow regimes, while no change in length was found in juvenile fish living in high flow. This suggests that, to some extent, caudal fins of anemonefish may be plastic to developmental flow, as observed in other fish species such as salmonids (Fischer-Rousseau et al., 2010). In environments with low (mean) but highly variable flow, unsteady swimming is likely to be the main mode adopted by fish, and this may elicit the higher growth of the caudal fin. Parental effects on presettlement fin shape and potentially developmental plasticity on postsettlement fin length highlight the role of parental–offspring environment mismatch in determining offspring phenotype at different stages across ontogeny. Parental effects on fin morphology seem stronger at early stages of development and weaken as offspring grow, and the effect of the developmental environment increases but in a different direction than parental environment. However, offspring were able to cope equally well in both developmental flow environments, with no differences in survival according to developmental flow. While we were only able to measure physiology and morphology on individuals that survived, the observed results suggest that anemonefish produce offspring that survive after settlement with phenotypes suited for heterogeneous environments, that is, irrespective of parental water flow, offspring had comparable survival across both developmental environments. Altogether, this suggests an absence of local adaptation based on water flow and highlights the environmental mismatch between parental and offspring environments, that is, offspring will not necessarily settle into anemones in the same water flow regime as their parents, as plasticity and the absence of any survival advantage negates any advantage of parental adaptation. This finding matches the range of flow environments in which anemones can be found (Fautin, 1992; Holbrook & Schmitt, 2005). While some tropical reef fish larvae are able to delay metamorphosis until they reach a suitable environment in which to settle (Victor, 1986), the probability of encountering anemones on reefs is relatively low (Chadwick & Arvedlund, 2005; Fautin, 1991). Therefore, the water flow environment may not be a key determinant of when settlement occurs. Settled anemonefish may have alternative ways of coping with the flow environment, including behavioural adjustments. Early postsettlement anemonefish mostly dwell among anemone tentacles (Ross, 1978), thus avoiding high-flow regimes in the same way as other coral reef fish use holes and the space among coral branches as shelter from strong currents (Fulton et al., 2001; Johansen et al., 2008). It appears that environmental factors other than water flow may be involved in determining individual morphology and physiology after settlement. However, our results may be conservative due to the use of cages that reduced the intensity of water flow, which was already lower than the intensity of water flow

measured in previous studies (12–18 cm/s in this study compared to 37–38 cm/s in Binning et al., 2014, 2015). Furthermore, the high variation in water flow at low-flow sites may buffer differences in plasticity in physiological traits among the two treatments. Plasticity may also not be visible at the whole organism scale occurring only at the cellular level, for example, in mitochondria via effects on ATP production (Chung & Schulte, 2020), or at the behavioural level, as previously mentioned, sheltering from water flow.

We detected adult anemonefish phenotypic variability across environments with water flow accentuating the differences between the sexes. These fish are a particularly interesting model to look at any sex-related morphological or physiological differences given that they are sequential protandrous hermaphrodites, that is, change from male to female depending on size and social rank (Buston, 2003; Hattori & Yanagisawa, 1991). Males had 5.7% more elongated bodies than females; at low water flow sites, the caudal fin length in relation to body length of females was 12.1% shorter than that in males; and finally, at high water flow sites, females had a 25.9% higher standard metabolic rate compared to males. The observed differences can be understood given the shifts in behaviour, dimension and spatial distribution of territory defence (Rueger et al., 2021), and potentially growth, when fish are male and female. Furthermore, males provide parental care which lasts on average 6 days (Beldade et al., 2017) during which they often chase off potential egg predators. Male behaviours entailing fast-starts, rapid turns and manoeuvres could benefit from longer caudal fins (Domenici & Blake, 1997; Videler, 1993). Females may need to stay further out in the water column to control the territory, and be exposed to higher flow regimes which would require a higher energetic demand and possibly increased standard metabolic rate (Weiner, 1992).

Overall, our study reveals the relative importance of parental and developmental environment in shaping offspring phenotypes along ontogeny and the fitness implications of living in different environments. Despite the developmental environment playing a greater role than parental environment in shaping morphology after settlement, parental environment is the main determinant of offspring survival and fitness. Indeed, a lower growth in one stage can have fitness implications beyond that stage, such as a smaller size which will decrease their reproductive potential (Barneche et al., 2018). Moreover, less offspring that survive at early stages of development will affect the number of reproductive adults with consequences on population dynamics. If offspring from a specific environment (high flow) have lower fitness (growth and survival), then selection against settlement in that specific environment should be expected. However, previous research on the same species found higher self-recruitment in high-flow environments (Beldade et al., 2016), suggesting trade-offs between parental investment into self-recruitment and postsettlement offspring fitness and survival (Livnat et al., 2005). Eventually, selection may maximise parental fitness in an environment that is energetically costly, such as high flow, at the cost of decreasing offspring fitness, a strategy observed in many animal taxa (Marshall & Uller, 2007).

AUTHOR CONTRIBUTIONS

Daphne Cortese, Amélie Crespel, Suzanne C. Mills, Tommy Norin, Shaun S. Killen and Ricardo Beldade designed the study and collected the data. Daphne Cortese and Amélie Crespel analysed the data. Daphne Cortese and Ricardo Beldade wrote the manuscript. All authors revised the manuscript.

ACKNOWLEDGEMENTS

Financial support was provided by the Agence National de la Recherche to Glenn Almany, SCM and RB (ANR-14-CE02-0005-01/Stay or Go) and to SCM (ANR-11-JSV7-012-01/Live and Let Die), and by LabEx 'CORAIL' to RB and SCM ('Where do we go now?'), by the Danish Council for Independent Research (now the 'Independent Research Fund Denmark'; DFF-4181-00297) to TN, by Natural Environment Research Council Advanced Fellowship to SSK (NE/J019100/1) and European Research Council starting grant to SSK (640004). We particularly thank Till Deuss for his invaluable knowledge in the aquarium facility. We are also thankful to Marguerite Taiarui, Isla Davidson, Jules Schligler, Nao Nakamura, Gilles Siu, Pascal Ung, Anne Haguenauer, Frederic Zuberer, Franck Lerouvreur and the CRIOBE student community for field support. We thank Peter Buston, Sinead English and David McKenzie for constructive comments on the manuscript and Paolo Domenici, Bruno Frédérich and Jacob Johansen for helpful discussions.

CONFLICT OF INTEREST

No conflict of interest declared.

DATA AVAILABILITY STATEMENT

Data and code (code used for figure and statistics) are available from Dryad Digital repository: https://doi.org/10.5061/dryad.j6q573nhp (Cortese et al., 2022).

ORCID

Daphne Cortese https://orcid.org/0000-0002-5746-3378
Amélie Crespel https://orcid.org/0000-0002-6351-9008
Suzanne C. Mills https://orcid.org/0000-0001-8948-3384
Tommy Norin https://orcid.org/0000-0003-4323-7254
Shaun S. Killen https://orcid.org/0000-0003-4949-3988
Ricardo Beldade https://orcid.org/0000-0003-1911-0122

REFERENCES

Allen, G. R. (1972). *The anemonefish: Their classification and biology*. T.F.H. Publ., Inc.

Arendt, J. D. (1997). Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, *72*(2), 149–177. https://doi.org/10.1086/419764

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*, 642–645. https://doi.org/10.1126/science.aao6868

Beldade, P., & Brakefield, P. M. (2002). The genetics and evo-devo of butterfly wing patterns. *Nature Reviews Genetics*, *3*(6), 442–452. https://doi.org/10.1038/nrg818

Beldade, R., Blandin, A., O'Donnell, R., & Mills, S. C. (2017). Cascading effects of thermally-induced anemone bleaching on associated anemonefish hormonal stress response and reproduction. *Nature Communications*, *8*(1), 1–9. https://doi.org/10.1038/s41467-017-00565-w

Beldade, R., Holbrook, S. J., Schmitt, R. J., Planes, S., & Bernardi, G. (2016). Spatial patterns of self-recruitment of a coral reef fish in relation to Island-scale retention mechanisms. *Molecular Ecology*, *25*(20), 5203–5211. https://doi.org/10.1111/mec.13823

Binning, S. A., Roche, D. G., & Fulton, C. J. (2014). Localised intraspecific variation in the swimming phenotype of a coral reef fish across different wave exposures. *Oecologia*, *174*(3), 623–630. https://doi.org/10.1007/s00442-013-2794-5

Binning, S. A., Ros, A. F. H., Nusbaumer, D., & Roche, D. G. (2015). Physiological plasticity to water flow habitat in the damselfish, *Acanthochromis polyacanthus*: Linking phenotype to performance. *PLoS ONE*, *10*(3), 1–19. https://doi.org/10.1371/journal.pone.0121983

Boisclair, D., & Tang, M. (1993). Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. *Journal of Fish Biology*, *42*(2), 169–183. https://doi.org/10.1111/j.1095-8649.1993.tb00319.x

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada*, *21*(5), 1183–1226. https://doi.org/10.1139/f64-103

Burgess, S. C., & Marshall, D. J. (2014). Adaptive parental effects: The importance of estimating environmental predictability and offspring fitness appropriately. *Oikos*, *123*(7), 769–776. https://doi.org/10.1111/oik.01235

Burgess, S. C., Treml, E. A., & Marshall, D. J. (2012). How do dispersal costs and habitat selection influence realized population connectivity? *Ecology*, *93*(6), 1378–1387. https://doi.org/10.1890/11-1656.1

Buston, P. M. (2003). Size and growth modification in clownfish. *Nature*, *424*(6945), 145–146. https://doi.org/10.1038/424145a

Chadwick, N. E., & Arvedlund, M. (2005). Abundance of giant sea anemones and patterns of association with anemonefish in the northern Red Sea. *Journal of the Marine Biological Association of the United Kingdom*, *85*(5), 1287–1292. https://doi.org/10.1017/S0025315405012440

Chung, D. J., & Schulte, P. M. (2020). Mitochondria and the thermal limits of ectotherms. *The Journal of Experimental Biology*, *223*(20), 1–14. https://doi.org/10.1242/jeb.227801

Clark, T. D., Sandblom, E., & Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. *Journal of Experimental Biology*, *216*(15), 2771–2782. https://doi.org/10.1242/jeb.084251

Cortese, D., Norin, T., Beldade, R., Crespel, A., Killen, S. S., & Mills, S. C. (2021). Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild. *Functional Ecology*, *35*(3), 663–674. https://doi.org/10.1111/1365-2435.13729

Cortese, D., Crespel, A., Mills, S., Norin, T., Killen, S., & Beldade, R. (2022). Data from: Adaptive effects of parental and developmental environments on offspring survival, growth, and phenotype. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.j6q573nhp

Domenici, P., & Blake, R. W. (1997). The kinematics and performance of fish fast-start swimming. *Journal of Experimental Biology*, *200*(8), 1165–1178.

Emms, M. A., Saenz-Agudelo, P., Giles, E. C., Gatins, R. A., Nanninga, G. B., Scott, A., Hobbs, J-P. A., Frish, A. J., Mills, S. C., Beldade, R., & Berumen, M. L. (2020). Comparative phylogeography of three host sea anemones in the Indo-Pacific. *Journal of Biogeography*, *47*(2), 487–500. https://doi.org/10.1111/jbi.13775

Farrell, A. P. (2008). Comparisons of swimming performance in rainbow trout using constant acceleration and critical swimming speed tests. *Journal of Fish Biology*, *72*(3), 693–710. https://doi.org/10.1111/j.1095-8649.2007.01759.x

Fautin, D. G. (1991). The anemonefish symbiosis: What is known and what is not. *Symbiosis*, *10*, 23–46.

Fautin, D. G. (1992). Anemonefish recruitment: The role of order and chance. *Symbiosis*, *14*, 143–160.

Fischer-Rousseau, L., Chu, K. P., & Cloutier, R. (2010). Developmental plasticity in fish exposed to a water velocity gradient: A complex response. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *314*(B), 67–85. https://doi.org/10.1002/jez.b.21311

Fulton, C. J., Bellwood, D. R., & Wainwright, P. C. (2001). The relationship between swimming ability and habitat use in wrasses (Labridae). *Marine Biology*, *139*(1), 25–33. https://doi.org/10.1007/s002270100565

Fulton, C. J., Bellwood, D. R., & Wainwright, P. C. (2005). Wave energy and swimming performance shape coral reef fish assemblages. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1565), 827–832. https://doi.org/10.1098/rspb.2004.3029

Galloway, L. F., & Etterson, J. R. (2007). Transgenerational plasticity is adaptive in the wild. *Science*, *318*(5853), 1134–1136. https://doi.org/10.1126/science.1148766

Green, B. S. (2008). Maternal effects in fish populations. *Advances in Marine Biology*, *54*(8), 1–105. https://doi.org/10.1016/S0065-2881(08)00001-1

Haguenauer, A., Zuberer, F., Siu, G., Cortese, D., Beldade, R., & Mills, S. C. (2021). Deep heat: A comparison of water temperature, anemone bleaching, anemonefish density and reproduction between shallow and mesophotic reefs. *Fishes*, *6*, 37. https://doi.org/10.3390/fishes6030037

Hattori, A., & Yanagisawa, Y. (1991). Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environmental Biology of Fishes*, *31*(2), 139–155. https://doi.org/10.1007/BF00001015

Hearn, C. J. (2011). Perspectives in coral reef hydrodynamics. *Coral Reefs*, *30*(SUPPL. 1), 1–9. https://doi.org/10.1007/s00338-011-0752-4

Holbrook, S. J., & Schmitt, R. J. (2005). Growth, reproduction and survival of a tropical sea anemone (Actiniaria): Benefits of hosting anemonefish. *Coral Reefs*, *24*(1), 67–73. https://doi.org/10.1007/s00338-004-0432-8

Hopkins, K. D. (1992). Reporting fish growth: A review of the basics. *Journal of the World Aquaculture Society*, *23*(3), 173–179. https://doi.org/10.1111/j.1749-7345.1992.tb00766.x

Johansen, J. L., Bellwood, D. R., & Fulton, C. J. (2008). Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology Progress Series*, *360*, 219–226. https://doi.org/10.3354/meps07482

Killen, S. S., Christensen, E. A. F., Cortese, D., Závorka, L., Norin, T., Cotgrove, L., Crespel, A., Munson, A., Nati, J. J. H., Papatheodoulou, M., & McKenzie, D. J. (2021). Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry. *Journal of Experimental Biology*, *224*(18), jeb242522.

Killen, S. S., Nati, J. J. H., & Suski, C. D. (2015). Vulnerability of individual fish to capture by trawling is influenced by capacity for anaerobic metabolism. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1813), 20150603. https://doi.org/10.1098/rspb.2015.0603

Langerhans, R. B. (2008). Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology*, *48*(6), 750–768. https://doi.org/10.1093/icb/icn092

Langerhans, R. B., Layman, C. A., Langerhans, A. K., & Dewitt, T. J. (2003). Habitat-associated morphological divergence in two Neotropical fish species. *Biological Journal of the Linnean Society*, *80*(4), 689–698. https://doi.org/10.1111/j.1095-8312.2003.00266.x

Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, *51*, 57–141. https://doi.org/10.1016/S0065-2881(06)51002-8

Leis, J. M., & McCormick, M. I. (2002). The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 171–199). https://doi.org/10.1643/0045-8511(2003)003[0214:]2.0.co;2

Lenhardt, X. (1991). Hydrodynamique des lagons d'atoll et d'ile haute en polynésie française. 127.

Lenth, R. (2020). *emmeans: Estimated marginal means, aka least-squares means*. R package. https://cran.r-project.org/package=emmeans

Lindholm, A. K., Hunt, J., & Brooks, R. (2006). Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. *Biology Letters*, *2*(4), 586–589. https://doi.org/10.1098/rsbl.2006.0546

Linhart, Y. B., & Grant, M. C. (1996). Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics*, *27*, 237–277. https://doi.org/10.1146/annurev.ecolsys.27.1.237

Lively, C. M. (1986). Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution*, *40*(2), 232–242. https://doi.org/10.1111/j.1558-5646.1986.tb00466.x

Livnat, A., Pacala, S. W., & Levin, S. A. (2005). The evolution of intergenerational discounting in offspring quality. *The American Naturalist*, *165*(3), 311–321. https://doi.org/10.1086/428294

Mariscal, R. N. (1970). The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. *Marine Biology*, *6*, 58–65.

Marshall, D. J. (2008). Transgenerational plasticity in the sea: Context-dependent maternal effects across the life history. *Ecology*, *89*(2), 418–427. https://doi.org/10.1890/07-0449.1

Marshall, D. J., & Uller, T. (2007). When is a maternal effect adaptive? *Oikos*, *116*(12), 1957–1963. https://doi.org/10.1111/j.2007.0030-1299.16203.x

Mills, S. C., Beldade, R., Henry, L., Laverty, D., Nedelec, S. L., Simpson, S. D., & Radford, A. N. (2020). Hormonal and behavioural effects of motorboat noise on wild coral reef fish. *Environmental Pollution*, *262*, 114250. https://doi.org/10.1016/j.envpol.2020.114250

Monismith, S. G., Genin, A., Reidenbach, M. A., Yahel, G., & Koseff, J. R. (2006). Thermally driven exchanges between a coral reef and the adjoining ocean. *Journal of Physical Oceanography*, *36*(7), 1332–1347. https://doi.org/10.1175/JPO2916.1

Mousseau, T. A., & Dingle, H. (1991). Maternal effects in insect life histories. *Annual Review of Entomology*, *36*(1), 511–534. https://doi.org/10.1146/annurev.en.36.010191.002455

Nadler, L. E., Killen, S. S., Domenici, P., & McCormick, M. I. (2018). Role of water flow regime in the swimming behaviour and escape performance of a schooling fish. *Biology Open*, *7*(10), bio031997. https://doi.org/10.1242/bio.031997

Norin, T., & Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*, *88*(1), 122–151. https://doi.org/10.1111/jfb.12796

Pakkasmaa, S., & Piironen, J. (2001). Water velocity shapes juveniles salmonids. *Evolutionary Ecology*, *14*, 721–730. https://doi.org/10.1023/A:1011691810801

Plaut, I. (2001). Critical swimming speed: Its ecophysiological relevance. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *131*(1), 41–50. https://doi.org/10.1016/S1095-6433(00)80239-1

R Core Team. (2019). *R: A language and environment for statistical computing*. R Fundation for Statistical Computing.

Reznick, D., Nunney, L., & Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution*, *15*(10), 421–425. https://doi.org/10.1016/S0169-5347(00)01941-8

Ross, R. M. (1978). Territorial behaviour and ecology of the anemonefish *Amphiprion melanopus* on Guam 1. *Zeitschrift für Tierpsychologie*, *46*(1), 71–83.

Rueger, T., Heatwole, S., & Wong, M. (2021). Cooperative and aggressive behaviours vary between ranks in anemonefish social hierarchies. *BioRxiv*.

Schligler, J., Cortese, D., Beldade, R., Swearer, S. E., & Mills, S. C. (2021). Long-term exposure to artificial light at night in the wild decreases survival and growth of a coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, *208*, 20210454.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science*, *60*(3), 1129–1157.

Svendsen, M. B. S., Bushnell, P. G., & Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system. *Journal of Fish Biology*, *88*, 26–50. https://doi.org/10.1111/jfb.12797

Therneau, T. M. (2020). *coxme: Mixed effects cox models*. R package. https://cran.r-project.org/package=coxme

Victor, B. C. (1986). Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(6), 1208–1213. https://doi.org/10.1139/f86-150

Videler, J. J. (1993). *Fish swimming*. Springer Science & Business Media.

Warner, D. A. (2014). Fitness consequences of maternal and embryonic responses to environmental variation: Using reptiles as models for studies of developmental plasticity. *Integrative and Comparative Biology*, *54*(5), 757–773. https://doi.org/10.1093/icb/icu099

Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*, *24*(1), 107–120. https://doi.org/10.1093/icb/24.1.107

Weiner, J. (1992). Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. *Trends in Ecology & Evolution*, *7*(11), 384–388. https://doi.org/10.1016/0169-5347(92)90009-Z

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News*, *2*(3), 7–10.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cortese, D., Crespel, A., Mills, S. C., Norin, T., Killen, S. S., & Beldade, R. (2022). Adaptive effects of parental and developmental environments on offspring survival, growth and phenotype. *Functional Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2435.14202