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Growth strategies across life-history stages and generational turnover of cryptobenthic coral reef fishes of the genus *Trimma*

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Abstract

Somatic growth influences survival and reproduction, with flow-on effects on population dynamics and energy fluxes within ecosystems. Small-bodied cryptobenthic reef fishes may contribute significantly to productivity due to their life-history traits, including growth rates and rapid generational turnover. However, comprehensive studies on growth that encompass all stages of life are rare. This study aimed to investigate growth patterns across life-history stages and generational turnover rates in three *Trimma* species that are abundant on coral reefs in the Pacific: *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi*. The *Trimma* species examined exhibited small body sizes of <25 mm and short life spans of <140 days, potentially enabling them to produce over three generations annually. Three growth models were compared (Modified Fry model, Body Proportional Hypothesis, and the Biological Intercept model) to back-calculate growth at ages prior to capture, and the Body Proportional Hypothesis performed the best in each species, indicated by the lowest residual sum of squares and mean squared error of the model. Each species displayed similar growth patterns, with growth rates varying across different life-history stages. Growth was most rapid during the pelagic larval phase, averaging 0.2 mm per day. The size at settlement was small, ranging from 7.6 to 8.4 mm. Growth was initially rapid post-settlement but gradually slowed, averaging 0.16 to 0.17 mm per day during the juvenile stage. In the adult phase, growth was non-asymptotic, averaging approximately 0.15 mm per day, with 31.3%–37.0% of total growth occurring during this stage. Growth decreased by 8.6%–11.7% following maturation, which is minor compared to the patterns observed in larger fish species. These findings support the expanding literature, suggesting cryptobenthic reef fishes exhibit unique life-history traits that could be associated with their small maximum body size.

KEYWORDS
coral reefs, CRFs, growth, growth models, small body size biodiversity

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1 | INTRODUCTION

There is a wide diversity of growth strategies in the animal kingdom that have important implications for a species' life history, behaviour and ecology (Peters, 1983). Somatic growth is the increase in body size or weight over time and is a critical trait that influences individual survival and reproduction, which has important implications for population dynamics and energy fluxes in the ecosystem (Anderson, 1988; Barneche et al., 2018; Brown et al., 1993; Savage et al., 2004). Divergent growth strategies are associated with fundamental trade-offs in life-history evolution. Rapid growth is often associated with early maturation, high reproductive effort, short life span and small body size, whereas slow growers may spread their breeding over long lives and reach large body sizes (Calder, 1984; Roff, 1992; Stearns, 1992). Many animals grow to their maximum body size early in life (determinate growth), whereas others, such as many fishes, continue to grow throughout their lives (indeterminate growth) (Lincoln et al., 1982; Sebens, 1987). Growth rates may also differ within a species, as they adopt distinct growth strategies across various life-history stages (Borgstein et al., 2020; Roff, 1992; Stamps et al., 1998; Stearns, 1992). Determining when and why animals grow fast, slow or not at all is critical to understanding their overall life history, population dynamics, turnover and roles within ecosystems.

Coral reef fishes have complex life histories that involve a short pelagic larval duration (PLD), an immature juvenile stage and a reproductive adult stage (Jones et al., 2002; Jones & McCormick, 2002; Leis & McCormick, 2002; Sale, 2002). Growth of fishes is likely to change as they transition between life-history stages, and is generally fastest in the larval stage, slower in the juvenile stage and decelerates or ceases altogether in the adult phase (Anderson, 1988). Rapid larval growth is usually selected for, as larvae with accelerated growth and development have an increased chance of survival and successful recruitment (Depczynski & Bellwood, 2006; Goatley & Bellwood, 2016). Growth in the juvenile phase generally slows following settlement onto the reef due to protective habitats, larger body size and decreased naivety to predators (Beeken et al., 2021; Depczynski & Bellwood, 2006; Leis & McCormick, 2002; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). Finally, most adult fishes experience asymptotic growth, where energy previously allocated to somatic growth is utilised in reproduction (Roff, 1992; Stamps et al., 1998; Stearns, 1992). However, although this may apply to some fishes, there is evidence that growth may persist linearly beyond maturity in some species (Beeken et al., 2021; Depczynski & Bellwood, 2006; Winterbottom et al., 2011; Winterbottom & Southcott, 2008).

Knowing the timing of life-history stages specific to different species is a crucial prerequisite to understanding growth changes that occur throughout these stages. Sagittal otoliths are calcified structures found within the brain cavity of fishes. These structures offer valuable insights into the timing of different life-history phases (Choat & Robertson, 2002; Goldsworthy et al., 2022; Wilson & McCormick, 1999). Sagittal otoliths accumulate increments either annually or daily in older and younger fish, respectively, and can therefore be used to determine fish age and life span (Choat & Robertson, 2002). Additionally, otoliths contain a settlement mark that defines the age boundary between the larval and juvenile stages. This mark is characterised by a decrease in otolith increment width and/or optical contrast after settlement (Goldsworthy et al., 2022; Wilson & McCormick, 1999). The age at maturation can be determined by fitting a logistic regression to the proportion of immature individuals versus mature females, which establishes the boundary between the juvenile and adult stages (Goldsworthy et al., 2022; Hernaman & Munday, 2005b; Lowe et al., 2021). The maximum age, determined by the fish with the greatest number of rings in each species, provides insights into the duration *of* the adult phase (Goldsworthy et al., 2022; Winterbottom & Southcott, 2008). A holistic overview of growth can be attained by modelling growth during these phases.

Examining the relationship between fish age and length at capture is the most utilised technique to model growth (Choat & Robertson, 2002; Green et al., 2009; Ogle, 2016). Yet, it can be difficult to collect specimens in the early life-history stages, and research is therefore mainly restricted to establishing post-settlement (Gwinn et al., 2010; Vigliola & Meekan, 2009). Alternatively, the early life-history growth of fishes can be reconstructed at ages prior to capture using historical evidence held in the otoliths. This is achieved by the application of back-calculation models to otolith increment width measurements to determine lengths at previous ages (Francis, 1990; Vigliola & Meekan, 2009). These models assume a relationship between otolith growth and somatic growth (OSG); therefore, it is essential to assess this relationship beforehand (Vigliola & Meekan, 2009). Several back-calculation methods have been reviewed by Vigliola and Meekan (2009), who determined that the Modified Fry (MF) back-calculation model was generally the most appropriate. However, other studies have shown that the optimal model varies depending on the species examined (Smedstad & Holm, 1996; Starrs et al., 2013; Vigliola et al., 2000; Wilson et al., 2009). As poorly fitting models can lead to incorrect interpretations of growth, it is important to validate these methods whenever possible, either experimentally (e.g., Roemer & Oliveira, 2007) or by comparing back-calculated datasets to ages and lengths at capture (e.g., Starrs et al., 2013). This is especially essential for fishes that may not conform to the general trends in growth seen across different life-history stages.

The cryptobenthic reef fishes (CRFs) are among the smallest and shortest-lived vertebrates on the planet, many with maximum adult body length of <50 mm and maximum life span of <150 days (Depczynski & Bellwood, 2003). Although these fishes exhibit the same three life-history stages of most coral reef fishes, CRFs have distinct traits, which may be associated with small body size, that are atypical to their larger counterparts. These traits include extreme mortality, reduced longevity, a long PLD relative to life span, early maturation, a short reproductive life and fast generational turnover rates (Depczynski & Bellwood, 2006; Hernaman & Munday, 2005a, 2005b; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). Additionally, many CRFs have unique growth patterns during certain life-history stages. Like larger fishes, CRFs tend to have rapid larval growth, then growth slows in the juvenile stage (Beeken et al., 2021). What distinguishes CRFs is their capacity to sustain continued growth throughout adulthood, in contrast to the majority of other fishes, where growth generally slows substantially after reaching reproductive maturity (Depczynski & Bellwood, 2006; Hernaman &

Munday, 2005a, 2005b; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). However, current literature of growth strategies in CRFs is mainly limited to post-settlement growth, with few studies encompassing growth across all life-history stages, including larval, juvenile and adult growth (but see Beeken et al., 2021). These strategies have clear implications for the high turnover of CRF populations and their functional roles as productive sources of nutrition for other reef organisms (Ackerman & Bellwood, 2000; Beeken et al., 2021; Brandl et al., 2018; Brandl et al., 2019; Depczynski et al., 2007; Depczynski & Bellwood, 2006; Galland et al., 2017; Winterbottom et al., 2011).

The aim of this study was to analyse growth during the larval, juvenile and adult life-history stages in three cryptobenthic goby species of the genus *Trimma* in Kimbe Bay, Papua New Guinea. *Trimma* is a speciose genus of Indo-Pacific CRFs, currently containing 113 species (Winterbottom, 2019; Winterbottom et al., 2024). *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi* are among the benthic group of *Trimma* species that perch on hard substrata and are highly abundant on coral reefs in Kimbe Bay (Goldsworthy et al., 2022; Winterbottom, 2019; Winterbottom et al., 2011). No studies have been conducted to evaluate the growth of CRFs in this biodiversity hotspot. Body size and age distributions were examined in all three species, predicting rapid growth, short life span and fast generational turnover. Three different otolith back-calculation methods were also assessed, with the expectation that the MF model would most appropriately describe ontogenetic changes in growth trajectories of *Trimma*. As is common in most coral reef fishes, we hypothesised that growth would be (1) most rapid in the larval stage; (2) remain rapid immediately following settlement due to the naivety and small size at settlement, then decrease throughout the juvenile stage; and (3) continuous during adulthood, as seen in some other CRFs.

2 | METHODS

2.1 | Study site, specimen collection and sample processing

The specimens used in this study were taken from the same samples analysed by Goldsworthy et al. (2022). Sampling was conducted during November and December 2019 at reefs in Kimbe Bay, Papua New Guinea (5.1667° S, 150.5000° E). A total of 129 *T. benjamini*, 102 *T. capostriatum* and 122 *T. yanoi* specimens were collected at random on SCUBA using a fine hand-net and 5:1 ethanol:clove oil anaesthetic solution. Fish were humanely euthanized by immersion in a 50% water, 50% ice slurry shortly after surfacing. Specimens were blotted dry, and then measured to 0.5 mm standard length (L_S). The head of each fish was sectioned from the body. Heads were preserved in 70% ethanol, and bodies were fixed in a formaldehyde 4%, acetic acid 5%, calcium chloride 1.3% (FAACC) solution for 3 days, and then transferred to 70% ethanol (Goldsworthy et al., 2022). The care and use of experimental animals complied with Papua New Guinea animal welfare laws, guidelines and policies, as approved by Mr. Thomas Koi (village elder and representative of the Local Marine Management Committee, Kilu) and Mrs. Cecilie Benjamin (Chair of the Board, Mahonia Na Dari Research and Conservation Centre, Kilu). All research endeavours were carried out in accordance with the James Cook University Animal Ethics Guidelines (approval numbers: A2665 and A2872) under a research visa allocated to Professor Geoffrey Jones and Nisha Goldsworthy issued by the government of Papua New Guinea.

2.2 | Otolith processing and determination of age and increment measurements

Otoliths were removed from the brain cavity, cleaned and fixed to glass slides using Crystalbond 509 thermoplastic glue with the convex side facing downwards. The surface of each otolith was polished using lapping film and water on a glass plate until a thin section was achieved (Figure 1a). Otoliths were coated in immersion oil, viewed on a BX43 Olympus microscope and photographed at 200× and 400× magnification using an Olympus EP50 digital camera. ImageJ software (Schneider et al., 2012) was used to count growth increments from the otolith primordium to edge (Figure 1b). Two counts of each otolith were undertaken, and the mean of these two counts was used. A third count was conducted if the two initial counts differed by >10% of the mean. The mean of the closest two counts was then used, provided that all three counts were within 10% of the mean. This value corresponded to the age of the fish in days, as growth increments were assumed to be deposited daily, as observed in other CRFs (e.g., Depczynski & Bellwood, 2005; Depczynski & Bellwood, 2006; Hernaman et al., 2000; Hernaman & Munday, 2005a; Longenecker & Langston, 2005; Winterbottom et al., 2011). Each count was conducted by a single observer on different occasions, and the observer was blinded to species and fish lengths to eliminate any biases.

The widths of otolith increments were measured using ImageJ software (Schneider et al., 2012) in a straight trajectory at 90° from the longest axis, as this was the trajectory with the greatest microstructure clarity in all otoliths (Figure 1c). Unmeasurable otoliths were omitted from the analysis. Otolith radius was taken as the total of all increment widths in each otolith.

2.3 | Establishing age at life-history milestones and generational turnover

Goldsworthy et al. (2022) established the life-history stages of *T. benjamini*, *T. capostriatum* and *T. yanoi*. Herein, the PLD (mean ± 95% confidence interval) was 32.9 ± 0.4 days in *T. benjamini*; 37.7 ± 0.4 days in *T. capostriatum*; and 36.1 ± 0.3 days in *T. yanoi*. We build on this study by validating the age at settlement using otolith growth increments. The average width of each growth increment was plotted against the age in days, with the expectation that these increments would decrease after the settlement mark, as a result of the transition from the pelagic larval stage to benthic life (Wilson & McCormick, 1999). The age at maturity (AM) for *T. benjamini*, *T. capostriatum* and *T. yanoi* was 74.1 ± 3.1,

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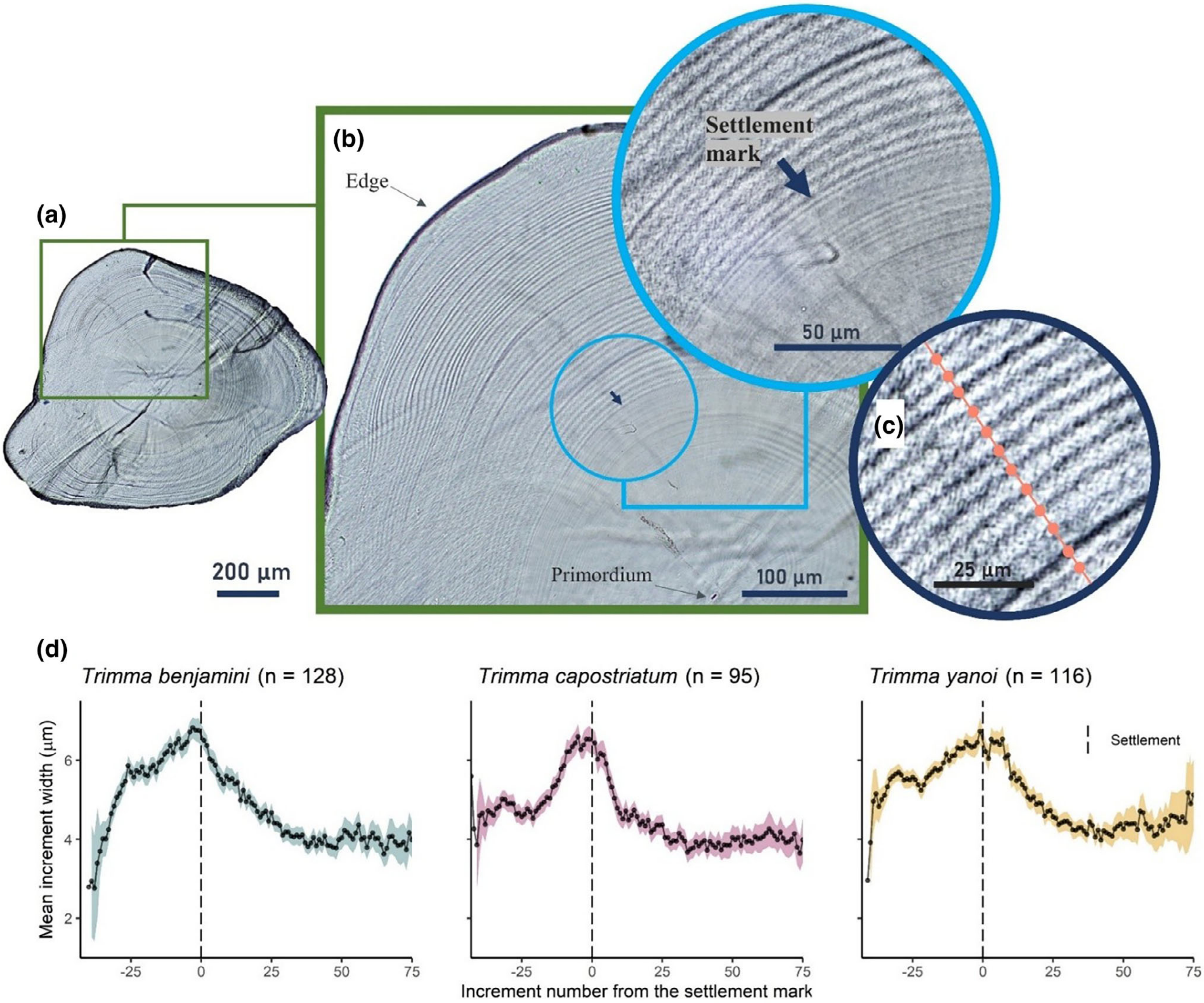

FIGURE 1 (a) Photograph of a whole processed *Trimma yanoi* otolith. (b) Enlarged image showing daily growth increments from the otolith primordium to edge. The settlement region is circled and enlarged. Arrow points to the settlement mark. Note that not all rings are visible at these magnifications. (c) Widths of growth increments measured in a straight line at 90 degrees from the longest axis. (d) Mean increment width (± 95% confidence intervals) at each increment number from the settlement mark (i.e., settlement = 0 indicated by the dashed line).

82.1 ± 3.4 and 81.7 ± 3.4 days, respectively (Goldsworthy et al., 2022). Maximum age (T_{max}) was defined as the age of the individual with the greatest number of growth rings for each species (Winterbottom et al., 2011).

Generational turnover was calculated from AM and T_{max} for each species using the following formula (Table S1.1):

$$\mathrm{GT} = \mathrm{AM} + \left(\frac{T_{\mathrm{max}} - \mathrm{AM}}{2}\right)$$

This equation estimated the number of days required for a new generation to be produced (Depczynski & Bellwood, 2006). The potential number of generations produced annually was calculated by dividing 365 by the generational turnover.

2.4 | Assessing the otolith-somatic growth relationship

To examine the nature of the OSG relationship, two different models were fit to the radius at length data for each species in R (R Core Team, 2021). A generalised linear model (Table S1.2) was used to determine if a linear relationship existed, and a second-degree polynomial model (Table S1.3) was used to establish if curvature existed. Akaike information criterion (AIC, Table S1.4) was used to determine the model of best fit. A difference in AIC scores of >2 units indicated variation in model fit, and a lower AIC score indicated a better fitting model. If the differences between AIC scores were <2 units, the most conservative model was used.

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2.5 | Back-calculation of lengths at previous ages

Three back-calculation methods were then applied to the otolith increment data to estimate fish L_s at previous ages: the experimental version of the MF model (Table S1.5) (Vigliola et al., 2000), the Biological Intercept model (BI model, Table S1.6) (Campana, 1990) and the Body Proportional Hypothesis model (BPH model, Table S1.7) (Francis, 1990). These three models were chosen as they were recommended by Vigliola and Meekan (2009) in a comprehensive review of back-calculation methods in fishes. Back-calculation methodology was used to determine growth as it produces more reliable estimates of growth than using otolith radius alone. Back-calculations were performed in R using the backCalc()function in the RFishBC package (Ogle, 2019; R Core Team, 2021). Uncertainty from the otolith counts was not propagated through back-calculation models. Measurement error was low, with variability <10% of the mean counts, which falls within the acceptable range established in similar growth modelling studies, and therefore influence on growth estimates would be minimal (Hernaman & Munday, 2005a; Vigliola & Meekan, 2009; Winterbottom et al., 2011; Winterbottom & Southcott, 2008).

2.6 | Population growth curves

Following back-calculations, polynomial mixed effect models of degrees 1–10 (Table S1.3) were fitted to back-calculated L_s for each species and back-calculation method to create population growth curves. Polynomial models were chosen over the traditional von Bertalanffy model as they are suitable for fishes where growth shows linearity (Ogle et al., 2017). In each polynomial model, growth ($L_s \sim$ age) was incorporated as a fixed factor to estimate population-level effects, and individual fish were included as a random factor, with variable intercept and slope parameters to estimate variability among individuals. This method also accounts for the longitudinal and autocorrelated nature of datasets generated from back-calculations, which originate from multiple observations per otolith (Ogle et al., 2017; Vigliola & Meekan, 2009). K-fold cross-validation (with $K = 10$ folds) was used to calculate the average mean squared error (MSE) for each polynomial model to identify the degree of polynomial that demonstrated both conservatism and a satisfactory fit. A lower cross-validated MSE indicated a superior model fit, where a difference exceeding 0.01 was deemed significant (Berrar, 2018). Using the optimum polynomial model, mean back-calculated L_s and 95% confidence intervals were made for the entire age range of each species using the emmeans package in R (Lenth, 2021). This was conducted for each species and back-calculation model, resulting in a population growth curve that transitioned through larval, juvenile and adult life-history phases for the MF, BI and BPH models.

2.7 | Back-calculation model selection

To determine which of the MF, BI or BPH methods best described growth in each species, population growth curves were compared to the observed L_s at capture. This could not be undertaken for larval growth because no individuals were captured, measured and aged in the larval phase; however, we assumed that models that adequately described post-settlement growth also described larval growth well. Residuals were calculated as $\text{back}-\text{calculated}\,L_S - L_S\,\text{at capture}$ and were plotted with fish age to examine the fit of each back-calculation method over the range of observed ages. A locally weighted regression smoother was added using the ggplot2 package to assist with uncovering patterns in the residuals. Residuals were squared and summed (RSS) and averaged to return the MSE, where lower RSS and MSE values provided further evidence of a better fitting population growth curve.

2.8 | Growth throughout larval, juvenile and adult life-history stages

Body size at settlement and maturity for each species was estimated from age at settlement and maturity using the optimum population growth model equation. For each species, the proportion of growth that occurred in each phase relative to the total growth was determined by:

$$\text{Larval phase}: \frac{L_s\,\text{at settlement}}{\text{Maximum}\,L_s}$$

$$\text{Juvenile phase}: \frac{L_s\,\text{at maturity} - L_s\,\text{at settlement}}{\text{Maximum}\,L_s}$$

$$\text{Adult phase}: \frac{\text{Maximum}\,L_s - L_s\,\text{at maturity}}{\text{Maximum}\,L_s}$$

where maximum L_s was defined as the maximum L_s on the growth curve.

Growth rate (G_i, mm/day) was determined by differentiating the optimum population growth model selected (Table S1.8) and applying the derived equation across the entire range of ages for each species (Vigliola et al., 2000). Differences in the mean daily growth rate among life-history stages were subsequently analysed using a generalised linear model (Table S1.2), and significance of these differences was assessed by pair-wise comparisons.

3 | RESULTS

3.1 | Body size, age and generational turnover

Each species attained a small adult body size. L_s of specimens ranged from 9.5 to 24 mm (mean ± 95% confidence interval $= 17.2 \pm 1.1$ mm) in *T. benjamini*, 10.5–24.5 mm (17.6 ± 1.2 mm) in *T. capostriatum* and 9–22 mm (15.6 ± 1.3 mm) in *T. yanoi* (Figure 2). As predicted, these fishes exhibited short life spans and fast generational turnover. Age ranged from 43 to 130 days (87.8 ± 6.9 days) in

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T. benjamini, 52.5–137.5 days (99.5 ± 7.6 days) in *T. capostriatum* and 37.5–126.5 (82.7 ± 8.7 days) in *T. yanoi* (Figure 2). Generational turnover ranged from 102 to 110 days (Table 1), indicating that each species could potentially produce 3.3–3.6 generations every year (Table 1).

3.2 | Validating age at settlement using increment widths

Increment widths and otolith radii were measured for 128 *T. benjamini*, 95 *T. capostriatum* and 116 *T. yanoi* individuals, and the settlement mark was determined in each (Figure 1b). As expected, increment widths increased leading up to settlement, reached a peak near settlement and then decreased significantly after settlement as individuals transitioned from pelagic to benthic life (Figure 1d).

3.3 | Assessing the otolith-somatic growth relationship

There was a positive OSG relationship in all species examined. This relationship was best described by a second-degree polynomial model in *T. benjamini*, generalised linear model in *T. capostriatum* and a

TABLE 1 Estimated generational turnover (days) and number of generations per year for *Trimma benjamini* ($n = 129$), *Trimma capostriatum* ($n = 102$) and *Trimma yanoi* ($n = 122$).

	Mean ± 95% confidence interval	
	Generational turnover (days)	**Generations per year**
T. benjamini	102 ± 1.5	3.58 ± 0.1
T. capostriatum	109.8 ± 1.7	3.32 ± 0.1
T. yanoi	104.1 ± 1.7	3.51 ± 0.1

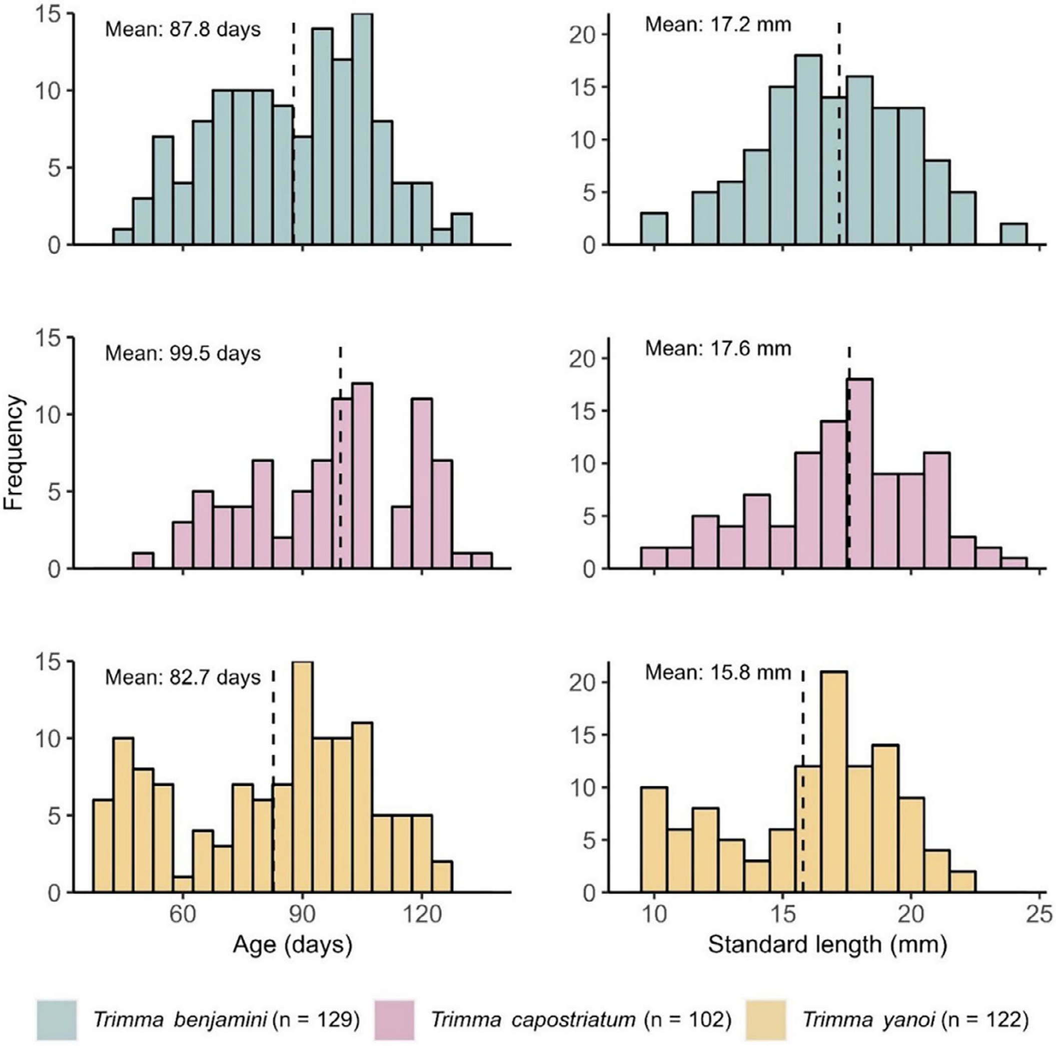

FIGURE 2 Age (days) and standard length (mm) frequency distributions in *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi*. Dashed line represents the mean.

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second-degree polynomial model in *T. yanoi* (Figure 3; Table S2). Nonetheless, curvature in the OSG relationship of *T. benjamini* and *T. yanoi* was weak, and a generalised linear model still provided a good fit (Table S2). A largely linear OSG relationship confirmed the use of the experimental version of the MF model and linear versions of the BI and BPH models.

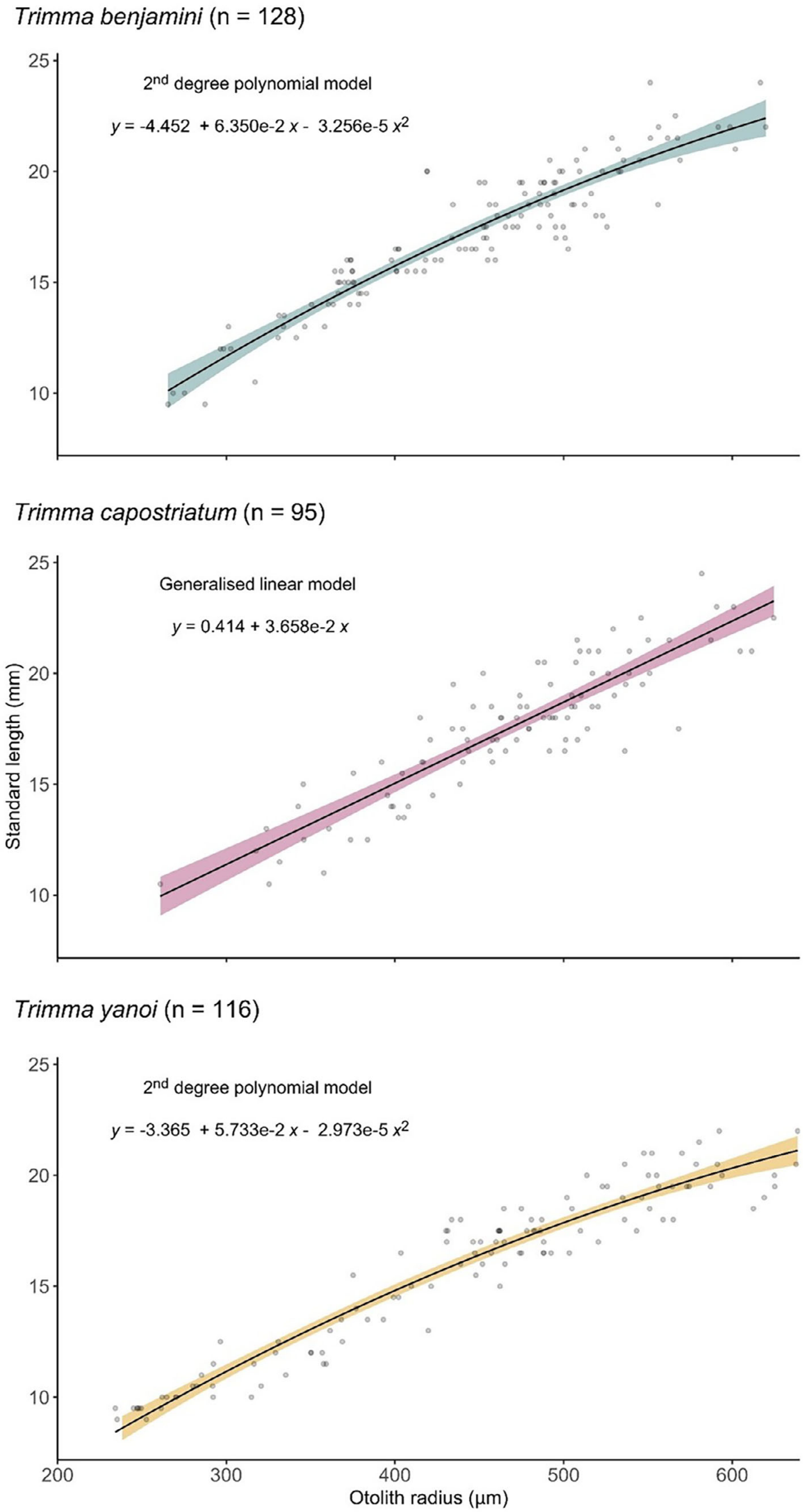

FIGURE 3 Relationship between otolith radius and somatic growth (OSG). The best-fitting models for each species are displayed: a second-degree polynomial in *Trimma benjamini* and *Trimma yanoi* and a generalised linear model in *Trimma capostriatum*.

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3.4 | Back-calculation of lengths at previous ages

Back-calculations were successfully applied to 128 *T. benjamini*, 95 *T. capostriatum* and 116 *T. yanoi* using the MF, BI and BPH models (Tables S1.5–S1.7), resulting in a total of 11,125 (*T. benjamini*), 9384 (*T. capostriatum*) and 9449 (*T. yanoi*) back-calculated *Ls* for each model. Each individual fish in the sample exhibited a unique growth trajectory that spanned its entire age range (Figures 4a, S1a, S2a).

3.5 | Population growth curves

For each species, a third-degree polynomial model was identified as optimal for back-calculated datasets generated by the MF model (Figures S1 and S3; Table S3). For back-calculated datasets generated by the BI model, polynomial models of the fourth degree were selected for each species (Figures S2 and S3; Table S3). Fourth-degree polynomial models were also selected for each species for back-calculated datasets generated by the BPH model (Figures 4 and S3; Table S3).

3.6 | Back-calculation model selection

The BPH model provided the most accurate trajectory of growth in all species (Figure 4; Table S4). Back-calculated L_s generated by the BPH model and analysed by polynomial mixed effect models of the fourth degree followed closely to the L_s of captured individuals, visualised by minimal patterning in the residuals versus age plots (Figure 4b). In addition, the BPH model had slightly lower RSS and MSR values than the BI model, and significantly lower values than MF model in all species examined (Table S4), providing additional evidence that the BPH model produced the best representation of growth. The MF model severely overestimated L_s at the lower end of the post-settlement age spectrum, and underestimated L_s in the older ages, demonstrated by a diagonal distribution of residuals (Figure S1; Table S4). The BI model provided the next best fit after the BPH model, showing comparable results but slightly greater deviations from ages and lengths at capture (Figure S2; Table S4).

3.7 | Growth throughout larval, juvenile and adult life-history stages

The larval phase accounted 31.3%–38% of total growth (Table 2). As hypothesised, out of all the life-history phases, growth curves were the steepest in the larval phase (Figure 4), where growth was 0.207 mm/day on average in each species (Figure 5; Table S5).

L_s at settlement was 8.3 ± 0.2 mm in *T. benjamini*, 7.6 ± 0.2 mm in *T. capostriatum* and 8.4 ± 0.2 mm in *T. yanoi* on average (Figure 4). We found that 29.8%–31.8% of growth occurred in the juvenile phase (Table 2). In all species, juvenile growth was high immediately after settlement and gradually decreased as the juvenile stage progressed (Figure 4). Growth in the juvenile stage was 0.171, 0.160 and 0.162 mm/day on average in *T. benjamini*, *T. capostriatum* and *T. yanoi*, respectively (Figure 5a). The growth rate of juvenile *T. benjamini* was 0.036 mm/day slower compared to larval growth, representing a 17.4% decrease. For *T. capostriatum*, juvenile growth rates were 0.047 mm/day slower than larval growth, corresponding to a 22.8% decrease. *T. yanoi* also showed a decrease in growth during the juvenile stage, with growth rates being 0.045 mm/day or 21.7% slower compared to larval growth (Figure 5b; Table S5).

Body size at maturity was 15.3 ± 0.4 mm in *T. benjamini*, 15.0 ± 0.4 mm in *T. capostriatum* and 15. ± 0.4 mm in *T. yanoi* (Figure 4). The adult phase accounted for 31.3%–37.0% of growth (Table 2), and growth rates were 0.151, 0.146 and 0.148 mm/day in *T. benjamini*, *T. capostriatum* and *T. yanoi*, respectively (Figure 5a). Growth was approximately linear throughout the adult life-history phase and did not reach a plateau (Figure 4). In contrast to juvenile growth, the adult growth decreased by an average of 11.7% (0.020 mm/day) in *T. benjamini*, 8.8% (0.014 mm/day) in *T. capostriatum* and 8.6% (0.014 mm/day) in *T. yanoi* (Figure 5b; Table S5).

4 | DISCUSSION

These findings contribute to a growing body of evidence that suggests CRFs, such as *Trimma*, exhibit extreme life-history traits that are unique from their larger counterparts. The *Trimma* species examined were characterised by distinct traits that could be related to their small body size of <25 mm, including reduced longevity of <140 days and the ability to produce over three generations annually. Each species exhibited similar growth patterns, where growth varied across different life-history stages. As expected, the highest growth rates were observed during the pelagic larval phase. Size at settlement was small at 7.6–8.4 mm, and growth slowed gradually following settlement. Adult growth was non-asymptotic, with 31.3%–37.0% of total growth occurring in this phase, and minor reductions (≤12%) in growth occurring after maturation relative to patterns seen in larger fishes. Here, we discuss the significance of such life-history traits and the flow-on implications for CRF survival and energy fluxes on coral reefs.

Larval growth in the *Trimma* species examined was the fastest out of all life-history stages, which is commonly observed among coral reef fishes (Leis & McCormick, 2002). Rapid larval growth may reduce the high mortality rates experienced in this stage (Anderson, 1988). Larval fish face mortality rates of over 99% due to factors such as predation and starvation, which can be attributed partially to body size (Leis & McCormick, 2002; Shima et al., 2021). Smaller larvae face increased vulnerability due to a higher number of predators capable of consuming them (Wilson & Meekan, 2002). In addition, smaller larvae have reduced prey availability and lower feeding success as a result of their small body and oral gape size (Pepin, 2023). Therefore, faster increases in larval body size can lead to greater survivorship and decreased mortality, which consequently may result in improved recruitment onto the reef (Bergenius et al., 2002; Leis & McCormick, 2002; Wilson & Meekan, 2002). Successful recruitment

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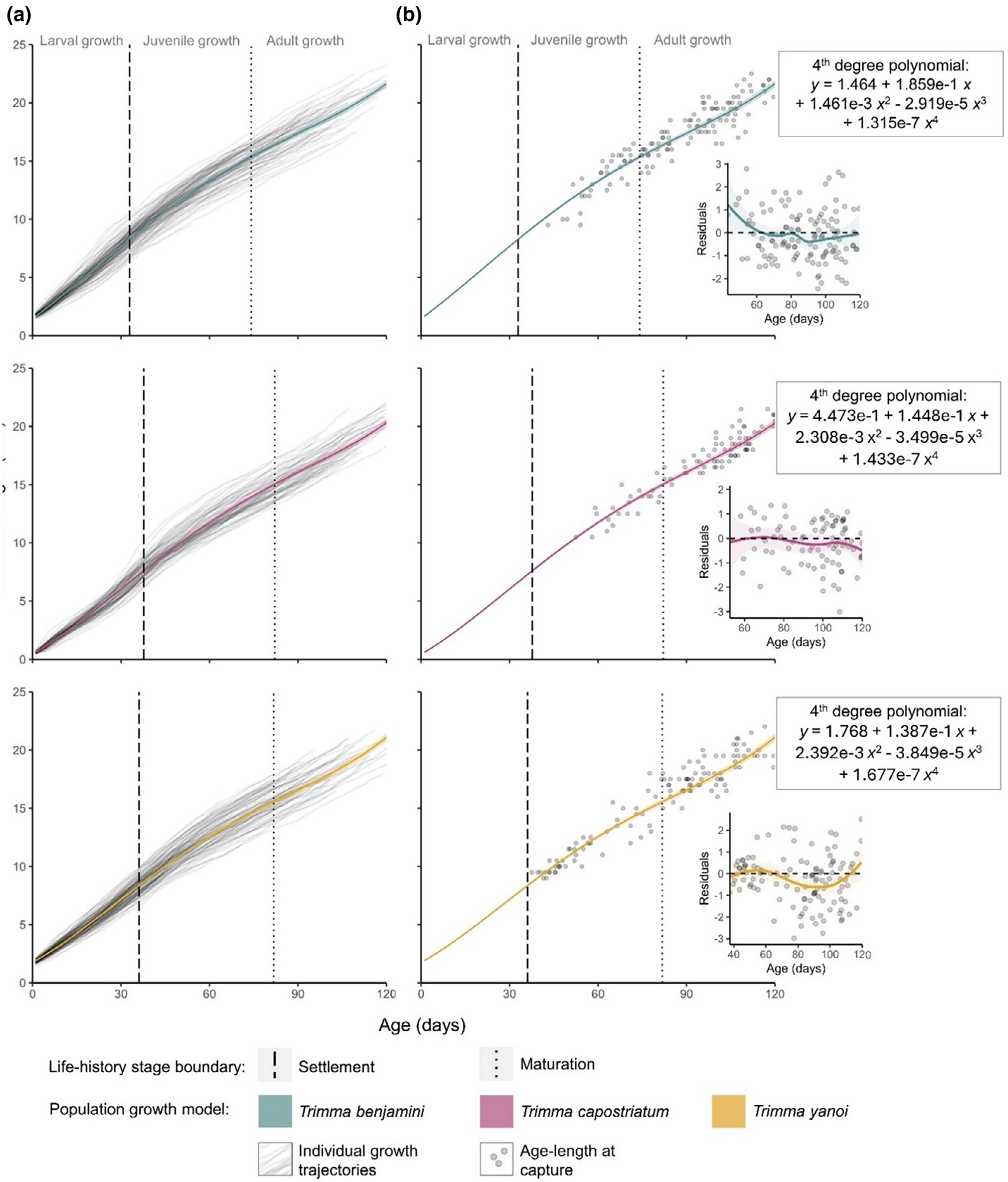

FIGURE 4 (a and b) Modelled population growth curves across larval, juvenile and adult life-history stages for *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi*. Solid regression lines and shaded ribbons represent polynomial mixed effects models of the fourth degree ± 95% confidence intervals (model equations for each species are displayed in a box). Dashed and dotted lines represent the age at settlement and maturity for each species, respectively. (a) Growth curves fitted to individual fish growth trajectories back-calculated using the Body Proportional Hypothesis model. (b) Growth curves against the ages (days) and standard lengths (mm) of individuals at the time of capture. Residual plots depict the deviations between the population growth model and observed ages and lengths at capture, with lines showing a locally weighted regression smoother applied to these residuals.

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from the plankton, mediated by larval growth, is necessary for the stability or growth of coral reef fish populations (Wilson & Meekan, 2002). However, this may be especially important for CRFs due to additional life-history pressures (Lefèvre et al., 2016). CRFs have high lifetime mortality, mainly due to their small body size (Depczynski & Bellwood, 2006; Goldsworthy et al., 2022; Winterbottom et al., 2011), which is offset by high population turnover rates of three to four and four to eight generations produced per year in *Trimma* and *Evitoa* (Depczynski & Bellwood, 2006), respectively. Therefore, to maintain stable populations, small fish species require a higher occurrence of successful recruitment events compared to larger species (Lefèvre et al., 2016). When confronted with environmental changes that affect larval growth, such as alterations in food availability (Platt et al., 2003), predator abundance (Anderson, 1988), temperature (Pepin, 1991), hydrodynamics (China & Holzman, 2014) or disruptions in lunar light emission (Shima et al., 2021), the population dynamics of small fish species may be more rapidly affected compared to their larger counterparts (Brandl et al., 2018; Goatley et al., 2016). One potential downside to faster larval growth is less time spent in the plankton (Leis & McCormick, 2002). *Trimma* and *Eviota*, along with many other CRFs, are expected to be substrate spawners and nest guarders, and less time in the plankton may have implications for dispersal potential in these predominantly sedentary fishes (Karino & Arai, 2006; Lester & Ruttenberg, 2005; Sunobe, 1995). However, *Trimma* still have a long pelagic larval duration of over 30 days, constituting over one-quarter of their lifetime (Goldsworthy et al., 2022). Therefore, further research is needed to understand the impact of faster-growing larvae on the dispersal of CRFs.

TABLE 2 Proportion of growth that occurred in larval, juvenile and adult life-history phases relative to total growth.

	Proportion of growth (%) in each life-history phase		
	Larvae	**Juvenile**	**Adult**
Trimma benjamini	35.4	29.8	34.8
Trimma capostriatum	38.0	30.7	31.3
Trimma yanoi	31.3	31.8	37.0

Note: Values are derived from the Body Proportional Hypothesis optimum growth equations (Figure 4).

Upon settlement, juvenile growth remained high immediately, then gradually declined as the juvenile stage advanced. This pattern was expected, considering that small and inexperienced recruits remain highly vulnerable to predation (Almany & Webster, 2006; Doherty et al., 2004). The small size at settlement, ranging from 7.7 to 8.4 mm, exposes them to a suite of predators. Additionally, fresh recruits often lack the skills and traits to effectively evade predators, as they are confronted with new reef predators that have different attack techniques compared to pelagic predators previously encountered in the larval stage. (Goatley & Bellwood, 2016; McCormick & Holmes, 2006). In such circumstances, mortality rates in this life-history stage can exceed 60% (Almany & Webster, 2006). Increases in growth during this phase can be an advantage, where 1-mm increases can reduce gape-limited predators and potentially extend their life span by approximately 11 days (Goatley & Bellwood, 2016). However, this phase of heightened mortality and rapid growth is typically short lived. As fishes encounter predation of conspecifics, they learn to avoid specific predators using visual and olfactory cues (McCormick & Holmes, 2006; McCormick & Manassa, 2008). Therefore, although the initial juvenile period is marked by extreme mortality and rapid growth, it may gradually subside as the fish grow and learn strategies to escape predation (Goatley & Bellwood, 2016).

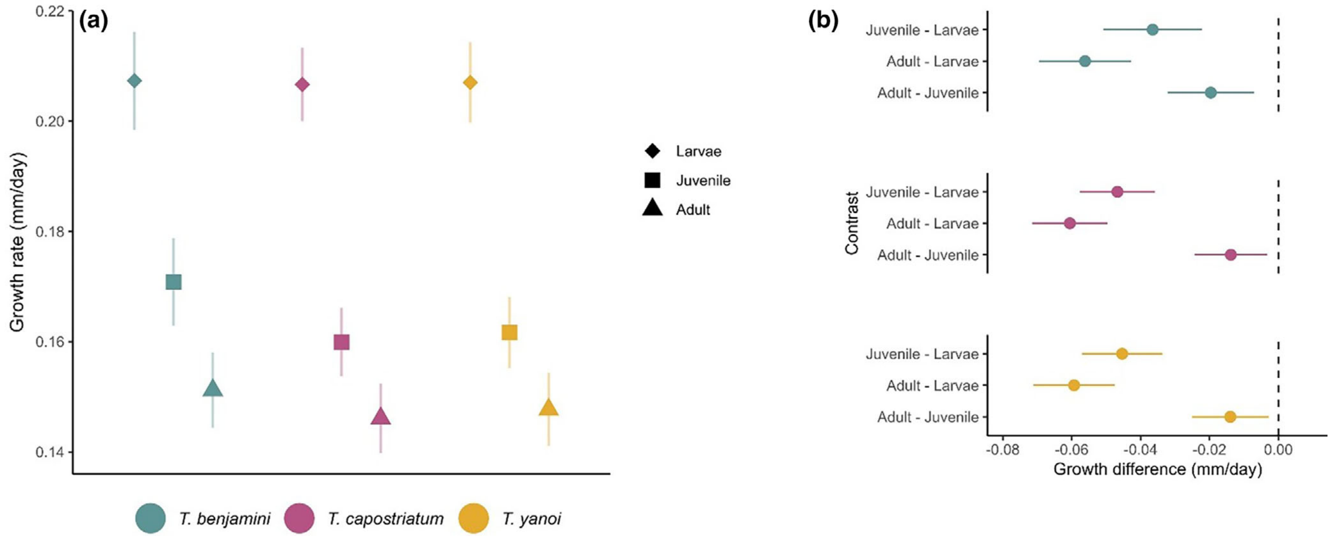

FIGURE 5 (a) Mean back-calculated growth rate (mm/day ±95% confidence intervals) in larvae, juvenile and adult life-history phases, derived from the Body Proportional Hypothesis optimum population growth equations (Figure 4). (b) Pair-wise comparisons showing the mean difference (mm/day ±95% confidence intervals) in growth between each life-history phase. In a and b, species *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi* are represented by different colours.

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Growth in each species did not plateau in adulthood, with 31.3%–37.0% of the total growth occurring during this phase and only minor (8.6%–11.7%) reductions in growth rates compared to the juvenile phase. Growth is determinate in many larger coral reef fishes such as lutjanids and acanthurids. These fishes exhibit rapid linear growth during early life history, where growth almost stops completely after maturation (Audzijonyte & Richards, 2018; Munday & Molony, 2002). Herein, just 20%–40% of growth occurs during the final 75% of the life span, as energy once utilised in somatic growth is directed to reproduction (Choat & Robertson, 2002). In other larger fishes such as *Plectropomus* spp., somatic growth takes place across a broader size range and decreases slowly following maturity and spawning (Fukuda & Sunobe, 2020; Fukuda, Tanazawa, & Sunobe, 2017; Manabe et al., 2008; Sakurai et al., 2009; Sunobe et al., 2017b; Sunobe & Nakazono, 1990a; Wong et al., 2008). CRFs, such as *Trimma* and *Eviota*, display contrasting growth patterns (Depczynski & Bellwood, 2006; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). The growth curves suggest that 77%–83% of growth occurs in the last 75% of life.

It is noteworthy that many CRFs can continue to grow substantially and reproduce simultaneously, as reproduction requires significant energy to find mates and sustain mature gonads (McCormick, 1998; Winterbottom et al., 2011). *Trimma* exhibit a diversity of reproductive modes. *Trimma* mating systems include harem polygyny (Fukuda, Tanazawa, & Sunobe, 2017; Sakurai et al., 2008; Sunobe & Nakazono, 1990b), multi-male groups (Tomatsu et al., 2018) and monogamy (Fukuda, Manabe, et al., 2017), and sex change patterns span from gonochorism to bidirectional (Sunobe et al., 2017a). As such, reproduction and the simultaneous maintenance of growth rates may be achievable by several mechanisms. Firstly, many CRFs have the capacity to feed on high-energy food such as plankton, which is abundant and requires minimal energy to forage. Therefore, energy needs to support continuous growth may be easily achieved (McCormick, 1998; Winterbottom et al., 2011). Secondly, CRFs, in general, have exponentially higher mass-specific metabolic rates (metabolic expenditure per gram of body mass) than larger fishes, which may facilitate a higher level of energy processing and allocation, allowing continuous growth (Brandl et al., 2018). Alongside this, the costs of reproduction may be significantly lower than that of larger fishes. Many CRFs, including *Trimma*, have low individual fecundity due to their small body size (Depczynski & Bellwood, 2006; Sunobe, 1995). *Eviota* have small clutch sizes and expected clutch production of two to four clutches in their lifetime, which is markedly low compared to other reef fishes. As a result, their overall reproductive energy investment is likely to be relatively low (Depczynski & Bellwood, 2006).

Non-asymptotic growth in the three *Trimma* species may be beneficial in the presence of life-history hardships, such as reproductive limitations and extreme mortality. Continuous growth may be advantageous with higher reproductive success that occurs with increasing body size. For example, increases in female body size can lead to a larger clutch size (Depczynski & Bellwood, 2006; Wootton, 1998), and larger individuals of both sexes may exhibit greater dominance where there is a competition (Fukuda & Sunobe, 2020; Fukuda, Tanazawa, & Sunobe, 2017; Manabe et al., 2008; Sakurai et al., 2009; Sunobe et al., 2017b; Sunobe & Nakazono, 1990a; Wong et al., 2008). Increases in the body size of *Trimma* and corresponding reproductive advantages throughout their lives may be beneficial due to their short reproductive life spans of <50 days and the need to reproduce efficiently (Goldsworthy et al., 2022).

Alongside reproductive benefits, this phenomenon may be an advantage with extreme lifetime mortality on coral reefs. It is well established that in early life-history stages fishes exhibit linear growth to account for the heavy predation rates that come with a small body size (Anderson, 1988; Goatley & Bellwood, 2016; Shima & Findlay, 2002; Wilson & Meekan, 2002). This theory may be applied to CRFs throughout all life-history stages because of their small size. The growth curves suggest that the *Trimma* examined mature at 15–15.5 mm and attain a maximum size of <25 mm, which is consistent with previous literature (Goldsworthy et al., 2022; Winterbottom et al., 2011). Goatley and Bellwood (2016) demonstrate that mortality rates decrease drastically after reaching a size threshold of 43 mm. However, the *Trimma* species examined, along with many other CRFs, never reach this size where mortality declines and growth asymptotes (Depczynski & Bellwood, 2006; Goldsworthy et al., 2022; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). Thus, *Trimma* remain at elevated risk of predation throughout their lives. Although predation is difficult to capture in situ, there are several points to support this, including (i) increased longevity of CRFs with the absence of predators (Randall & Delbeek, 2009); (ii) reproductively active individuals present even at maximum longevities (Depczynski & Bellwood, 2006; Goldsworthy et al., 2022; Winterbottom et al., 2011; Winterbottom & Southcott, 2008); (iii) exhibition of extreme mortality rates of up to 8% per day and short life spans <140 days (Depczynski & Bellwood, 2006; Goldsworthy et al., 2022; Winterbottom et al., 2011; Winterbottom & Southcott, 2008); and finally, (iv) CRFs are consumed by any predator that is able to catch them (Goatley et al., 2017), which invites the possibility that these fishes are important prey species on coral reefs (Brandl et al., 2018).

Surprisingly, the BPH back-calculation model followed by the BI model outperformed the MF model in all species, contrary to the expectation that the MF model would be superior (Vigliola & Meekan, 2009). Indeed, the MF model produced the best estimates of size in *Elacatinus evelynae* and *Elacatinus prochilos* (Wilson et al., 2009), as well as *Diplodus sargus*, *Diplodus vulgaris* and *Diplodus puntazzo* (Vigliola et al., 2000). However, there are exceptions where other methods were adequate. For example, the best estimates of size were obtained by the BI and time-varying growth models in early life history of *Mogurnda adspersa* (Starrs et al., 2013), and the Age Effect model in *Salvelinus leucomaenis* (Morita & Matsuishi, 2001). Starrs et al. (2013) explain that fishes with longer life spans and more complex OSG relationships may be more suitably modelled by the MF model, whereas simpler methods may be better where the OSG relationship is near linear. Therefore, the superior performance of the simple BPH model may be attributed to the linear or near-linear OSG relationships observed in the examined *Trimma* species. This highlights the need for a review of the most appropriate back-calculation model in small and short-lived coral reef fishes with atypical growth patterns compared to larger fishes. Although the BPH back-calculation model provided a good fit, it is important to note that there may be a modest

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under- or overestimation of back-calculated lengths at age extremes due to slight deviations from strict linearity.

Extreme life-history characteristics associated with a small adult body size of three *Trimma* species are prevalent among other CRFs and highlight their potential to be large players in energy flow on coral reefs (Beeken et al., 2021; Brandl et al., 2019; Depczynski et al., 2007; Depczynski & Bellwood, 2006; Winterbottom et al., 2011; Winterbottom & Southcott, 2008). With more than three generations produced annually and continuous growth throughout life, CRFs, such as *Trimma*, may be a continuous and regenerative source of nutrients and energy for other reef consumers (Brandl et al., 2018; Depczynski et al., 2007; Depczynski & Bellwood, 2003; Morais & Bellwood, 2020). Investigating the spawning dynamics of *Trimma* should be a focus of future research, as a comprehensive understanding of these patterns is crucial for population dynamics and their ecosystem implications. When CRF life-history traits and population dynamics are considered, it is estimated that juveniles and adults can deliver productivity of up to 2.31 kg ha^{-1} d^{-1} on healthy coral reefs (Brandl et al., 2020; Morais & Bellwood, 2019, 2020), and account for almost 60% of fish biomass consumed on the reef (Brandl et al., 2019). Although this study is a long way away from underpinning the ecosystem importance of *Trimma*, determining growth across life-history stages is one step closer to identifying their impact on coral reefs and better understanding the ecosystem processes influenced by growth.

AUTHOR CONTRIBUTIONS

Nisha C. Goldsworthy: conducted data collection, experimental design, data analysis, and writing. **Maya Srinivasan:** contributed to conceptual design, analysis, and writing. **Patrick Smallhorn-West:** contributed to experimental design, data analysis, and writing. **Geoffrey P. Jones:** contributed to conceptual design, data analysis, and writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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REFERENCES

Ackerman, J. L., & Bellwood, D. R. (2000). Reef fish assemblages: A re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series*, *206*, 227–237. https://doi.org/10.3354/meps206227

Almany, G. R., & Webster, M. S. (2006). The predation gauntlet: Early post-settlement mortality in reef fishes. *Coral Reefs*, *25*, 19–22. https://doi.org/10.1007/s00338-005-0044-y

Anderson, J. T. (1988). A review of size dependant survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*, *8*, 55–56.

Audzijonyte, A., & Richards, S. A. (2018). The energetic cost of reproduction and its effect on optimal life-history strategies. *The American Naturalist*, *192*(4), 150–162. https://doi.org/10.1086/698655

Barneche, D. R., Allen, A. P., & Mumby, P. (2018). The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters*, *21*(6), 836–844. https://doi.org/10.1111/ele.12947

Beeken, N. S., Selwyn, J. D., & Hogan, J. D. (2021). Determining the life history strategy of the cryptobenthic reef gobies *Coryphopterus hyalinus* and *C. Personatus*. *Marine Ecology Progress Series*, *659*, 161–173. https://doi.org/10.3354/meps13573

Bergenius, M. A. J., Meekan, M. G., Robertson, D. R., & McCormick, M. I. (2002). Larval growth predicts the recruitment success of a coral reef fish. *Oecologia*, *131*, 521–525. https://doi.org/10.1007/s00442-002-0918-4

Berrar, D. (2018). Cross-Validation. In D. Berrar (Ed.), *Encyclopedia of bioinformatics and computational biology* (Vol. 1, pp. 542–545). Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.20349-X

Borgstein, N., Beltrán, D. M., & Prada, C. (2020). Variable growth across species and life stages in Caribbean reef octocorals. *Frontiers in Marine Science*, *7*(483), 1–11. https://doi.org/10.3389/fmars.2020.00483

Brandl, S. J., Goatley, C. H. R., Bellwood, D. R., & Tornabene, L. (2018). The hidden half: Ecology and evolution of cryptobenthic fishes on coral reefs. *Biological Reviews*, *93*, 1846–1873. https://doi.org/10.1111/brv.12423

Brandl, S. J., Johansen, J. L., Casey, J. M., Tornabene, L., Morais, R. A., & Burt, J. A. (2020). Extreme environmental conditions reduce coral reef fish biodiversity and productivity. *Nature Communications*, *11*, 1–14. https://doi.org/10.1038/s41467-020-17731-2

Brandl, S. J., Tornabene, L., Goatley, C. H. R., Casey, J. M., Morais, R. A., Côté, I. M., Baldwin, C. C., Parravicini, V., Schiettekatte, N. M. D., & Bellwood, D. R. (2019). Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science*, *364*, 1189–1192. https://doi.org/10.1126/science.aav3384

Brown, J. H., Marquet, P. A., & Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *The American Naturalist*, *142*(4), 573–584. https://doi.org/10.1086/285558

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Calder, W. A. (1984). *Size, function, and life history*. Harvard University Press.

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, *47*, 2219–2227.

China, V., & Holzman, R. (2014). Hydrodynamic starvation in first-feeding larval fishes. *Proceedings of the National Academy of Sciences*, *111*(22), 8083–8088. https://doi.org/10.1073/pnas.1323205111

Choat, J. H., & Robertson, D. R. (2002). Age-based studies. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 57–80). Elsevier.

Depczynski, M., & Bellwood, D. (2006). Extremes, plasticity, and invariance in vertebrate life history traits: Insights from coral reef fishes. *Ecology*, *87*(12), 3119–3127. https://doi.org/10.1890/0012-9658(2006)87[3119:EPAIIV]2.0.CO;2

Depczynski, M., & Bellwood, D. R. (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series*, *256*, 183–191. https://doi.org/10.3354/meps256183

Depczynski, M., & Bellwood, D. R. (2005). Shortest recorded vertebrate lifespan found in a coral reef fish. *Current Biology*, *15*(8), 288–289. https://doi.org/10.1016/j.cub.2005.04.016

Depczynski, M., Fulton, C., Marnane, M. J., & Bellwood, D. R. (2007). Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia*, *153*, 111–120. https://doi.org/10.1007/s00442-007-0714-2

Doherty, P. J., Dufour, V., Galzin, R., Hixon, M. A., Meekan, M. G., & Planes, S. (2004). High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology*, *85*(9), 2422–2428. https://doi.org/10.1890/04-0366

Francis, R. (1990). Back-calculation of fish length: A critical review. *Journal of Fish Biology*, *36*(6), 883–902. https://doi.org/10.1111/j.1095-8649.1990.tb05636.x

Fukuda, K., Manabe, H., Sakurai, M., Dewa, S.-i., Shinomiya, A., & Sunobe, T. (2017). Monogamous mating system and sexuality in the gobiid fish, *Trimma marinae* (Actinopterygii: Gobiidae). *Journal of Ethology*, *35*(1), 121–130. https://doi.org/10.1007/s10164-016-0499-z

Fukuda, K., & Sunobe, T. (2020). Group structure and putative mating system of three hermaphrodite gobiid fish, *Priolepis akihitoi*, *Trimma emeryi*, and *Trimma hayashii* (Actinopterygii: Gobiiformes). *Ichthyological Research*, *67*, 552–558. https://doi.org/10.1007/s10228-020-00750-w

Fukuda, K., Tanazawa, T., & Sunobe, T. (2017). Polygynous mating system and field evidence for bidirectional sex change in the gobiid fish *Trimma grammistes*. *International Journal of Pure and Applied Zoology*, *5*(3), 92–99.

Galland, G. R., Erisman, B., Aburto-Oropeza, O., & Hastings, P. A. (2017). Contribution of cryptobenthic fishes to estimating community dynamics of sub-tropical reefs. *Marine Ecology Progress Series*, *584*, 175–184. https://doi.org/10.3354/meps12364

Goatley, C. H. R., & Bellwood, D. R. (2016). Body size and mortality rates in coral reef fishes: A three-phase relationship. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1841), 1–6. https://doi.org/10.1098/rspb.2016.1858

Goatley, C. H. R., González-Cabello, A., & Bellwood, D. R. (2016). Reef-scale partitioning of cryptobenthic fish assemblages across the great barrier reef, Australia. *Marine Ecology Progress Series*, *544*, 271–280. https://doi.org/10.3354/meps11614

Goatley, C. H. R., González-Cabello, A., & Bellwood, D. R. (2017). Small cryptopredators contribute to high predation rates on coral reefs. *Coral Reefs*, *36*, 207–212. https://doi.org/10.1007/s00338-016-1521-1

Goldsworthy, N. C., Srinivasan, M., Smallhorn-West, P., Cheah, L.-C., Munday, P. L., & Jones, G. P. (2022). Life-history constraints, short adult life span and reproductive strategies in coral reef gobies of the genus *Trimma*. *Journal of Fish Biology*, *101*, 996–1007. https://doi.org/10.1111/jfb.15161

Green, B. S., Mapstone, B. D., Carlos, G., & Begg, G. A. (2009). Tropical fish otoliths: Information for assessment, management and ecology. In *Reviews: Methods and Technologies in Fish Biology and Fisheries*. Springer. https://doi.org/10.1007/978-1-4020-5775-5

Gwinn, D. C., Allen, M. S., & Rogers, M. W. (2010). Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research*, *105*(2), 75–79. https://doi.org/10.1016/j.fishres.2010.03.005

Hernaman, V., & Munday, P. L. (2005a). Life-history characteristics of coral reef gobies: I. Growth and life-span. *Marine Ecology Progress Series*, *290*, 207–221. https://doi.org/10.3354/meps290207

Hernaman, V., & Munday, P. L. (2005b). Life-history characteristics of coral reef gobies: II. Mortality rate, mating system and timing of maturation. *Marine Ecology Progress Series*, *290*, 223–237. https://doi.org/10.3354/meps290223

Hernaman, V., Munday, P. L., & Schläppy, M. L. (2000). Validation of otolith growth-increment periodicity in tropical gobies. *Marine Biology*, *137*, 715–726. https://doi.org/10.1007/s002270000387

Jones, G. P., & McCormick, M. I. (2002). Numerical and energetic processes in the ecology of coral reef fishes. In P. F. Sale (Ed.), *Coral reef fishes* (pp. 221–238). Academic Press. https://doi.org/10.1016/B978-012615185-5/50013-X

Jones, G. P., Munday, P. L., & Julian, C. M. (2002). Rarity in coral reef fish communities. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 81–101). Academic Press. https://doi.org/10.1016/B978-012615185-5/50006-2

Karino, K., & Arai, R. (2006). Effect of clutch size on male egg-fanning behavior and hatching success in the goby, *Eviota prasina* (Klunzinger). *Journal of Experimental Marine Biology and Ecology*, *334*(1), 43–50. https://doi.org/10.1016/j.jembe.2006.01.018

Lefèvre, C. D., Nash, K. L., González-Cabello, A., & Bellwood, D. R. (2016). Consequences of extreme life history traits on population persistence: Do short-lived gobies face demographic bottlenecks? *Coral Reefs*, *35*(2), 399–409. https://doi.org/10.1007/s00338-016-1406-3

Leis, J. M., & McCormick, M. I. (2002). The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 171–199). Academic Press. https://doi.org/10.1016/B978-012615185-5/50011-6

Lenth, R. V. (2021). emmeans: estimated marginal means, aka least-squares means. R package version 1.7.1–1. https://CRAN.R-project.org/package=emmeans

Lester, S. E., & Ruttenberg, B. I. (2005). The relationship between pelagic larval duration and range size in tropical reef fishes: A synthetic analysis. *Proceedings of the Royal Society B*, *272*(1563), 585–591. https://doi.org/10.1098/rspb.2004.2985

Lincoln, R. J., Boxshall, G. A., & Clark, P. F. (1982). *Dictionary of ecology, evolution, and systematics* (2nd ed.). Cambridge University Press.

Longenecker, K., & Langston, R. (2005). Life history of the Hawaiian blackhead triplefin, *Enneapterygius atriceps* (Blennioidei, Tripterygiidae). *Environmental Biology of Fishes*, *73*, 243–251. https://doi.org/10.1007/s10641-004-5332-9

Lowe, J. R., Russ, G. R., Bucol, A. A., Abesamis, R. A., & Choat, J. H. (2021). Geographic variability in the gonadal development and sexual ontogeny of *Hemigymnus*, *Cheilinus*, and *Oxycheilinus* wrasses among Indo-Pacific coral reefs. *Journal of Fish Biology*, *99*, 1348–1363. https://doi.org/10.1111/jfb.14842

Manabe, H., Matsuoka, M., Goto, K., Dewa, S.-I., Shinomiya, A., Sakurai, M., & Sunobe, T. (2008). Bi-directional sex change in the gobiid fish *Trimma* sp.: Does size-advantage exist? *Behaviour*, *145*(1), 99–113. https://doi.org/10.1163/156853908782687214

McCormick, M. I. (1998). Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: Relationship between feeding mechanics, microhabitat selection and growth. *Marine Biology*, *132*(1), 9–20. https://doi.org/10.1007/s002270050367

10958649, 2026, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.70224 by James Cook University, Wiley Online Library on [08/07/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

McCormick, M. I., & Holmes, T. H. (2006). Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*. *Journal of Fish Biology*, *68*(3), 969–974. https://doi.org/10.1111/j.0022-1112.2006.00982.x

McCormick, M. I., & Manassa, R. (2008). Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*, *27*(1), 105–113. https://doi.org/10.1007/s00338-007-0296-9

Morais, R. A., & Bellwood, D. R. (2019). Pelagic subsidies underpin fish productivity on a degraded coral reef. *Current Biology*, *29*(9), 1521–1527. https://doi.org/10.1016/j.cub.2019.03.044

Morais, R. A., & Bellwood, D. R. (2020). Principles for estimating fish productivity on coral reefs. *Coral Reefs*, *39*(5), 1221–1231. https://doi.org/10.1007/s00338-020-01969-9

Morita, K., & Matsuishi, T. (2001). A new model of growth back-calculation incorporating age effect based on otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(9), 1805–1811. https://doi.org/10.1139/cjfas-58-9-1805

Munday, P. L., & Molony, B. W. (2002). The energetic cost of protogynous versus protandrous sex change in the bi-directional sex-changing fish *Gobiodon histrio*. *Marine Biology*, *141*, 1011–1017. https://doi.org/10.1007/s00227-002-0904-8

Ogle, D. H. (2016). *Introductory fisheries analyses with R*. CRC Press.

Ogle, D. H. (2019). RFishBC. R package version 0.2.3. http://derekogle.com/RFishBC

Ogle, D. H., Brenden, T. O., & McCormick, J. L. (2017). Chapter 12 - growth estimation: Growth models and statistical inference. In *Age and growth of fishes: Principles and techniques*. American Fisheries Society.

Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(3), 503–518. https://doi.org/10.1139/f91-065

Pepin, P. (2023). Feeding by larval fish: How taxonomy, body length, mouth size, and behaviour contribute to differences among individuals and species from a coastal ecosystem. *ICES Journal of Marine Science*, *80*(1), 91–106. https://doi.org/10.1093/icesjms/fsac215

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.

Platt, T., Fuentes-Yaco, C., & Frank, K. T. (2003). Spring algal bloom and larval fish survival. *Nature*, *423*(6938), 398–399. https://doi.org/10.1038/423398b

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Randall, J. E., & Delbeek, J. C. (2009). Comments on the extremes in longevity in fishes, with special reference to the Gobiidae. *Proceedings of the California Academy of Sciences*, *60*(13), 447–454.

Roemer, M. E., & Oliveira, K. (2007). Validation of back-calculation equations for juvenile bluefish with the use of tetracycline-marked otoliths. *Fishery Bulletin*, *105*(2), 305–309.

Roff, D. A. (1992). *The evolution of life histories: Theory and analysis*. Chapman & Hall.

Sakurai, M., Manabe, H., Dewa, S.-I., Sunobe, T., Matsuoka, M., Shinomiya, A., & Goto, K. (2008). Bi-directional sex change in the gobiid fish Trimma sp.: Does size-advantage exist? *Behaviour*, *145*(1), 99–113. https://doi.org/10.1163/156853908782687214

Sakurai, M., Nakakoji, S., Manabe, H., Dewa, S.-i., Shinomiya, A., & Sunobe, T. (2009). Bi-directional sex change and gonad structure in the gobiid fish *Trimma yanagitai*. *Ichthyological Research*, *56*, 82–86. https://doi.org/10.1007/s10228-008-0054-1

Sale, P. F. (2002). *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (2nd ed.). Elsevier.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, *163*(3), 429–441. https://doi.org/10.1086/381872

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, *18*(1), 371–407.

Shima, J. S., & Findlay, A. M. (2002). Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Marine Ecology Progress Series*, *235*, 303–309. https://doi.org/10.3354/meps235303

Shima, J. S., Osenberg, C. W., Noonburg, E. G., Alonzo, S. H., & Swearer, S. E. (2021). Lunar rhythms in growth of larval fish. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 1–9. https://doi.org/10.1098/rspb.2020.2609

Smedstad, O. M., & Holm, J. C. (1996). Validation of back-calculation formulae for cod otoliths. *Journal of Fish Biology*, *49*(5), 973–985. https://doi.org/10.1111/j.1095-8649.1996.tb00094.x

Stamps, J. A., Mangel, M., & Phillips, J. A. (1998). A new look at relationships between size at maturity and asymptotic size. *The American Naturalist*, *152*(3), 470–479. https://doi.org/10.1086/286183

Starrs, D., Ebner, B. C., & Fulton, C. J. (2013). Can backcalculation models unravel complex larval growth histories in a tropical freshwater fish? *Journal of Fish Biology*, *83*(1), 96–110. https://doi.org/10.1111/jfb.12152

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Sunobe, T. (1995). Embryonic development and larvae of three gobiid fish, *Trimma okinawae*, *Trimma grammistes* and *Trimmatom sp*. *Japanese Journal of Ichthyology*, *42*(1), 11–16. https://doi.org/10.11369/jji1950.42.11

Sunobe, T., & Nakazono, A. (1990). Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan with a note on sex change. *Ethology*, *84*, 133–143. https://doi.org/10.1111/j.1439-0310.1990.tb00790.x

Sunobe, T., Sado, T., Hagiwara, K., Manabe, H., Suzuki, T., Kobayashi, Y., Sakurai, M., Dewa, S., Matsuoka, M., Shinomiya, A., Fukuda, K., & Miya, M. (2017). Evolution of bidirectional sex change and gonochorism in fishes of the gobiid genera *Trimma*, *Priolepis*, and *Trimmatom*. *The Science of Nature*, *104*, 1–11. https://doi.org/10.1007/s00114-017-1434-z

Tomatsu, S., Ogiso, K., Fukuda, K., Deki, M., Dewa, S.-I., Manabe, H., Sakurai, M., Shinomiya, A., & Sunobe, T. (2018). Multi-male group and bidirectional sex change in the gobiid fish, Trimma caudomaculatum. *Ichthyological Research*, *65*(4), 502–506. https://doi.org/10.1007/s10228-018-0631-x

Vigliola, L., Harmelin-Vivien, M., & Meekan, M. G. (2000). Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(6), 1291–1299. https://doi.org/10.1139/f00-055

Vigliola, L., & Meekan, M. G. (2009). The back-calculation of fish growth from otoliths. In *Tropical fish otoliths: Information for assessment, management and ecology* (pp. 174–211). Springer. https://doi.org/10.1007/978-1-4020-5775-5_6

Wilson, D. T., & McCormick, M. I. (1999). Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Marine Biology*, *134*, 29–41. https://doi.org/10.1007/s002270050522

Wilson, D. T., & Meekan, M. G. (2002). Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). *Marine Ecology Progress Series*, *231*, 247–260. https://doi.org/10.3354/meps231247

Wilson, J. A., Vigliola, L., & Meekan, M. G. (2009). The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. *Journal of Experimental Marine Biology and Ecology*, *368*(1), 9–21. https://doi.org/10.1016/j.jembe.2008.09.005

Winterbottom, R. (2019). An illustrated key to the described valid species of *Trimma* (Teleostei: Gobiidae). *Journal of the Ocean Science Foundation*, *34*, 1–61. https://doi.org/10.5281/zenodo.3525430

Winterbottom, R., Alofs, K. M., & Marseu, A. (2011). Life span, growth and mortality in the western Pacific goby *Trimma benjamini*, and

10958649, 2026, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.70224 by James Cook University, Wiley Online Library on [08/07/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

comparisons with *T. Nasa*. *Environmental Biology of Fishes*, *91*, 295–301. https://doi.org/10.1007/s10641-011-9782-6

Winterbottom, R., Brighton, E., & Mason-Parker, C. (2024). A new species of Trimma (Teleostei: Gobiidae) from the Seychelles, Indian Ocean. *Journal of the Ocean Science Foundation*, *41*, 37–45.

Winterbottom, R., & Southcott, L. (2008). Short lifespan and high mortality in the western Pacific coral reef goby *Trimma nasa*. *Marine Ecology Progress Series*, *366*, 203–208. https://doi.org/10.3354/meps07517

Wong, M. Y. L., Munday, P. L., Buston, P. M., & Jones, G. P. (2008). Monogamy when there is potential for polygyny: Tests of multiple hypotheses in a group-living fish. *Behavioral Ecology*, *19*, 353–361. https://doi.org/10.1093/beheco/arm141

Wootton, R. J. (1998). *Ecology of teleost fishes* (2nd ed.). Kluwer Academic.

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