


# Life-history constraints, short adult life span and reproductive strategies in coral reef gobies of the genus *Trimma*

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## Abstract

Body size influences many life-history traits, with small-bodied animals tending to have short life spans, high mortality and greater reproductive effort early in life. In this study, the authors investigated the life-history traits and reproductive strategies of three small-bodied coral reef gobies of the genus *Trimma*: *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi*. The authors found all *Trimma* species studied attained a small body size of <25 mm, had a short life span of <140 days and experienced high estimated daily mortality of 3.0%–6.7%. Furthermore, the pelagic larval phase accounted for 25.3%–28.5% of the maximum life span, and maturation occurred between 74.1 and 82.1 days at 15.2–15.8 mm, leaving only 35%–43% of the total life span as a reproductively viable adult. All mature individuals had gonad structures consistent with bidirectional sex change, with bisexual gonads including both ovarian and testicular portions separated by a thin wall of connective tissue. In the female and male phases, only ovaries or testes were mature, whereas gonadal tissue of the non-active sex remained. One *T. benjamini* individual and one *T. yanoi* individual had ovarian and testicular tissue active simultaneously. The results of this study highlight the life-history challenges small CRFs face on their path to reproduction and reproductive strategies that could be beneficial in fishes with high and unpredictable mortality and short reproductive life spans.

## KEYWORDS

body size, maturity, mortality, pelagic larval duration, reproduction, *Trimma*

## 1 | INTRODUCTION

Body size has broad ecological and evolutionary implications for animals, impacting on their diversity, abundance, ecological specialization and life-history traits (Hanken & Wake, 1993; Marzluff & Dial, 1991; May, 1978; Peters, 1983; Roff, 1992). Large-bodied organisms tend to exhibit prolonged life spans, reduced mortality and late maturation. In contrast, small-bodied animals tend to exhibit short life spans and

high mortality, resulting in limited time available to reproduce and the selection for greater reproductive effort earlier in life (Calder, 1984; Roff, 1992; Stearns, 1992). Small animals must adopt strategies to develop quickly and reproduce early and successfully before their short life ends (Fisher *et al.*, 2013). Nonetheless, for small species, there may be ecological and physiological constraints on how short development and maturation times can be (Bernardo, 1993; Charnov *et al.*, 2001; Roff, 1992).

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On coral reefs, fishes that occupy benthic habitats and are small bodied (*i.e.*, <50 mm) are known as cryptobenthic reef fishes (CRFs; Goatley & Brandl, 2017). The majority of coral reef fish species have a small body size (Munday & Jones, 1998), and they can be highly abundant on coral reefs (Ackerman & Bellwood, 2000; Galland *et al.*, 2017). Although considerable attention has been given to the ecological implications of small body size, including diversity, abundance, habitat specialization and predation risk (Jones *et al.*, 2002; Munday & Jones, 1998), much less is known about their life-history strategies to compensate for high mortality and short life span. There is increasing evidence which shows CRFs have vital ecological roles in maintaining coral reef energy flow, providing 60% of consumer biomass through their extraordinarily fast-paced life-history dynamics (Brandl *et al.*, 2019; Depczynski *et al.*, 2007). However, a fast-paced life history requires time to transition from the larval stage, reach reproductive maturity and reproduce successfully. How extremely small coral reef fishes partition their life history is poorly understood.

CRFs face several obstacles throughout their life that potentially limit their ability to survive and reproduce. Firstly, their small body size is associated with reduced longevity compared to larger coral reef fishes, and therefore a small maximum window for reproduction (Depczynski & Bellwood, 2006). Second, CRFs also experience high mortality rates as a result of their small size (Depczynski & Bellwood, 2006; Goatley *et al.*, 2017; Goatley & Bellwood, 2016; Winterbottom *et al.*, 2011). Mortality in reef fishes decreases exponentially after reaching a size threshold of *c.* 43 mm (Goatley & Bellwood, 2016). Many CRFs thus experience high mortality throughout their entire lives as this threshold is never surpassed (Depczynski & Bellwood, 2006; Winterbottom *et al.*, 2011), leading to an increased chance of perishing before reaching reproductive maturity.

In addition to a short life span and high mortality, CRFs encounter two main physiological constraints which reduce their reproductive lifetime, the first being the length of their pelagic larval duration (PLD). Reef fishes have a two-part life cycle, comprising a pelagic larval phase before settlement onto the reef (Leis & McCormick, 2002). PLD is broadly similar across most reef fish species, despite vast differences in overall longevity (Depczynski & Bellwood, 2006). For example, *Bolbometopon muricatum* can live up to 37 years (Andrews *et al.*, 2015) and has a PLD of just 25 days (Taylor *et al.*, 2018), representing 0.2% of the maximum life span. By contrast, the pygmy goby, *Trimma nasa*, lives <90 days and has a PLD of 34 days, representing 38.7% of its life span (Winterbottom & Southcott, 2008). PLD may be constrained among fishes to attain a critical size or developmental stage before settlement onto the reef (Beeken *et al.*, 2021; Depczynski & Bellwood, 2006). Consequently, PLD, which is a significant time in early life not available for reproduction, potentially makes up a large proportion of the maximum life span of CRFs.

The second physiological constraint for CRFs is their length/age at maturity. According to life-history theory, early maturation should be selected for in small-bodied individuals with high mortality rates to increase the probability that individuals will survive until they reproduce (Ricklefs, 2010; Roff, 1992; Stearns, 1992). Yet, early maturation

has disadvantages associated with maturing at a smaller body size. For example, female fecundity is low with a small body size, or a larger body size may be selected for where intraspecific competition is present (Hernaman & Munday, 2005b; Wong *et al.*, 2008). As a result, CRFs face a dilemma regarding the best overall reproductive strategy to adopt, either: (a) mature early to increase the overall chance of surviving to reproduce (*e.g.*, Depczynski & Bellwood, 2006), or (b) delay maturation and attain a larger body size to improve size-related reproductive outputs (*e.g.*, Kunishima *et al.*, 2021). Delaying maturation, however, further reduces the reproductive time available to CRFs and could be a risky strategy when mortality rates remain high throughout life.

Many coral reef fishes are capable of enhancing lifetime reproductive outputs using various sex change strategies (Benvenuto *et al.*, 2017). The size-advantage model (SA model, Ghiselin, 1969; Warner, 1975) suggests protogyny will be favoured in polygynous groups, where large males achieve the highest reproductive success as a result of intrasexual competition for mates or breeding sites. Conversely, protandry is favoured where male body size does not affect reproductive success and larger individuals have higher reproductive success as females, because of the positive relationship between body size and fecundity (Ghiselin, 1969; Warner, 1975). In addition, bidirectional sex change can occur in polygynous groups, where a large female can transition to male when the dominant male is lost. Reverse sex change can occur if a single male infiltrates a group with a larger male (Manabe *et al.*, 2007). In small fishes with high and erratic mortality rates, a male may abruptly lose every female in his harem. A solitary male may have an indefinite window for reproduction because of the high likelihood of predation, and delays in locating new breeding partners may significantly reduce his reproductive value. By becoming female and reproducing in an established group, his reproductive outputs may be higher than remaining male and waiting for a new harem to form (Munday *et al.*, 2010).

Sex change comes at a cost of time and energy to convert the gonads from one sex to another, which can place further pressure on reproduction (Munday & Molony, 2002). Some CRFs have minimised these costs by evolving bisexual gonads with female and male tissues, containing developed tissues of the active sex, and regressed tissues of the non-functional sex (Sunobe & Nakazono, 1993). This avoids entire gonad reconstruction and allows for rapid sex change, thus saving time and energy (Munday *et al.*, 2010; Yamaguchi & Iwasa, 2017), which may be beneficial in species when social conditions experienced by males might change dramatically and unpredictably, and when a delay in finding a new partner could result in a substantial loss of reproductive output (Munday *et al.*, 2010).

The genus *Trimma* (family Gobiidae) is a group of hyper-diverse Indo-Pacific CRFs, consisting of 105 species (Winterbottom, 2019). These small-bodied fishes have a standard length ( $L_S$ ) of <30 mm and are among the smallest vertebrates on Earth. Despite extensive research describing mating systems and sex change strategies of *Trimma* (Fukuda *et al.*, 2017a, 2017b; Fukuda & Sunobe, 2020; Kobayashi *et al.*, 2005; Manabe *et al.*, 2007, 2008; Sakurai *et al.*, 2009; Sunobe *et al.*, 2017; Sunobe & Nakazono, 1990; Tomatsu

*et al.*, 2018), there have been limited attempts to describe other aspects of their ecology and life history (but see Winterbottom *et al.*, 2011; Winterbottom & Southcott, 2008). Consequently, little is known about the challenges they face on their path to reproduction. Because of their small body size, it is expected that *Trimma* species may also experience traits associated with other small-bodied fishes, such as: (a) reduced longevity; (b) high mortality rates; (c) long PLD relative to life span and (d) early or delayed maturation, depending on the presence of advantages favouring either strategy. A combination of (a)–(d) can lead to a short reproductive life. In this study, the authors investigate these life-history obstacles and reproductive strategies in three species of *Trimma*: *Trimma benjamini*, *Trimma capostriatum* and *Trimma yanoi*.

## 2 | MATERIALS AND METHODS

### 2.1 | Species, specimen collection and ethical statement

*Trimma* are speciose and abundant on Indo-Pacific coral reefs and adjacent habitats. All three species studied here are sedentary benthic species which perch on hard substrata, as opposed to hovering in the water column above the benthos like several other members of this genus. A total of 353 individuals (129 *T. benjamini*, 102 *T. capostriatum* and 122 *T. yanoi*) were collected between November and December 2019 from inshore and offshore reefs in Kimbe Bay, Papua New Guinea. All individuals were captured on SCUBA using a fine-mesh (2 mm) hand-net and clove oil anaesthetic solution (5:1, ethanol:clove oil), and euthanized by immersion in an ice slurry (50% water, 50% ice) immediately after surfacing. Fish collections were compliant with James Cook University Ethics Approval A2665 and were collected under a research visa allocated to Professor Geoffrey Jones issued by the government of Papua New Guinea. Permissions were granted by Mrs. Cecilie Benjamin (chair of the Board, Mahonia Na Dari Research and Conservation Centre, Kilu) and Mr. Thomas Koi (village elder and representative of the Local Marine Management Committee, Kilu).

### 2.2 | Body size, longevity and mortality

Fresh specimens were blotted dry and measured to 0.5 mm  $L_S$ . The head of each fish was removed from the body by sectioning between the operculum and pectoral fins and was preserved in 70% ethanol. Fish age and PLD were determined using sagittal otoliths, which were removed from the brain cavity, cleaned using water and stored dry in vials. Thermoplastic glue (Crystalbond 509™) was used to mount otoliths sulcus-down on glass slides. The surface of each otolith was polished using 9, 3 and 0.3  $\mu\text{m}$  lapping film to obtain a thin, flat section of a whole otolith with growth rings clearly visible from the otolith primordium to edge. Sections were coated in immersion oil to improve microstructure clarity and photographed at 200 $\times$  and 400 $\times$  magnification with an Olympus EP50 digital camera attached to

a BX43 Olympus microscope. Growth rings were counted in ImageJ (Schneider *et al.*, 2012) from the core outwards, beginning at the first increment which was assumed to be deposited at hatching (Winterbottom *et al.*, 2011). Although this could not be validated experimentally for *Trimma*, growth increments were assumed to be daily deposits, as seen in ecologically similar CRFs (e.g. Depczynski & Bellwood, 2005; Depczynski & Bellwood, 2006; Hernaman & Munday, 2005a; Longenecker & Langston, 2005; Vigliola & Meekan, 2009; Winterbottom *et al.*, 2011; Winterbottom & Southcott, 2008). For each individual, two counts of each otolith were made on separate occasions and the mean was calculated. If the initial counts differed by >10% of the mean, a third count was made. The average of the closest two counts was then taken assuming all were within 10% of the mean, and this value represented the age of the fish in days. The maximum life span was defined as the fish with the greatest number of rings in each species (Winterbottom *et al.*, 2011).

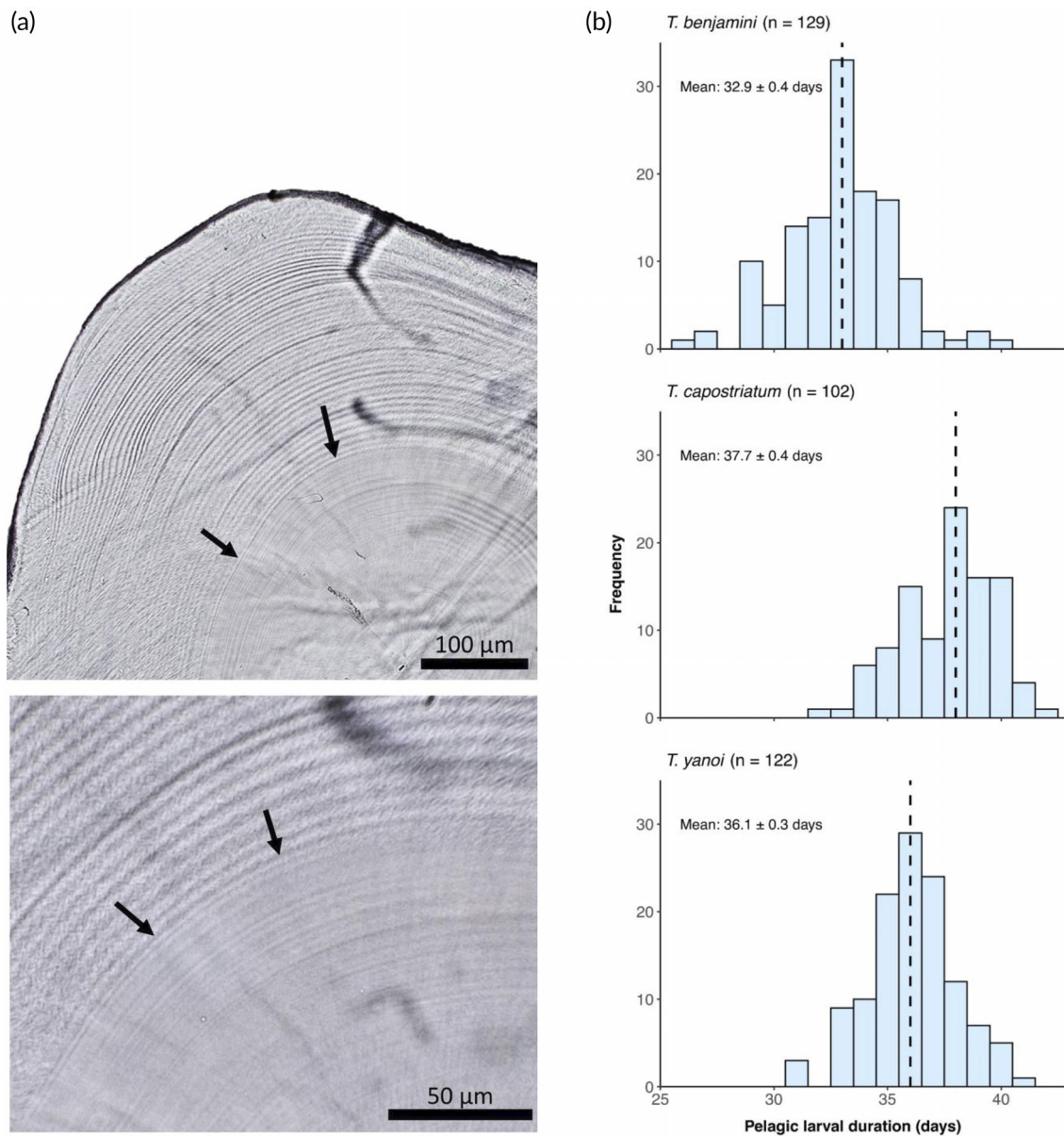
Natural daily mortality was estimated by three methods and was calculated separately for each species. The first method calculated mortality rate according to Hoenig's equation, which is derived from experimental evidence over a broad range of marine taxa ( $r^2 = 0.82$ ):  $\ln Z = 1.46 - 1.01 \ln T_{\max} \cdot Z$  is the instantaneous mortality rate and  $T_{\max}$  the maximum age (Hoenig, 1983). Secondly, mortality was calculated with the Chapman and Robson estimator using the frequency of individuals in 10 day age class bins. This model is based on the concept that the descending section of the catch-at-age data followed a geometric probability distribution, which was used to estimate the survival ( $S$ ) parameter.  $Z$  was calculated from these estimates of  $S$ , where  $S = e^{-Z}$  (Chapman & Robson, 1960; Winterbottom *et al.*, 2011). Finally, mortality was calculated using the catch curve regression estimator (Dunn *et al.*, 2002) by fitting a linear regression to the descending section of a 10 day age frequency plot after log transformation to obtain estimates of  $Z$ . Estimates of  $Z$  from the Chapman and Robson estimator and the catch curve regression estimator were converted to daily mortality using  $\frac{(1-e^{-Z})}{10}$  and expressed as a percentage.

### 2.3 | Pelagic larval duration

Settlement was determined by a change in contrast from more opaque (pre-settlement) to less opaque (post-settlement) and/or a decrease in increment width in each otolith (Figure 1a, Wilson & McCormick, 1999). The number of rings pre-settlement indicated the PLD and the maximum post-settlement life span was the difference between the PLD and maximum age. Differences in mean PLD among species were assessed using a one-way ANOVA and *post hoc* Tukey's honestly significant difference (HSD) test.

### 2.4 | Maturation

Length and age at maturity were defined as the  $L_S$  and age at which 50% of specimens were sexually mature females (sex determined by gonad structure, see below). Estimations of maturity were obtained by



**FIGURE 1** (a) *Trimma yanoi* otolith showing daily growth increments and a change in optical density pre- and post-settlement. Arrows indicate settlement mark. Not all pre-settlement increments are visible in this focal plane. (b) Frequency distribution of pelagic larval duration (PLD) in *Trimma benjamini* ( $n = 129$ ), *Trimma capostriatum* ( $n = 102$ ) and *T. yanoi* ( $n = 122$ )

fitting a logistic regression function to the proportional frequency of juveniles to females in 1 mm  $L_S$  class intervals and 10 day age class intervals (Lowe *et al.*, 2021). Individual logistic regression curves were fitted for each species, and 95% C.I. were determined using a Gaussian error distribution (Antle *et al.*, 1970). For each species, time spent as a juvenile was calculated as the difference between the mean PLD and the age at maturity, and time spent as a reproductively viable adult was taken as the difference between the age at maturity and the maximum life span. Finally, the dimensionless ratio  $\frac{\text{length at maturity}}{\text{maximum } L_S}$  was calculated for each species, which shows the proportional lengths that are expended before and after maturation (Tsikliras & Stergiou, 2014).

## 2.5 | Reproduction

Reproductive phases and strategies were assessed by histological examination of the gonads. After capture of specimens, abdomen sections were dissected just anterior to the anus and were placed in a formaldehyde 4%, acetic acid 5%, calcium chloride 1.3% (FAACC) fixative for 3 days, and then transferred to 70% ethanol. At the time of processing, abdomens were placed in a tissue processor, embedded in paraffin wax with the body cavity facing down, sectioned to 5 μm using a microtome, mounted on glass microscope slides and stained with Mayer's haematoxylin and Young's eosin-erythrosine (H&E). 5–15 sections were taken per specimen, separated by 50–200 μm to

**TABLE 1** Results for *Trimma benjamini* ( $n = 129$ ), *Trimma capostriatum* ( $n = 102$ ) and *Trimma yanoi* ( $n = 122$ ) showing (a) maximum recorded life span (days) and body size ( $L_S$ , mm), (b) daily mortality estimated by Hoenig's equation, the Chapman–Robson estimator and catch-curve regression estimator and (c) age (days) and length (mm, proportion of max  $L_S$ ) at maturity

		<i>T. benjamini</i> $n = 129$	<i>T. capostriatum</i> $n = 102$	<i>T. yanoi</i> $n = 122$
a. Body size and life span	Maximum life span (days)	130.0	137.5	126.5
	Maximum $L_S$ (mm)	24.0	24.5	22.0
b. Daily mortality	Hoenig's equation (%)	3.2	3.0	3.2
	Chapman–Robson estimator (%) <sup>a</sup>	5.4 ± 1.0	6.1 ± 0.6	4.4 ± 1.1
	Catch-curve regression (%) <sup>a</sup>	5.1 ± 2.8	6.7 ± 3.0	4.4 ± 2.8
c. Maturity	Age at maturity (days) <sup>a</sup>	74.1 ± 3.1	82.1 ± 3.4	81.7 ± 3.4
	Length at maturity (mm) <sup>a</sup>	15.4 ± 0.7	15.2 ± 0.9	15.8 ± 0.4
	(proportion of max $L_S$ ) <sup>a</sup>	0.64 ± 0.03	0.62 ± 0.04	0.72 ± 0.02

<sup>a</sup>Mean ± 95% C.I.

ensure an adequate representation of each gonad was captured. Histological samples were examined under a high-power microscope with transmitted light.

Ovaries and testes were classed as mature or undeveloped according to Sunobe *et al.* (2005) and Sakurai *et al.* (2009). Ovaries were classed as mature when the most advanced oocyte present in the gonads was vitellogenic or hydrated, and undeveloped when ovaries contained only previtellogenic oocytes. Testes were classed as mature when consisting of expanded sperm ducts containing many free spermatozoa, and a developed, lobed and secreting accessory gonadal structure (AGS) attached to each testis was evident (Cole, 1990). Testes were classed as undeveloped when spermatozoa were absent or present in small amounts with no sperm ducts evident, and the testes-associated AGS was undeveloped and was non-lobed and non-secreting. The term bisexual refers to a gonad structure consisting of both ovarian and testicular tissue, and does not refer to bisexual function (Lowe *et al.*, 2021).

### 3 | RESULTS

#### 3.1 | Body size, longevity and mortality

*T. benjamini*, *T. capostriatum* and *T. yanoi* exhibited small body sizes ( $L_S$ ) of  $17.2 \pm 0.5$  mm (mean ± 95% C.I.),  $17.6 \pm 0.6$  mm and  $15.8 \pm 0.7$  mm, and reached a maximum  $L_S$  of 24, 24.5 and 22 mm, respectively (Table 1a). All species were short-lived, with maximum ages of 130, 137.5 and 126.5 days in *T. benjamini*, *T. capostriatum* and *T. yanoi*, respectively (Table 1a).

Daily mortality estimates obtained from the focal *Trimma* species were high, ranging from 3.2% to 5.4% in *T. benjamini*, 3.0% to 6.7% in *T. capostriatum* and 3.2% to 4.4% in *T. yanoi* (Table 1b). Specimens younger than 95 days in *T. benjamini*, 105 days in *T. capostriatum* and 85 days in *T. yanoi* were not included in the Chapman–Robson and Catch curve analysis

(Figure 2), as their frequency suggests they may have been under sampled (Winterbottom *et al.*, 2011).

#### 3.2 | Pelagic larval duration

Clear settlement marks were able to be determined in all individuals (Figure 1a). PLD differed significantly among the three species ( $F_{(2,350)} = 148.72$ ,  $P < 0.001$ ) and ranged from 26 to 40 days in *T. benjamini*, 32 to 42 days in *T. capostriatum* and 31 to 41 days in *T. yanoi* (Figure 1b). The mean PLD (32.9–37.7 days) represented over one-fourth of the maximum life span in all species (Figure 3). Accordingly, the post-settlement life span in each species was less than 100 days (Figure 3).

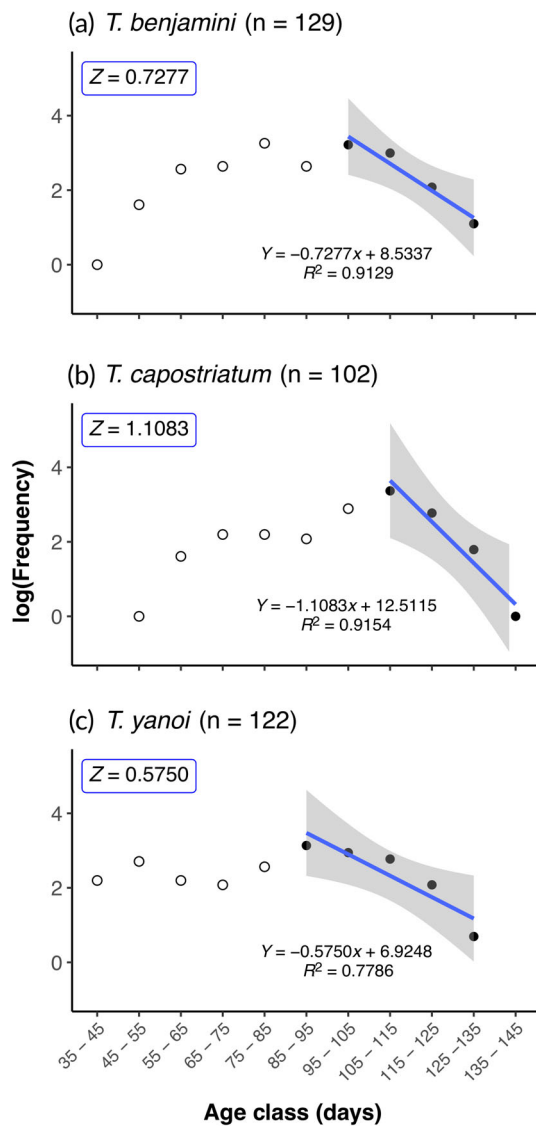
#### 3.3 | Maturation

Length at maturity (Figure 4) was similar for all three species (15.2–15.8 mm) and ranged from 0.62 to 0.72 as a proportion of the maximum  $L_S$  (Table 1c). *T. benjamini* matured the earliest at 74.1 days, followed by *T. capostriatum* and *T. yanoi*, which matured at similar ages of 82.1 and 81.7 days, respectively (Table 1c, Figure 4).

Thus, mean duration as a reproductively redundant juvenile in the species examined was 41.1–45.7 days, representing 31.7%–36.1% of the maximum life span (Figure 3). The mean reproductive window was therefore a narrow 44.8–55.9 days, representing 35.4%–43.0% of the maximum life span (Figure 3).

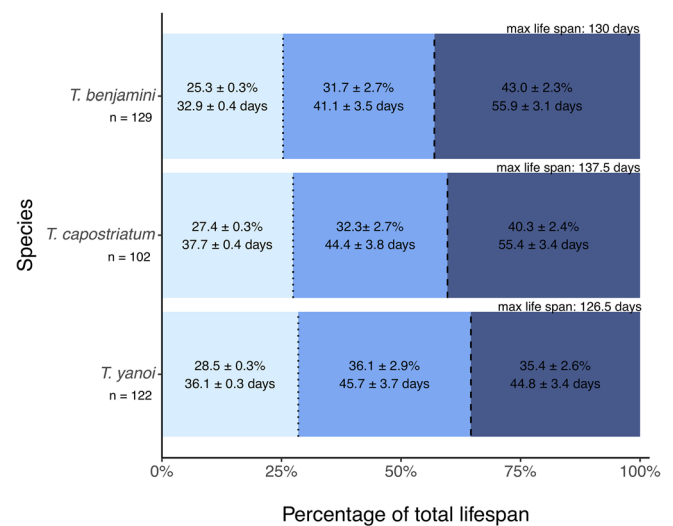
#### 3.4 | Reproduction

In total, 353 *Trimma* gonads (129 *T. benjamini*, 102 *T. capostriatum* and 122 *T. yanoi*) were analysed histologically. Aside from juveniles with undifferentiated gonadal cells, all individuals had bisexual gonads,



**FIGURE 2** Ten day age-frequency catch curve regression for the estimation of instantaneous mortality ( $Z$ ) for (a) *Trimma benjamini* ( $n = 129$ ), (b) *Trimma capostriatum* and (c) *Trimma yanoi* ( $n = 122$ ). White points show ascending limb values which were not included in the analysis and black points show descending limb values that were included in the analysis

which consisted of both ovarian and testicular portions, partitioned by a thin wall of connective tissue, and an AGS connected to each testis. This gonad arrangement was the same in all species. In female and male phase specimens, only ovaries or testes were mature at a single point in time, while gonadal tissue of the non-active sex remained; 55 (*T. benjamini*), 61 (*T. capostriatum*) and 39 (*T. yanoi*) individuals were female phase, evident by mature ovaries and undeveloped testes. The testes consisted of spermatogonia, spermatocytes spermatids and few spermatozoa, indicating that spermatogenesis continued in the female phase. Nonetheless, no sperm ducts were evident and the AGS was undeveloped and was non-lobed and non-secreting (Figure 5a,b); 25 (*T. benjamini*), 14 (*T. capostriatum*) and 26 (*T. yanoi*) specimens were male phase. These individuals had mature testes and undeveloped

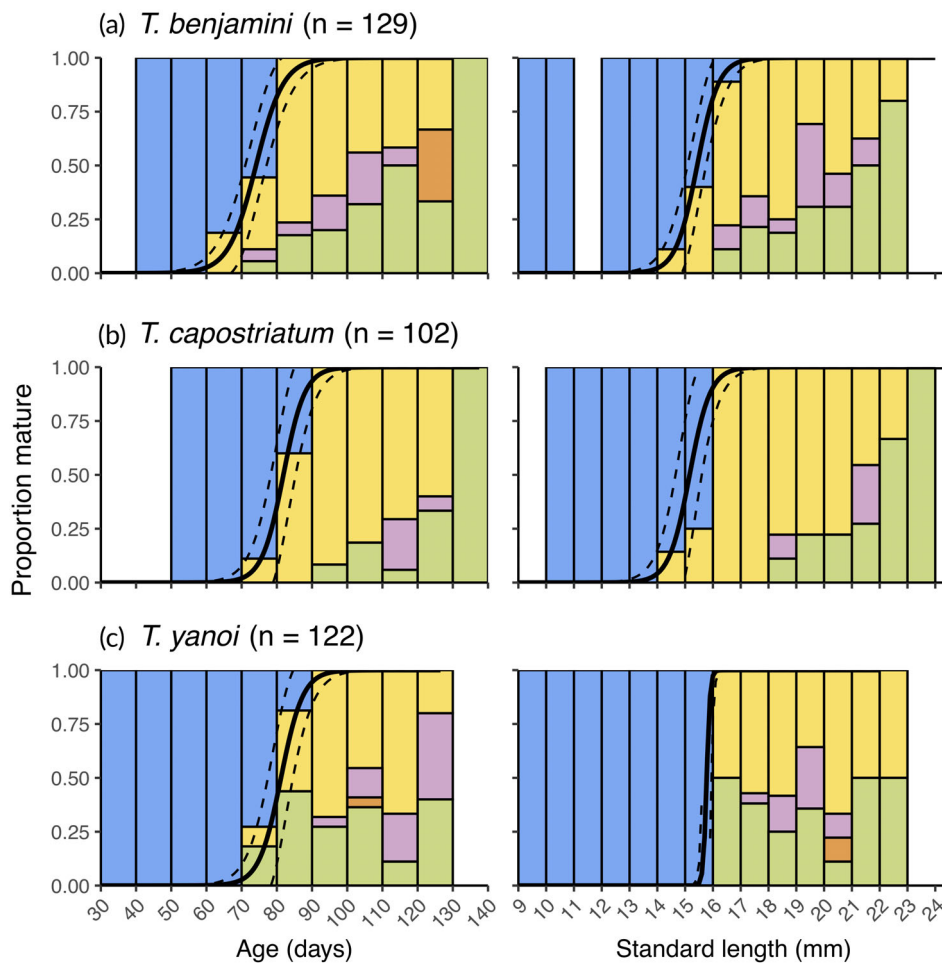


**FIGURE 3** Number of days and percentage of maximum life span (mean  $\pm$  95% C.I.) spent in each life stage (pelagic larvae, juvenile and adult) for *Trimma benjamini* ( $n = 129$ ), *Trimma capostriatum* ( $n = 102$ ) and *Trimma yanoi* ( $n = 122$ ). Dotted and dashed lines represent settlement and maturity, respectively. Life stage: ( ) pelagic larvae, (■) juvenile and (■) adult. (---) Settlement and (---) maturity

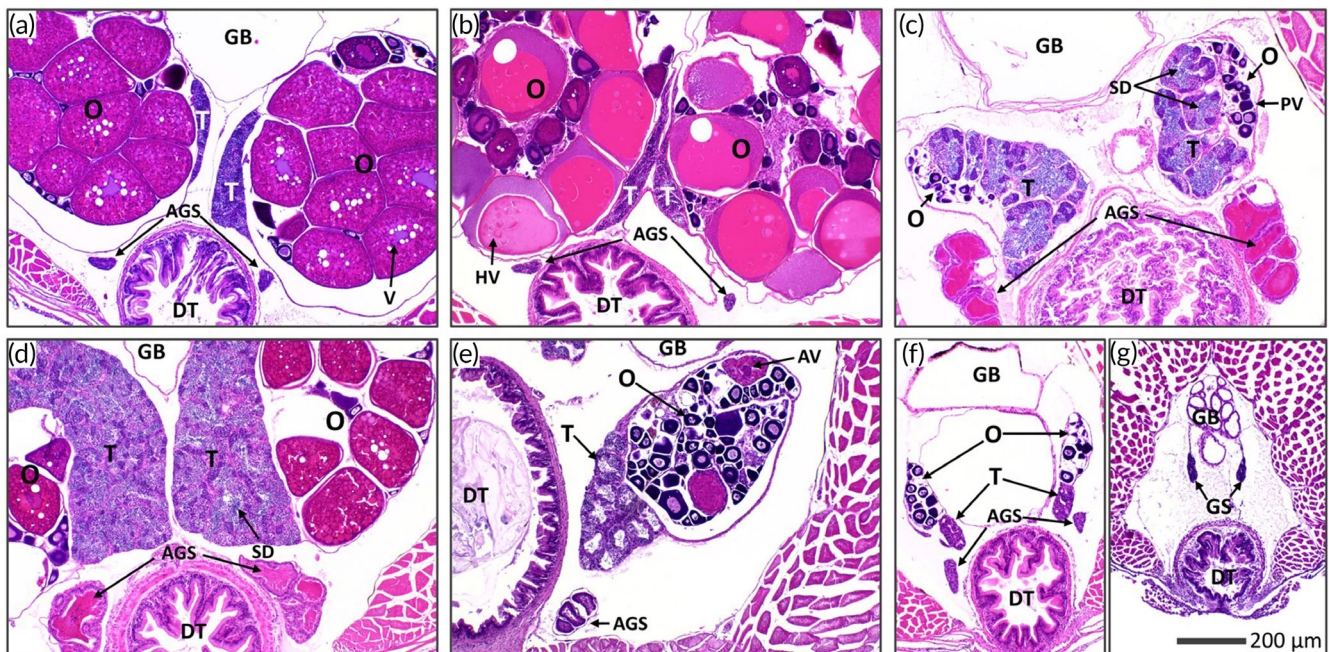
ovaries, which consisted of a small section containing few previtellogenic oocytes (Figure 5c). The male:female sex ratios were 1:2.2 in *T. benjamini*, 1:4.4 in *T. capostriatum* and 1:1.5 in *T. yanoi*. Two specimens (one each of *T. benjamini* and *T. yanoi*) had both mature ovaries and testes simultaneously and were thus labelled as a hermaphrodite (referring to gonad structure and not necessarily function; Figure 5d). Thirteen *T. benjamini*, five *T. capostriatum* and eight *T. yanoi* individuals had ovaries and testes at intermediate levels of development and were thus labelled as transitional phase. Gonads in this phase consisted of ovaries with degenerating atretic oocytes and testes with proliferating spermatogenic tissue or degenerating spermatogenic tissue and proliferating oocytes. The AGS was lobed but non-secreting or secreting small amounts (Figure 5e). Thirty-five (*T. benjamini*), 22 (*T. capostriatum*) and 48 (*T. yanoi*) specimens had no mature ovarian or testicular tissue present and were classified as juveniles. Gonads of these individuals were either bisexual, with ovaries that contained previtellogenic oocytes, testes with spermatogonia and an undeveloped AGS (Figure 5f), or consisted entirely of undifferentiated gonadal germ cells (Figure 5g).

## 4 | DISCUSSION

The findings of this study indicate that the most prominent feature of *Trimma* spp. life histories is an extreme constraint on the time available for reproduction. All three species examined were characterized by small body size, short life span and high mortality, relatively long PLD, time taken to mature after settlement and bisexual gonad development. Only 35%–43% of the total life span was available for reproduction. Together, these life-history characteristics



**FIGURE 4** Proportional frequency distributions of the sexual phase-specific age and length structure of (a) *Trimma benjamini* (n = 129), (b) *Trimma capostriatum* (n = 102) and (c) *Trimma yanoi* (n = 122). Estimated age and length at maturity trajectory are shown by solid logistic regression lines and the associated 95% C.I. is shown by dashed lines. (—) Maturity, (■) juvenile, (■) female, (■) intermediate, (■) hermaphrodite and (■) male



**FIGURE 5** Gonadal structures of female (a, b), male (c), hermaphrodite (d), transitional (e) and juvenile (f, g) phases in *Trimma benjamini* (a, d, f), *Trimma capostriatum* (c) and *Trimma yanoi* (b, e, g). AGS: accessory gonadal structure; AV: atretic vitellogenic oocyte; DT: digestive tract; GB: gas bladder; GS: germ cells; HV: hydrated vitellogenic oocyte; O: ovary; PV: previtellogenic oocyte; SD: sperm ducts filled with spermatozoa; T: testis; V: vitellogenic oocyte. n = 129 *T. benjamini*, 102 *T. capostriatum* and 122 *T. yanoi*. Scale bar 200  $\mu$ m

imply the genera is constrained both by a large proportion of life span unavailable to reproduce and high mortality owing to their small size. The results of this study conform to a previous study by Winterbottom *et al.* (2011) examining the life-history characteristics of *T. benjamini*.

The *Trimma* species in this study are among the smallest and shortest-lived fishes on coral reefs, with all individuals examined having an  $L_5$  of less than 25 mm and living less than 140 days. Small body size comes with many constraints including a short life span, high mortality risk, a long PLD relative to life span and, consequently, a short reproductive life. Because the age of coral reef fishes ranges from 59 days in *Eviota sigillata* (Depczynski & Bellwood, 2006) to 81 years in *Macolor macularis* (Taylor *et al.*, 2021), *Trimma* were at the lower end of the spectrum, which is also seen in other small CRFs (e.g., Beeken *et al.*, 2021; Depczynski *et al.*, 2007; Longenecker & Langston, 2005). Consequently, the maximum window available for reproduction is very narrow.

Estimated daily mortality of 3.0%–6.7% per day is comparable to high mortality rates seen in other small-bodied CRFs (Depczynski & Bellwood, 2006). With a small body size of <25 mm, *Trimma* species never reach the size threshold of c. 43 mm where mortality in larger species has been observed to decline. Consequently, they remain at high risk of mortality throughout their entire life. Predation is assumed to be the main cause of mortality in CRFs. Furthermore, Goatley *et al.* (2017) propose predation rates are variable as a result of habitat or behavioural differences between species. *Trimma* species inhabit exposed reef slopes and drop offs on coral reefs, where they predominantly perch on hard substrata (Winterbottom, 2019), and may be victims of predation because of limited sheltering opportunities (Brandl *et al.*, 2018). Moreover, the average size difference between predator and prey is strikingly small at 12.1 mm (Goatley *et al.*, 2017). Therefore, *Trimma* species may be subject to predation by not only large fishes, but also small ones.

The PLDs of the three *Trimma* species examined represented a substantial proportion of their maximum life span (>25%), which is high, compared with the <1% demonstrated by many larger coral reef fishes (Depczynski & Bellwood, 2006). Yet, spending over a quarter of the life span as pelagic larvae is not unique to *Trimma* and is seen in other CRFs such as the genera *Coryphopterus* (Beeken *et al.*, 2021), *Eviota* (Depczynski & Bellwood, 2006) and *Enneapterygius* (Longenecker & Langston, 2005). An extensive PLD to allow growth to a sufficient size may be a strategy to decrease extreme mortality of small recruits (Beeken *et al.*, 2021). Some fishes that settle into protective habitats with lower post-settlement mortality have a reduced PLD (Depczynski & Bellwood, 2006). For example, *Amphiprion melanopus* settle directly into anemone hosts that provide protection from predators. Thus, they experience short PLDs of <15 days and are capable of settlement at <7 mm (Job & Bellwood, 2000). In contrast, *Trimma* species mainly settle onto hard substrata on exposed reef slopes and drop offs, which are not well protected (Winterbottom, 2019), and may suggest a minimum size threshold to reduce post-recruitment mortality (Depczynski & Bellwood, 2006; Goatley & Bellwood, 2016). Accordingly, their PLD reduces their post-settlement life on coral reefs to just 90–100 days,

during which they need to complete metamorphosis, find a suitable home, grow, mature and reproduce.

Maturation in the *Trimma* spp. examined was fast compared to most fishes. For example, mean age and lengths at maturity of Mediterranean Actinopterygii were 2.2 years and 20.7 cm, respectively, with maximum maturity at 12 years in *Epinephelus marginatus* (Tsikliras & Stergiou, 2015) and 223.5 cm in *Xiphias gladius* (Tsikliras & Stergiou, 2014). The ability for *Trimma* to rapidly mature in 74.1–82.1 days at 15.2–15.8 mm allows them to complete reproduction despite extremely short life spans. Nonetheless, length at maturity as a proportion of the maximum  $L_5$  was 0.62–0.72 in the three *Trimma* species, which was notably later than the average of 0.59 (s.d. = 0.122,  $n = 471$ ) for Actinopterygii (Tsikliras & Stergiou, 2014). Several CRFs with short life spans mature earlier than this average, which is consistent with life-history theory. For example, *Eviota queenslandica* mature at 0.51 of the maximum length and 0.42 in *Eviota melasma* (Depczynski & Bellwood, 2006). However, like the *Trimma* species examined, some CRFs mature later than this average. For example, *E. sigillata* mature at 0.62 of the maximum length (Depczynski & Bellwood, 2006). Maturation in such fishes can occur later than the average for several reasons. Firstly, fecundity may be low near the minimum body size threshold for maturation, because of female fecundity declining with decreasing body cavity size as they produce and carry fewer eggs (Hernaman & Munday, 2005b). At the same time, reproduction is energetically costly and may come at the risk of heightened mortality as a result of increased foraging activity to fuel reproduction. It may therefore be beneficial for these small fishes to delay reproduction to attain a larger size where fecundity is greater (Audzijonyte & Richards, 2018). In addition, intrasexual competition may favour a delay in maturation. Harem polygyny is the most common mating system recorded in *Trimma* (Sunobe *et al.*, 2017), where larger males achieve a higher level of reproductive success than smaller males because of being more competitive for mates or territory (Fukuda *et al.*, 2017b; Fukuda & Sunobe, 2020; Manabe *et al.*, 2008; Sakurai *et al.*, 2009, 2017; Sunobe & Nakazono, 1990). Moreover, females in polygynous groups may compete for breeding resources such as breeding sites, food and paternal care by males. Accordingly, small subordinate females may be largely excluded from breeding, thus favouring maturation at a larger size (Wong *et al.*, 2008). Delaying maturation therefore may have several benefits; yet, it severely decreases the time these fishes have as reproductively viable adults to just 45–56 days. It also exposes them to increased risk of mortality before any reproduction is achieved.

Sex change strategies can be inferred by gonad structure (Lowe *et al.*, 2021; Sunobe *et al.*, 2017). The high number of individuals with gonads in a transitional state indicates that sex change may occur frequently in the three species examined here. Excluding the two individuals with hermaphrodite phase gonads, all mature individuals had testes or ovaries active at any one time, while the tissue of the non-functional sex was retained, as has been described previously (Cole, 1990; Fukuda *et al.*, 2017b; Manabe *et al.*, 2008; Sakurai *et al.*, 2009; Sunobe *et al.*, 2017; Sunobe & Nakazono, 1993). In protandrous species, bisexual gonads occur in initial phase males, which have an inactive ovarian portion. Nonetheless, ovarian tissue



completely displaces testicular tissue after transition to the female phase, leaving no remaining testicular tissue (Chang & Yueh, 1990; Law & Sadovy de Mitcheson, 2017; Sunobe *et al.*, 2016). In the initial female phase of protogynous species, some individuals have small sections of germ cells or spermatogonia, whereas others contain no spermatogenic tissue. In all species, no ovarian tissue is retained after sexual transition (Bhandari *et al.*, 2003; Nakamura *et al.*, 1989; Sundberg *et al.*, 2009). Retention of bisexual gonads in both female and male phases indicates that the *Trimma* species examined are always potentially capable of functioning as either female or male and thus likely exhibit bidirectional sex change (Munday *et al.*, 2010; Sunobe *et al.*, 2017).

Bidirectional sex change is reported as rare in coral reef fishes (Yamaguchi & Iwasa, 2018), occurring in just 4.1% of known hermaphroditic species outside of the *Gobiidae* (16 of 395 species; Kuwamura *et al.*, 2020). Yet, it is the most common type of hermaphroditism in the *Gobiidae*, with *c.* 75% of known hermaphroditic gobies (50 of 66 species) displaying sex change in both directions (Kuwamura *et al.*, 2020). In polygynous *Trimma okinawae*, sex change is induced by a change in social status (Kobayashi *et al.*, 2009), where individuals become the sex that will result in the highest reproductive success in accordance with the size-advantage hypothesis of sex change (Munday *et al.*, 2006). The loss of the dominant male from a polygynous group can result in the largest female changing sex to become the dominant male (Manabe *et al.*, 2007; Sunobe & Nakazono, 1993) and reverse sex change from male to female occurs when all females in a group disappear, and the resultant bachelor male enters a group with a larger residing male (Manabe *et al.*, 2007). The *Trimma* species examined have female-biased sex ratios indicating polygyny is a likely mating system (Winterbottom *et al.*, 2011), and therefore the benefits of bidirectional sex change in these species may be akin to other polygynous members of the genus. Bidirectional sex change can be valuable when a male's social circumstances may change drastically and unexpectedly and when a delay in selecting new mates may cause a significant decrease in reproductive output. Because of high and unpredictable mortality in the three *Trimma* species examined, the loss of individuals and changes to mating circumstances is likely a common phenomenon. Thus, the ability to change sex in both directions depending on the social circumstances present may increase overall reproductive value.

Possessing ovarian and testicular portions in both female and male phase individuals can avoid entire gonad reconstruction and may allow for rapid sex change in small gobies with short life spans and high mortality rate (Munday *et al.*, 2010; Munday & Molony, 2002; Yamaguchi & Iwasa, 2017). In contrast, the *Trimma* species examined retain ovarian and testicular portions in both male and female phases. Sex change in *Trimma* involves the tissue of one sex rapidly proliferating while tissue of the other sex degenerates, and total gonad repurposing is avoided (Sunobe *et al.*, 2005). Sex change can occur in as little as 4 days (female to male) and 6 days (male to female) in *T. okinawae* (Sunobe & Nakazono, 1993; Yamaguchi, 2016). Bisexual gonads in both male and female phases are seen in other small fishes with short reproductive life spans and high mortality, such as the genera *Eviota* (Maxfield & Cole, 2019a; Schemmel & Cole, 2016),

*Lythrypnus* (Maxfield & Cole, 2019b; Muñoz-Arroyo *et al.*, 2019), *Bryanninops* (Munday *et al.*, 2002), *Priolepis* (Manabe *et al.*, 2013) and multiple other *Trimma* species (Sunobe *et al.*, 2017). High and unpredictable mortality can mean that an individual's social circumstances can quickly change. Therefore, rapid change from one sex to another may be an advantage with the limited reproductive period these fishes experience (Munday *et al.*, 2010; Yamaguchi, 2016; Yamaguchi & Iwasa, 2017).

One *T. benjamini* individual and one *T. yanoi* individual exhibited gonads with both active ovarian and testicular regions, which has not been observed in this genus before. This gonadal structure may indicate rare occurrences of simultaneous hermaphroditism, where individuals can function as both female and male simultaneously (Sakakura *et al.*, 2006; Tuset *et al.*, 2005). Alternatively, it could represent a period where individuals are capable of acting as both female and male during sexual transition. This could maximize the available reproductive time, as individuals can remain reproductively active rather than being reproductively redundant for the duration of the sex change process. However, in other species of *Trimma* the tissue of one sex degenerates while the tissue of the other sex proliferates, and there is no evidence of simultaneous hermaphroditism during this process (Sunobe *et al.*, 2005). Periods of simultaneous hermaphroditism during sex change may be a rare occurrence, or happen quickly, which may explain why this stage has not been captured in previous studies. Moreover, having the gonad structure of a simultaneous hermaphrodite does not necessarily mean they function as one. For example, most *Lythrypnus zebra* individuals have a gonad structure comparable to that of a simultaneous hermaphrodite, despite functioning as a single sex (Munday *et al.*, 2010; St. Mary, 1996). Further population histological studies in *Trimma* are warranted to confirm if these rare individuals are functional or non-functional simultaneous hermaphrodites, or if this phenomenon occurs only during sex change.

Despite the life-history constraints associated with small body size, small-bodied fishes still persist. Furthermore, the majority of reef fishes are small, with the average length being just 45 mm (Bellwood *et al.*, 2017). There may be several reasons for this, including the ability to exploit a range of small habitats, increased agility, low energy demands per individual and the ability to grow and reproduce quickly, leading to a high rate of population increase (Blanckenhorn, 2000; Brandl *et al.*, 2018, 2019; Depczynski & Bellwood, 2006; Winterbottom *et al.*, 2011). Here, the authors show that an expanding number of small CRFs maintain a dual-gonad arrangement, which may be advantageous to maximize reproductive potential in species where a short reproductive life is combined with high and unpredictable rates of mortality that can dramatically and unpredictably alter social living conditions that individuals experience.

#### AUTHOR CONTRIBUTIONS

N.C.G., M.S., P.L.M. and G.P.J. contributed to initial project conceptualization. N.C.G., M.S., L.C.C., P.L.M. and G.P.J. formulated methodology. N.C.G. collected specimens, and N.C.G. and L.C.C. performed laboratory work. N.C.G. analysed data and wrote the manuscript. All authors contributed to final manuscript preparation.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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