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RESEARCH ARTICLE

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Larval traits show temporally consistent constraints, but are decoupled from postsettlement juvenile growth, in an intertidal fish

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Abstract

1. Complex life cycles may evolve to dissociate distinct developmental phases in an organism's lifetime. However, genetic or environmental factors may restrict trait independence across life stages, constraining ontogenetic trajectories. Quantifying covariance across life stages and their temporal variability is fundamental in understanding life-history phenotypes and potential distributions and consequences for selection.
2. We studied developmental constraints in an intertidal fish (*Bathygobius cocosensis*: Gobiidae) with a discrete pelagic larval phase and benthic juvenile phase. We tested whether traits occurring earlier in life affected those expressed later, and whether larval traits were decoupled from postsettlement juvenile traits. Sampling distinct cohorts from three annual breeding seasons afforded tests of temporally variability in trait covariance.
3. From otoliths (fish ear stones), we measured hatch size, larval duration, pelagic growth (larval traits) and early postsettlement growth (juvenile trait) in 124 juvenile *B. cocoensis*. We used path analyses to model trait relationships with respect to their chronological expression, comparing models among seasons. We also modelled the effect of season and hatch date on each individual trait to quantify their inherent variability.
4. Our path analyses demonstrated a decoupling of larval traits on juvenile growth. Within the larval phase, longer larval durations resulted in greater pelagic growth, and larger size-at-settlement. There was also evidence that larger hatch size might reduce larval durations, but this effect was only marginally significant. Although pelagic and postsettlement growth were decoupled, pelagic growth had postsettlement consequences: individuals with high pelagic growth were among the largest fish at settlement, and remained among the largest early postsettlement. We observed no evidence that trait relationships varied among breeding seasons, but larval duration differed among breeding seasons, and was shorter for larvae hatching later within each season.
5. Overall, we demonstrate mixed support for the expectation that traits in different life stages are independent. While postsettlement growth was decoupled from

larval traits, pelagic development had consequences for the size of newly settled juveniles. Temporal consistency in trait covariances implies that genetic and/or environmental factors influencing them were stable over our three-year study. Our work highlights the importance of individual developmental experiences and temporal variability in understanding population distributions of life-history traits.

KEYWORDS

Bathygobius cocosensis, complex life cycles, early life-history traits, ontogenetic trajectory, otolith analysis, path analysis, planktonic larvae, trait covariance

1 | INTRODUCTION

Many organisms possess complex life cycles whereby the developmental path of an individual is partitioned into distinct morphological and ecological stages. Such complex life cycles may allow fitness to be maximised at each stage in development (Ebenman, 1992; Moran, 1994); life-history traits beneficial in one stage may not be beneficial in another, so metamorphosis might serve to partition the life cycle and allow stage-specific traits to evolve independently (Campero, De Block, Ollevier, & Stoks, 2008b; Johansson, Lederer, & Lind, 2010; Pechenik, Hilbish, Eyster, & Marshall, 1996; Phillips, 1998). Independence of developmental phases, therefore, compartmentalises selection in each life stage (Campero et al., 2008b). However, the underlying genetic architecture and physiological processes that govern development may be constrained and unable to fully dissociate trait variation across the life cycle (Campero, De Block, Ollevier, & Stoks, 2008a; Ebenman, 1992; Moran, 1994; Sponaugle & Grorud-Colvert, 2006). Furthermore, traits expressed at one life stage can have opposing effects on fitness in subsequent life stages (Miles & Wayne, 2009; Schluter, Price, & Rowe, 1991). For example, Crean, Monro, and Marshall (2011) identified conflicting selection with regard to larval growth rates in an ascidian. Larvae with slower growth rates had greater survival to reproduction, but these individuals attained smaller average size at reproduction (which was expected to influence fecundity) relative to those individuals that grew more rapidly as larvae. Therefore, trait distributions may exist at some intermediate range that optimises total fitness at the expense of maximising fitness in any one stage (Marshall & Morgan, 2011; Schluter et al., 1991). Hence, determining developmental constraints among traits provides insights into how selection shapes life-history phenotype distributions across the life cycle and the resulting consequences on population dynamics.

An additional layer of complexity comes from the fact that environmental variation may affect the correlations among life-history traits (Gutteling et al., 2007; Schluter et al., 1991; Sgrò & Hoffmann, 2004). For example, De Block and Stoks (2005) demonstrated this in damselflies by manipulating two larval developmental environments: the photoperiod and food availability. Not only did these environmental factors affect traits associated with metamorphosis (age and mass at emergence) but also the way these traits correlated with fitness. In particular, at a given mass, females fed more in their larval stage had greater lifetime mating success than food-deprived individuals. In other words, the relationship between mass and fitness was modulated by larval environment. Such findings hint at how environmental differences across time may impact the way life histories are correlated. Few studies, however, explicitly consider how environmental changes through time may lead to temporal variability in trait covariance in wild populations (Giménez, 2010; Pechenik et al., 1996).

Many marine organisms have complex life cycles: While adults may be largely—if not entirely—restricted to the benthos, offspring are typically pelagic at their earliest life stages. For such species, eggs or larvae disperse and develop as part of the plankton. Larvae then undergo metamorphosis to become young juveniles and return to the benthic environment to continue development in their post-settlement phase. Studies of life-history trait distributions between life stages have revealed that fitness after metamorphosis can depend on trait variation and developmental environments in the larval phase (Allen & Marshall, 2010; Marshall & Keough, 2003; Raventós & Macpherson, 2005; Shima & Swearer, 2010), which is contrary to predictions of independent fitness consequences in complex life cycles. Therefore, the demographic properties of marine populations might be strongly governed by early developmental processes (Bergenius, Meekan, Robertson, & McCormick, 2002; D'Alessandro, Sponaugle, & Cowen, 2013; Hamilton, Regetz, & Warner, 2008; Searcy & Sponaugle, 2001; Shima & Swearer, 2010; Torres et al., 2016). For example, Gagliano, McCormick, and Meekan (2007) showed that selective mortality in a damselfish—occurring weeks to months after settlement—can be traced back to variation in hatch size or pelagic growth. Marine organisms are thus excellent systems to investigate constraints and related fitness consequences in ontogenetic trajectories, but studies to date have primarily focused on comparing age-related shifts in trait distributions. A void exists for research that quantifies the inherent correlations among early life-history traits and their associated trade-offs (Marshall & Morgan, 2011; Pineda, Hare, & Sponaugle, 2007). Moreover, the difficulty in conducting manipulative experiments in organisms with planktonic larvae restricts studying fitness consequences of life-history variation to observational inferences (e.g., Bergenius et al., 2002; Caie, 2016; D'Alessandro et al., 2013) or to more manageable invertebrate species with absent or very short planktonic phases (e.g., Allen & Marshall, 2010; Crean et al., 2011; Marshall & Keough, 2004).

Our study focuses on larval and juvenile traits in the intertidal fish, Cocos frillgoby (*Bathygobius cocosensis*: Gobiidae), collected over three annual breeding seasons. As in many marine fish (McCormick, 1993; Tanaka, Kawai, Seikai, & Burke, 1996), transition from the larval to juvenile stage in *B. cocosensis* represents a time of dramatic morphological, physiological and behavioural change, accompanying occupation of a different habitat (the pelagic versus benthic environment) and niche. Larvae disperse in the open ocean for ~25 days (preliminary data) where coastal and pelagic conditions influence their development. Following metamorphosis, juveniles settle on rocky intertidal shorelines, which are highly variable environments due to daily tidal fluctuations and variability in physical factors (e.g., salinity and temperature) and biological stressors (e.g., predation mode). The distinct biotic and abiotic factors affecting larvae versus juveniles highlight the potential benefits of fully dissociated life stages. We analysed four early life-history traits measured from otoliths (fish ear stones), in the pelagic larval and benthic juvenile stages (Table 1, Fig. 1), to address two key knowledge gaps regarding trait variation in wild populations of organisms with complex life cycles.

We characterised the extent of trait covariance—and hence developmental constraints in ontogenetic trajectories—across larval and juvenile life stages in *B. cocosensis*, with the null hypothesis that traits are uncorrelated. Substantial effort has been invested into understanding how selection reshapes early life-history trait distributions postsettlement in marine organisms, but studies explicitly quantifying the magnitude of constraints across life stages

TABLE 1 Early life-history traits examined in *Bathygobius cocosensis*. The coefficient of variation (CV) for each trait was calculated for the entire sample (across seasons), with a sample size of $n = 124$. See Supporting Information Figure S2 for illustration of trait definitions

Trait	Units	Description	CV
Hatch size	μm	The distance between the otolith nucleus and the hatch check; a proxy for somatic size-at-hatching and maternal investment.	0.145
Larval duration	days	The number of days larvae spent as plankton; this was calculated as the number of daily increments from, and including, the hatch check to settlement check.	0.126
Pelagic growth	μm	The distance between the hatch check and the settlement check; the amount of growth attained during the pelagic stage.	0.114
Settlement size	μm	The distance between the nucleus and the settlement check; a proxy for somatic size-at-settlement.	0.104
Postsettlement growth	μm	The distance between the settlement check and the fourth-day-postsettlement increment; the amount of growth attained in the 4 days after settlement.	0.161
Postsettlement size	μm	The distance between the nucleus and the fourth-day-postsettlement increment; a proxy for somatic size 4 days after settlement.	0.090

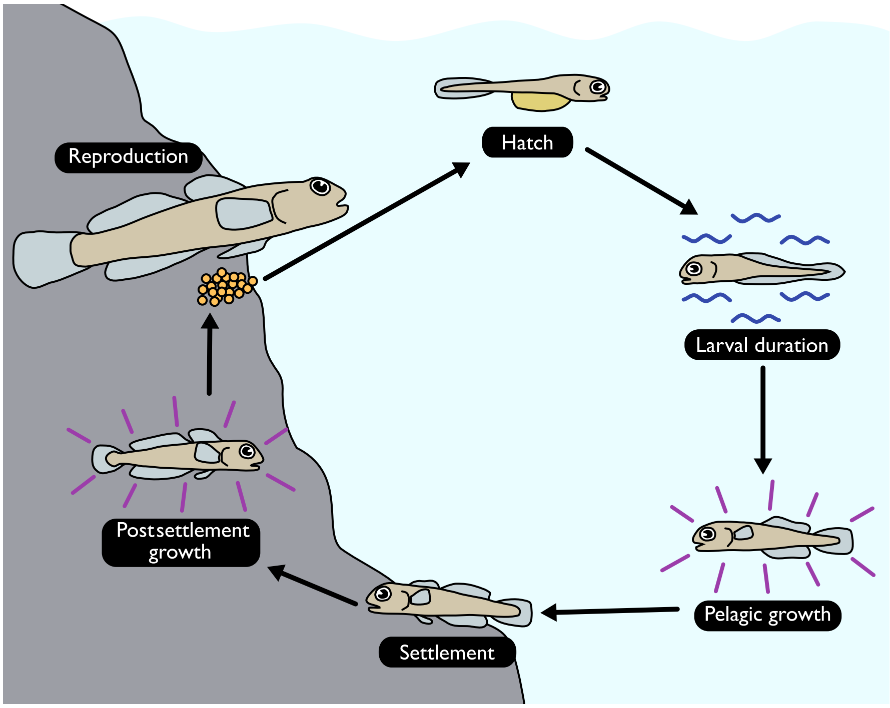

FIGURE 1 The life cycle of *Bathygobius cocosensis*. Reproduction occurs on the benthos. Larvae hatch and undergo a pelagic larval phase. After this period of pelagic development, larvae return to the benthos, where they settle and undergo a metamorphosis into young juveniles. Further growth and development occur on the benthos, the postsettlement phase, until fish reach adulthood [Colour figure can be viewed at wileyonlinelibrary.com]

are scarce (but see Pechenik et al., 1996; Giménez, 2010; Aguirre, Blows, & Marshall, 2014). Here, we explicitly quantify how much variation in later expressed traits can be explained by variation in earlier life-history traits. We determined whether patterns of trait covariance were temporally variable, testing the null hypothesis that the direction and magnitude of trait relationships across different life stages showed no differences among breeding seasons. Traits themselves may also temporally vary due to environmental differences experienced by individuals: Different hatch dates within a breeding season may coincide with fine-scale temporal environmental changes, whilst at a broader temporal scale, different seasonal cohorts may be affected by year-to-year changes in environmental conditions. We therefore tested the null hypothesis that traits were invariant across breeding seasons and were unrelated to hatch date. Assessing this temporal variability in traits and their covariance is crucial to understanding trait evolution and recruitment dynamics in organisms with complex life cycles.

2 | MATERIALS AND METHODS

2.1 | Study species and study site

Bathygobius cocosensis is a demersal intertidal fish with a wide distribution across the Indo-Pacific region. In Australia, it inhabits rocky coasts throughout tropical and temperate waters and this study focuses on a population at Hastings Point (28°21′45″S 153°34′47″E), New South Wales. Breeding occurs from November to March (personal observations). Eggs are laid and fertilised on the benthos, and larvae hatch and undergo a ~25 day pelagic phase (preliminary data) before metamorphosing into juvenile fish, settling in intertidal and shallow subtidal habitat. We collected settled juvenile fish across three breeding seasons: 28 March 2014 ($n = 26$), 17 January 2015 ($n = 48$) and 27 January 2016 ($n = 50$). Juveniles (standard length < 20 mm) were caught using hand nets. Fish were euthanised using eugenol at 100 mg/L in seawater before being preserved in 100% ethanol.

2.2 | Data collection

Early life-history traits were obtained from otoliths (fish ear stones). Development of these calcified structures is characterised by the deposition of growth increments, and analysis of the number and distance between increments affords study of various traits across a fish's ontogenetic trajectory without direct observation (Brothers, Mathews, & Lasker, 1976; Campana & Neilssra, 1985; Shima & Swearer, 2010; Sponaugle & Cowen, 1997). Otolith extraction and acquisition of otolith-derived traits were conducted by the Barcelona Otolith Reading Services, Blanes, Girona, Spain. Fish have three otolith pairs: the sagittae, lapilli and asterisci (David, Isley, & Grimes, 1994). Work by Shafer (2000) in the congener *B. coalitus* suggests that *Bathygobius* species produce reliable daily growth increments and distinct marks at settlement on their sagittae. Our own preliminary investigations indicated that the lapilli provided much clearer daily growth increments relative to the sagittae (see Supplementary Material for further details of otolith-related methods). Therefore, we conducted all analyses on traits derived from lapilli.

Data manipulation and analyses were conducted in *R* (R Core Team 2016). At first, linear regressions between all pairwise combinations of estimated age (days), standard length (mm) and maximum lapillus otolith size (μm) were conducted to verify that growth was isometric. This is necessary to ensure that measurements of otolith size are proportionally correlated with age and body size for accurate back-calculation of size-at-age and growth estimation (Shafer, 2000) and ensuring no bias in otolith readings with age. In all cases, the linear relationship between any two of these variables was highly significant with a large amount of explained variation ($R^2 > 0.85$); scatter plots also provided visual validation of a linear relationship (Supporting Information Figure S1).

We collected measurements from six early life-history traits (Table 1; Supporting Information Figure S2) that have demonstrated fitness consequences in other marine studies. Pelagic larval traits were hatch size, larval duration and pelagic growth. Hatch size was inferred as the distance from the otolith nucleus to hatch check. The hatch check can be a proxy of larval somatic size upon hatching and maternal investment (D'Alessandro et al., 2013; Gagliano et al., 2007; Shima & Swearer, 2009), which might influence predator-mediated mortality or ability to navigate the pelagic environment (Allen, 2008; Marshall & Steinberg, 2014; Paradis, Pepin, & Brown, 1996). Larval duration was defined as the number of days (daily increments) from hatching to settlement, including both the hatch check and settlement check. This represents the time individuals spend in the pelagic environment; longer larval durations might reduce fitness because of greater exposure to physical stressors (Pechenik, 1999). At last, we derived pelagic growth as the distance between the hatch and settlement check. Pelagic growth rates can be important determinants of mortality after metamorphosis in marine fish (Gagliano et al., 2007; Searcy & Sponaugle, 2001).

We also measured three traits occurring at, or after, settlement (Table 1; Supporting Information Figure S2). Settlement size was measured as the distance between the otolith nucleus and the settlement check, a proxy for somatic size-at-settlement. Size can be important in dictating predator-mediated selection on juvenile fish (Holmes & McCormick, 2006). We also defined two postsettlement phase traits, growth and size. Both growth rates and size postsettlement have been found to be important targets of selection in juvenile fish (Gagliano et al., 2007). Postsettlement growth was determined over the first 4 days postsettlement as the distance between the settlement check and the fourth otolith increment after the settlement check. Postsettlement size was defined as the distance between the nucleus and the fourth-day-postsettlement increment.

2.3 | Temporal variation in traits

We tested generally for temporal variability in traits at broad (between seasons) and fine (within seasons over different hatch dates) timescales in *B. cocosensis*. We took the age (days post-hatch) of an individual and subtracted this from the date of collection to get an estimated hatch date. These back-calculated hatch dates produced a spread of values from 16 December through to 20 February across breeding seasons (Supporting Information Figure S3A). Due to differences in the month of sampling, the distribution of hatch dates differed among seasons: Fish collected in 2013/14 generally had later hatch dates than those collected in the 2014/15 and 2015/16 seasons. The average number of days postsettlement for collected juveniles was around 23 days, with a minimum and maximum of 5 and 46 days, respectively (Supporting Information Figure S3B,C). We analysed trait variation using individual ANCOVA models, testing the effects of Season (categorical factor), Hatch date (continuous variable) and their interaction. The interaction term was nonsignificant for all traits (Table S1), indicating that any hatch date effects were consistent among seasons; models were rerun without the interaction. We represented Hatch date as a numerical vector, where 1 = 1 December and 90 = 28 February. Significance was tested using Type II Sum of Squares with the *R* package *car* (Fox et al., 2016).

2.4 | Trait covariance across life stages

We considered how earlier occurring traits affect the variation of traits later in the life cycle of *B. cocosensis* using a path analysis. Because of the way in which we defined settlement size and postsettlement size, these traits contained a measurement dependency on hatch size and on growth (Supporting Information Figure S2). Therefore, we excluded these two traits from our path analyses, considering only the four traits free of autocorrelation. We subsequently considered the consequences for settlement and postsettlement sizes of variation in the other traits by (a) determining the correlation between pelagic growth and postsettlement size and (b) determining the relationship between size and life stage.

The *R* package *plspm* (Sanchez, Trinchera, & Russolillo, 2013) was used for path analyses. Path analyses describe the directed dependence among a set of variables, such that the total effect (β_{TOT}) of one variable on another is the sum of their direct (β_{DIR}) and indirect (β_{IND}) effects (Lleras, 2005). Each trait was allowed to directly affect any trait that occurred after it in the life cycle (Hatch size → Larval duration → Pelagic growth → Postsettlement growth; Figure 1). Each trait was given its own "block" (latent factor), coded as a "reflective" variable and standardised (mean = 0, variance = 1) using the *scaled* argument in *plspm*. We constructed four different models: the three seasons (2013/14, 2014/15 and 2015/16) each modelled separately and the full dataset (seasons pooled). The *boot.val* argument in *plspm* was used to generate 95% confidence intervals (the 2.5% and 97.5% percentiles) for 1,000 bootstrap replicates for trait effects in each model.

To test the null hypothesis that traits nonsignificantly covaried within a model, we evaluated whether the bootstrap confidence interval around mean direct (β_{DIR}) and total (β_{TOT}) trait effects overlapped with zero. Furthermore, we tested the null hypothesis that patterns of covariance did not show temporal variation; that is, that there is no difference in the bootstrap mean of β_{DIR} or β_{TOT} between pairs of seasons. To do this, we implemented Welch's *t* test (Welch, 1947, 1951) between pairs of years for each pathway. Welch's *t* test was deemed appropriate for our analysis because the variances differed among seasons (Ruxton, 2006). See the supplementary information for more details on the calculation and significance testing of Welch's *t*.

3 | RESULTS

3.1 | Temporal variation in traits

ANCOVA for each of our measured traits found little evidence for temporal variation, either within or among breeding seasons, in early life-history traits (Table 2). Only Larval duration exhibited temporal variation, with a significant effect of Season ($F_{2,120} = 7.156$, $p = 0.001$) and a negative effect of Hatch date (standardised $\beta = -0.094$, $F_{1,120} = 17.831$, $p < 0.001$). On average, larvae spent longer in the pelagic in the 2013/2014 breeding season, and, across all three breeding seasons, larvae born later in the season had shorter larval durations.

3.2 | Trait covariance across life stages

The path analyses provided no evidence that covariance patterns varied among breeding seasons, with no significant differences in direct (β_{DIR}) or total (β_{TOT}) trait effects among seasons (Figure 2; Supporting Information Tables S2 and S3); therefore, we focus on reporting results for the pooled dataset. Overall, the path analysis revealed little effect of earlier traits on later traits (Figures 2 and 3). Only the direct relationship of Larval duration on Pelagic growth ($\beta_{DIR} = 0.669$) was significant (Figure 2). Consistent with this, Pelagic growth was also the only trait for which substantial variation was predicted by the path analysis ($R^2 = 0.445$; Table 3). Variation in Larval duration was poorly predicted by Hatch size ($R^2 = 0.020$; Table 3); however, in two seasons (2014/15 and 2015/16) and in the pooled dataset, the bootstrap 95% CI only just overlapped zero and beta coefficients were

TABLE 2 ANCOVA table for early life-history trait variation in juvenile *Bathygobius cocosensis* as a function of breeding season (Season: broad-scale temporal variation) and hatch dates (Hatch date: fine-scale temporal variation). Significant *p*-values ($\alpha = 0.05$) are indicated with an asterisk

	Season *df* = 2, 120		Hatch date *df* = 1, 120	
Trait	*F*	*p*	*F*	*p*
Hatch size	0.119	0.889	0.713	0.401
Larval duration	7.156	0.001*	17.831	<0.001*
Pelagic growth	2.035	0.135	3.038	0.084
Postsettlement growth	2.826	0.063	0.477	0.491
Settlement size	1.998	0.140	2.724	0.101
Postsettlement size	0.470	0.626	2.912	0.090

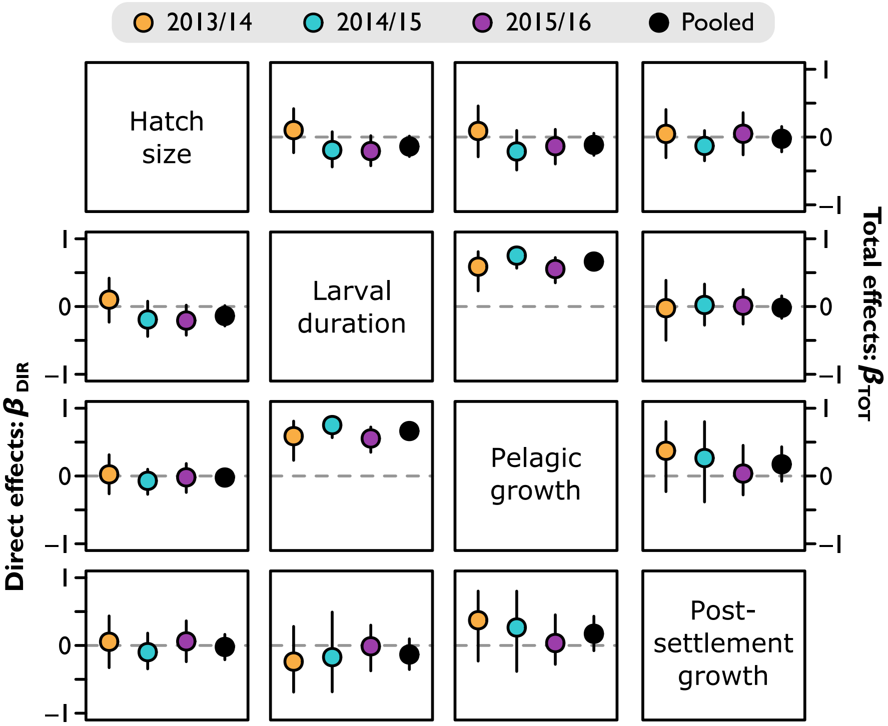

FIGURE 2 Estimates of standardised direct effects (β_{DIR}: below the diagonal) and total effects (β_{TOT}: above the diagonal) quantifying the effect of an earlier expressed trait on a later expressed trait in *Bathygobius cocosensis*, as estimated from path models in different breeding seasons (see key): 2013/14 (n = 26); 2014/15 (n = 48); 2015/16 (n = 50); and pooled (n = 124). Traits are arranged in chronological order from left to right and the plot should be interpreted as earlier expressed traits affecting later expressed traits. Error bars are bootstrap 95% confidence intervals. Dashed lines indicate an effect size of zero [Colour figure can be viewed at wileyonlinelibrary.com]

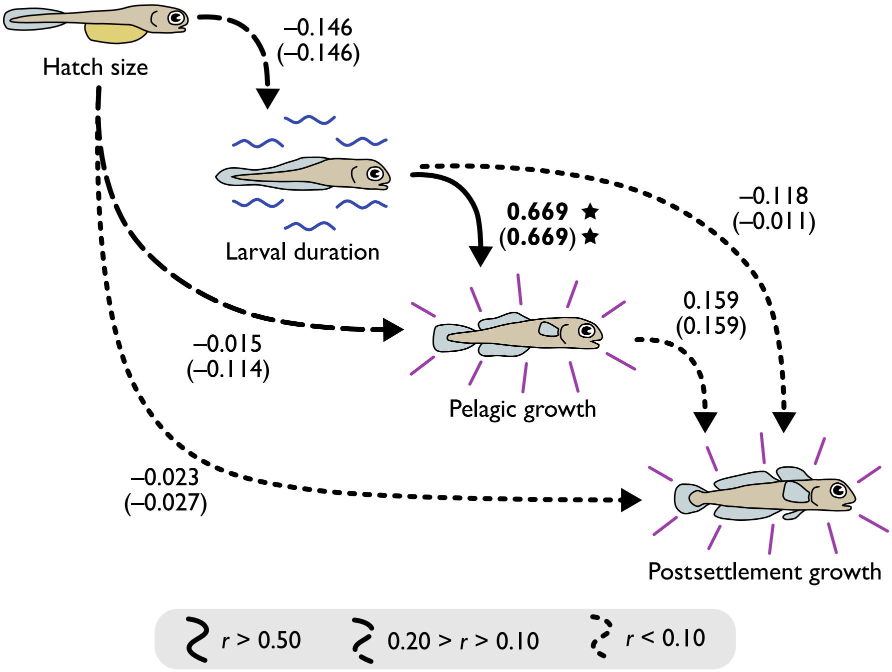

FIGURE 3 Relationships among early life-history traits in *Bathygobius cocosensis*, as determined from path analyses, in our pooled dataset (all breeding seasons, n = 124). Traits are arranged in chronological order from left to right. Arrows indicate direction of effect, and the line type (dotted, dashed or solid) for each arrow represents the strength of correlation (r, see legend) between the two traits. Numbers are the bootstrap mean standardised effect sizes reported as “direct effect (total effect)”, that is, β_{DIR} (β_{TOT}), where the TOTAL EFFECT = DIRECT EFFECT + INDIRECT EFFECT. Bold values marked with a “★” are statistically significant (where the bootstrap 95% confidence interval does not contain zero) [Colour figure can be viewed at wileyonlinelibrary.com]

moderately strong, suggesting that larger hatch sizes might reduce larval duration (Figure 2). Variation in POSTSETTLEMENT GROWTH was also poorly explained by pelagic phase traits (R^2 = 0.016) (Table 3).

We further considered the consequences of the observed variation in our pelagic traits on size-at-settlement and size-postsettlement, both traits known to have fitness consequences in fish. Consistent with the inference from the path analysis, there was no evidence that variation in HATCH SIZE contributed any significant variation later in life (r = 0.005 and −0.007 for SETTLEMENT SIZE and POSTSETTLEMENT SIZE, respectively). Variation in SETTLEMENT SIZE was entirely driven by PELAGIC GROWTH, which the path analysis indicated was strongly predicted by LARVAL DURATION. That is, irrespective of size-at-hatch, the larger fish at settlement were those that grew the most (and spent the most time) in the plankton. A moderate amount of variation in POSTSETTLEMENT SIZE was explained by POSTSETTLEMENT GROWTH (R^2 = 0.272) (Figure 4a), which the path analysis indicated was independent of PELAGIC GROWTH

TABLE 3 Predictability of early life-history trait variation in juvenile *Bathygobius cocosensis* based on variation in preceding traits. The total explained variation (R^2-values, range from 0–1) in a trait based on path analyses (combination of indirect and direct effects) is presented for each breeding season and the pooled dataset

Trait	2013/14	2014/15	2015/16	Pooled
Larval duration	0.008	0.036	0.046	0.020
Pelagic growth	0.358	0.600	0.322	0.445
Postsettlement growth	0.100	0.051	0.004	0.016

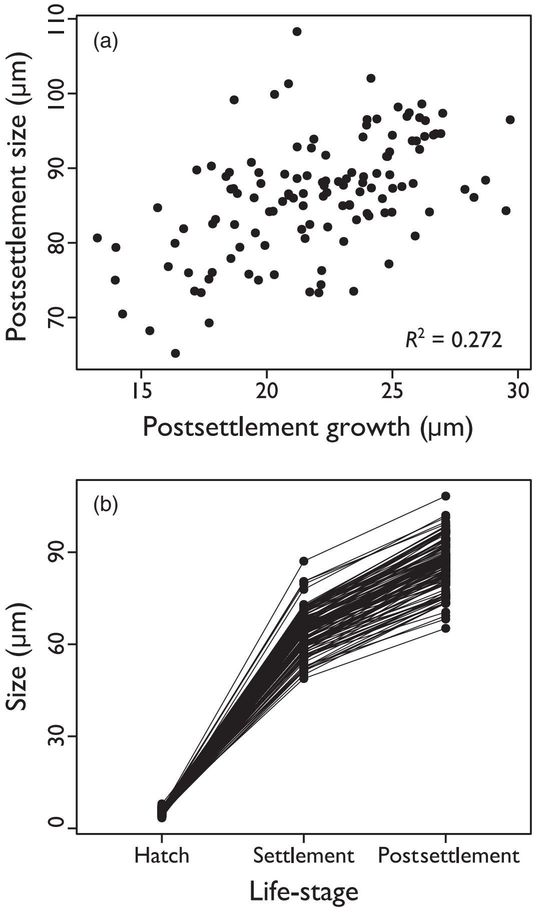

FIGURE 4 Size and growth of *Bathygobius cocosensis* juveniles pooled across seasons (n = 124). (a) The correlation between postsettlement growth with postsettlement size and the associated R^2. (b) The lapilli otolith size for each individual plotted against life stage based on the distance from the nucleus to a specific increment: "Hatch" = the hatch check; "Settlement" = the settlement check; and "Postsettlement" = the fourth increment after the settlement check (see Supporting Information Figure S2)

(Figures 2 and 3). However, individuals with larger size-at-settlement were still among the largest early postsettlement (Figure 4b), indicating that postsettlement growth does not overwrite size differences generated by pelagic growth variation.

4 | DISCUSSION

The partitioning of complex life cycles into discrete stages creates the potential for selection to maximise fitness in different developmental phases (Aguirre et al., 2014; Pechenik et al., 1996; Phillips, 1998). Inherent physiological and genetic constraints may, however, limit the degree to which traits important within each life stage are truly independent (Ebenman, 1992; Moran, 1994). For the intertidal fish, *Bathygobius cocosensis* (Cocos frillgoby), our path analyses evidenced significant trait covariance among larval traits, but independence of postsettlement juvenile growth. However, we note that, despite the ability for individuals to decouple postsettlement growth from pelagic phase variation, there appears to be little evidence of compensatory growth to attenuate size differences among individuals in the first few days following settlement. Therefore, individuals that settle small remain small. Trait relationships did not differ significantly across breading seasons, suggesting that the underlying environmental and genetic processes governing ontogenetic trajectories in our study population were temporally stable. In addition, there was little evidence that traits themselves exhibited temporal variation. We consider the potential causes and consequences of our observed ontogenetic patterns, their variation and their impact on demography and trait evolution.

4.1 | Larval traits covary consistently across seasons and are dissociated from postsettlement growth

Our path analyses demonstrated a clear disconnect between trait variation in the pelagic larval phase and postsettlement growth in *B. cocosensis*. We note, however, that we have only been able to observe phenotypic patterns of surviving settlers and are unable to discern whether these covariance patterns are representative of the full distribution of ontogenetic trajectories possible in this species.

The only significant relationship observed among traits was the effect of the larval duration on pelagic growth, which are both pelagic phase traits, indicating that individuals with longer planktonic development attain a greater amount of absolute growth (Figures 2 and 3) and settle larger (Figure 4b). Whether larger size-at-settlement is selectively beneficial would require further testing as the direction and magnitude of size-selective mortality in marine organisms are ecologically dependent and variable with ontogeny (Caie, 2016; D'Alessandro et al., 2013; Holmes & McCormick, 2006; Johnson & Hixon, 2010). The effect of hatch size on larval duration of *B. cocosensis* was not statistically significant, but confidence intervals only just included zero in two of the three breeding seasons (2014/15 and 2015/16) and the pooled dataset (Figures 2 and 3), and a study with greater power (sample size) might have inferred a significant dependency. The moderate negative effect of hatch size on larval duration (Figures 2 and 3; Table 3) suggests individuals hatching larger might spend less time in the plankton.

Despite there being potential growth benefits of a longer larval duration in *B. cocosensis*, the planktonic environment can be perilous for small larvae (Gaines & Roughgarden, 1987; Paradis et al., 1996); therefore, reducing the larval duration might have fitness benefits (Pechenik, 1999; Pepin & Myers, 1991). Other marine studies have reported the importance of hatch size on postsettlement mortality (D'Alessandro et al., 2013; Gagliano et al., 2007; Raventós & Macpherson, 2005), suggesting potential carry-over effects of maternal investment. However, in this study, path analyses revealed no effect of hatch size on postsettlement growth (Figures 2 and 3); size-at-settlement and size-4-days-postsettlement were also uncorrelated with hatch size, despite their measurements containing hatch size variation (Supporting Information Figure S2), indicating that variable growth mitigates later size consequences of maternal investment.

Although 27% of the variation in postsettlement size was explained by postsettlement growth (Figure 4a), *B. cocosensis* juveniles that settled large were generally among the largest fish early after settlement (Figure 4b). That is, growth within the first 4 days postsettlement did not overwrite pelagic developmental variation. A similar effect of decoupled growth rates, but persistent size effects, has been observed in other studies. For instance, work by Johansson et al. (2010) on the frog *Rana temporaria* demonstrated that though metamorphosis facilitates decoupling of performance measures between life stages, size as a trait *per se* carried over from tadpoles to froglets, which affected froglet performance traits due to their dependence on body size.

While compensatory growth has been observed in marine fish postsettlement (Gagliano & McCormick, 2007), our results suggest that smaller individuals were unable to elevate their growth early postsettlement to attenuate their larval developmental history. An important point of consideration is that the time interval over which we measured postsettlement growth and size was only 4 days (relative to the 16–31 days range of larval duration over which pelagic growth occurred). However, mortality can be considerable early postsettlement (Allen & Marshall, 2010; Holmes & McCormick, 2006), and hence, the ability to rapidly compensate for poor larval growth may be important if there is strong size-dependent postsettlement selection. Nonetheless, there can be costs associated with compensation mechanisms (Campero et al., 2008a), and conflicting selection across multiple paths to fitness (Crean et al., 2011; Marshall & Morgan, 2011) may govern their presence or absence.

4.2 | Birthdays are important for larval duration

Larval duration was the only trait that exhibited temporal variation in *B. cocosensis*, which differed among our sampling seasons (least squares mean larval duration in 2013/14 was three and two days longer than in 2014/15 and 2015/16, respectively), and later hatching individuals spent less time in the plankton. This temporal variability of larval duration is consistent with other studies in marine fishes that demonstrate within- and between-season variation in this trait (Kingsford, Smith, & Flood, 2011; Radtke, Kinzie, & Shafer, 2001). The lack of an interaction between season and hatch date (Table S1) suggests that hatch dates had similar effects on larval duration in all seasons. We expect that warming waters and greater food availability from early to late summer may promote more rapid development and earlier metamorphosis. Otherwise, fish with later hatch dates may need to reduce their larval durations in order to time their metamorphosis before the end of the settlement season. Indeed, empirical evidence suggests that hatch dates in fish can be under selection (Einum & Fleming, 2000; Wright & Gibb, 2005) and larval traits may be under pressure to coincide metamorphosis with particular environmental events that favour settlement success (Robertson, Green, & Victor, 1988; Robertson, Swearer, Kaufmann, & Brothers, 1999).

4.3 | Perspectives and future directions

Understanding how early developmental and environmental experiences shape life-history trait variation, and influence population dynamics, has been the focus of a large number of studies, particularly in marine systems (Allen & Marshall, 2010; Hamilton et al., 2008; Pechenik, 2006; Shima, Noonburg, & Swearer, 2015; Shima & Swearer, 2009; Sponaugle & Grorud-Colvert, 2006; Sponaugle, Grorud-Colvert, & Pinkard, 2006; Torres et al., 2016). Such studies have been concerned with changes in population trait means over life stages and less well studied is the extent to which traits expressed at different life stages share variation (covary), the fitness consequences of covariance across stages and processes that modulate these relationships (Aguirre et al., 2014; Crean et al., 2011; Marshall & Morgan, 2011).

Our results provide mixed support for the theoretical expectation that complex life cycles compartmentalise trait variation (Ebenman, 1992; Moran, 1994). Although no pelagic phase traits exerted constraints on postsettlement growth in *B. cocossensis*, fish that were relatively large (small) at settlement tended to still be relatively large (small) shortly after settlement. Therefore, while growth itself appears dissociated across early life stages, growth in the pelagic phase constrains size in the postsettlement phase. Understanding the fitness consequences of this constraint will require assessment of how selection acts on size (Caie, 2016; Johnson & Hixon, 2010) in settled *B. cocosensis* juveniles.

The general lack of temporal variability exhibited by *B. cocosensis* in individual traits and their covariance patterns suggests a marked amount of stability in the mechanisms that influence these life-history traits. Although few studies have considered trait covariances across life stages, these studies have demonstrated the contrary pattern, where uncharacterised natural variation and known (experimentally manipulated) environmental variation both generated different relationships among early life-history traits (Giménez, 2010; Pechenik et al., 1996). Life-history trait means have been shown to respond to environmental differences across time and space at small (weeks to months, or kilometres) to large (years, or 100s kilometres) scales (Caie, 2016; Di Franco & Guidetti, 2011; Di Franco et al., 2012; Searcy & Sponaugle, 2001; Sponaugle & Cowen, 1997; Sponaugle & Grorud-Colvert, 2006). In addition, spatiotemporal variability in the sources of recruits in different cohorts (Gerlach, Atema, Kingsford, Black, & Miller-Sims, 2007; Kingsford et al., 2011;

Shima & Swearer, 2016) might impact the underlying genetic variation represented in each cohort. The mechanistic causes and long-term consequences of the temporal stability that we have observed require further investigation; we are currently characterising temporal patterns of genetic variation in *B. cocosensis* to determine the potential contribution of recruit source variability.

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AUTHORS' CONTRIBUTIONS

J.A.T., C.R., L.L. and K.M. were involved in the conceptualisation and design of this experiment; W.F.F. provided support for sampling and critical insights; J.A.T. carried out the analyses and wrote the original draft of this manuscript; all authors contributed towards revisions and approved the final draft for publication.

DATA ACCESSIBILITY

Data are accessible via figshare, https://doi.org/10.6084/m9.figshare.6105827 (Thia, Riginos, Liggins, Figueira, & McGuigan, 2018).

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