

Hatch date and growth rate drives reproductive success in nest-guarding males of a temperate reef fish

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ABSTRACT: Identifying sources of variation in individual reproductive success is crucial to our understanding of population dynamics and evolutionary ecology. We evaluated sources of variation in reproductive success of the common triplefin *Forsterygion lapillum*, a species with male parental care. We characterised breeding success of adult males during the breeding season (using presence of eggs and/or breeding territories as proxies for success), measured their phenotypic traits (body size and condition) and used their otoliths to reconstruct life history characteristics (hatch dates and average growth rates). Our reconstructions of life history traits suggested at least 2 alternative pathways to success for adult males. More successful males hatched earlier and therefore had a developmental head-start over less successful males (age of males with eggs > age of male territory holders without eggs > age of males without territories, i.e. 'floaters'). Alternatively, our reconstructions suggested that reproductive success of males was predicted by growth rates: for males born in the same month, those with eggs grew faster than those with territories and no eggs, and both groups grew faster than floaters. These results suggest that accelerated growth rate may compensate for the effects of a later hatch date, and that both hatch dates and growth rates influence the success of adult males, likely through proximate effects on individual phenotypes.

KEY WORDS: Reproduction · Life history · Parental care · Reef fish · Otolith microstructure · Demographic history · Common triplefin · *Forsterygion lapillum*

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INTRODUCTION

Variation in individual reproductive success is a cornerstone of evolutionary theory (Williams 1992). Although much research has evaluated determinants of reproductive success for a wide variety of organisms and systems, these remain poorly known for many species (Clutton-Brock 1988). Body size, condition, growth and timing of birth/hatching/germination are among the many factors identified as important contributors to reproductive success across many different taxa, including plants (Warwick & Brock 2003, Winter et al. 2008), reptiles (Ruby 1984, Mad-

sen et al. 1993, Olsson & Shine 1996), mammals (Wauters & Dhondt 1989, Hodge et al. 2008), birds (Lozano et al. 1996, Mauck et al. 2004) and fishes (Jacob et al. 2009, Buston & Elith 2011).

In many animal systems, females select male mates in an attempt to maximise their own fitness (Andersson 1994). Sexual selection theory (Andersson 1994) suggests that females are likely to favour males with traits that signal fitness benefits to the female (i.e. traits that could increase the number of offspring that survive to reproductive age). Female choice is particularly common in species where males defend nests or care for young (and indeed, female choice can

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drive the evolution of male parental care; Alonzo 2012). In these systems, male reproductive success may also be determined by the quality of care that males are able to provide to their offspring (Andersson 1994, Møller & Thornhill 1998).

The question of 'what makes a good male' has been addressed for many species with male parental care. For example, females of the sand goby *Pomatoschistus minutus* appear to prefer males with better nesting sites (Lehtonen & Lindström 2009). In other species, females may assess male quality based on courtship and parental behaviour patterns of males (Oliveira et al. 2000, Reid et al. 2004), or by the choices made by other females (Alonzo 2008). For many species with male parental care, females tend to favour males with larger body size and/or greater body condition (e.g. Bisazza & Marconato 1988, Magnhagen & Kvarnemo 1989). Body size and/or condition may be good indicators of sufficient energetic reserves that enable males to care for offspring over longer durations (Côte & Hunte 1989, Lindström & Hellström 1993). For pouch-brooding males, larger body size (and a larger pouch) is associated with improved survival of offspring (Dzyuba et al. 2006). Larger males often rank more highly in social dominance hierarchies, which can reduce likelihood of egg predation by conspecifics (Bisazza et al. 1989) and ensure access to better nesting sites (Perrone 1978, Magnhagen & Kvarnemo 1989, Rowland 1989, Candolin & Voigt 2001). Similarly, increased body condition may provide honest signals to females of a male's increased reproductive output (Chastel et al. 1995), attractiveness to other females (Morales et al. 2003) or prolonged lifespan (Kasumovic et al. 2009).

Body size and condition are often functions of age and growth rate. 'Age', in turn, is a function of an individual's birth (or hatch) date. Individuals born earlier will have more time to grow and may attain a larger size by the onset of a breeding season (Lindholm et al. 1994, Cargnelli & Gross 1996, Taborsky 1998). However, age may become decoupled from size if an earlier birth date means that important periods of growth happen under less opportune conditions (e.g. where scope for growth is highly seasonal). For this reason, a consideration of absolute birth (or hatch) date may be useful. If female choice favours males with increased body size and/or condition, then birth (or hatch) dates and/or growth rates may shape the reproductive success of males (Taborsky 1998).

Additionally, the potential influence of birth dates and growth rates may extend beyond body size and condition. Variation in growth rate can influence longevity (reviewed by Metcalfe & Monaghan 2003)

and/or timing of maturation (Rowe & Thorpe 1990). Similarly, variation in hatch dates can affect timing of maturation (Uller & Olsson 2010), vulnerability to predators (Kurban 1982) and/or future reproductive tactics (Fagundes et al. 2015, Welsh et al. 2017).

Alternative reproductive tactics are an important aspect of many fishes with male parental care. For example, males of the ocellated wrasse *Symphodus ocellatus* use different reproductive tactics based on their size and age (Alonzo et al. 2000); the largest males construct and defend nests, and are often aided by intermediate-sized 'satellite males' that attract females and defend the nest from the smallest males that employ a 'sneaker' (i.e. parasitic) tactic (reviewed by Alonzo & Warner 2000a). Fitness pay-offs vary among male tactics, and detailed studies of this system have contributed greatly to our understanding of the evolution of life history strategies (e.g. Alonzo & Warner 2000a,b, Alonzo & Heckman 2010, Alonzo 2012). Importantly, tactics used by males appear to be shaped by their age (birth date) and by their growth history (Alonzo et al. 2000).

The 'birthdate effect' (sensu Taborsky 1998) has also been evaluated for the peacock blenny *Salaria pavo*, another well-studied reef fish with alternative reproductive tactics (males may defend nests or engage in a sneaker strategy; Goncalves et al. 1996). Fagundes et al. (2015) conducted an extended mark-recapture study of peacock blennies and concluded that nest-holding males were born earlier in the season, but had similar growth rates to sneaker males.

Here, we investigated a set of age-based demographic traits that may contribute to male reproductive success in the common triplefin *Forsterygion lapillum*. This species has male parental care and an accessible record of life-history traits associated with developmental history (provided by the growth increments recorded within the 'ear stones', or otoliths). We quantified morphological traits and reconstructed life-history traits of adult males that differed in their breeding status. We evaluated a set of non-mutually exclusive hypotheses that male breeding status is predicted by (1) body size and/or condition, (2) timing of hatching and/or (3) growth rate during development.

MATERIALS AND METHODS

Study species

The common triplefin is a small temperate reef fish, widely distributed around the New Zealand coast

(Francis 2001). Common triplefin are exposed to a range of environments associated with ontogenetic shifts throughout their lifetime. Eggs are laid over much of the year, on cobble substrate of coastal rocky reefs (Feary & Clements 2006, Wellenreuther & Clements 2007) and larvae hatch after ~2–3 wk (Francis 2001). After ~52 d, larvae return to rocky reefs (Shima & Swearer 2009) and settle within fronds of brown algae (McDermott & Shima 2006). Juveniles migrate from algal canopies to benthic cobble habitats and become reproductively mature after several months (typical life expectancy is ~1–1.5 yr, Moginie 2016).

During the main spawning season (August to November for the study location), sexually mature males develop 'nuptial pigmentation', characterised by a change from a mottled, pale-brown body colouration to a more uniformly black body colouration, typically with a blue margin along the anal fin (Wellenreuther & Clements 2007). Sexually mature males often defend small territories (~1 m²) that contain potential nesting sites (typically the underside of a cobble; Francis 2001), and will actively court passing females (Handford 1979). Adult females lay eggs within the nest of a chosen male, and thereafter, the male provides sole parental care that consists of aeration and defence of eggs until hatching. Males routinely guard clutches of ~2000 eggs (likely from multiple females), and may care for multiple clutches throughout their reproductive lifetime (Mensink et al. 2014). Alternative male reproductive tactics (e.g. sneaker males, satellite males; Alonzo & Warner 2000a) have not been documented for this species and it is not known if these are a feature of this system (although alternative reproductive strategies have been documented for other triplefin species; de Jonge et al. 1989).

Sampling the breeding population

We sampled a breeding population of the common triplefin to evaluate relationships between 'breeding status' and a set of life history traits. We collected adult males from a single site with a large population of common triplefin (Kau Bay in Wellington Harbour, 41° 17' 12" S, 174° 49' 43" E). Collected individuals were immediately euthanized in accordance with ethical standards (AEC 2012R10). Collections of new individuals were made repeatedly over a 4 mo period during a breeding season (August to November 2014). Males were identified from nuptial pigmentation (gender was confirmed with subsequent dissection). We sampled males haphazardly (individuals were targeted and collected using hand nets) on

a permanently marked transect running parallel to the shoreline for 60 m, along a 5 m depth contour. This breeding population was sampled repeatedly over 15 sampling dates between August and November. We estimated that each collection removed ~0.6 % of the local population (we make an assumption that our collections had minimal effects on the social interactions and mating opportunities of resident fish).

Characterising breeding status

We used 2 criteria to characterise the 'breeding status' of each sampled male prior to collection. Firstly, we classified each fish as either 'territorial' or 'non-territorial' based on visual observations of focal individuals (3 min duration). Fish classified as territorial showed evidence of site attachment (i.e. returns after displacement; Maher & Lott 1995), exclusive habitat use (i.e. the sole occupant of the cobble; Petty & Grossman 2007) and behaviour patterns consistent with territorial defence (i.e. chases directed at other encroaching individuals; Maher & Lott 1995). Secondly, for all fish that were characterised as territorial, we scored the presence or absence of eggs at their nesting site. This method facilitated categorisation of 'breeding status' as follows: (1) non-territorial males ('floaters'), (2) territorial males without eggs or (3) territorial males with eggs. We acknowledge that this approach categorises the breeding status of individuals based on a single observation (and this point sampling introduces a source of error). However, we make an assumption that (1) this error is randomly distributed, and (2) our sampling effort is sufficient to enable us to evaluate a potential relationship between breeding status and measured traits despite this error.

Estimating predictors of breeding success

We quantified a set of phenotypic and life-history traits for sampled males and evaluated their ability to predict variation in breeding status. Specifically, we measured the size (standard length, SL) of fish to the nearest millimetre using callipers, and quantified mass (wet weight) to 0.0001 g using a microbalance. We calculated body condition (Fulton's *K*; Ricker 1975) as:

$$K = \frac{\text{wet weight}}{\text{SL}^3} \quad (1)$$

Additionally, we used otoliths to reconstruct individual life histories (dates of hatching and lifetime

growth rates). Specifically, we extracted sagittal otoliths from each fish and placed them in 15 % mol H_2O_2 for 12 h to remove adhered tissue. Otoliths were then mounted on plastic discs in a clear resin and hand-polished with 9 μm diamond lapping film (3M) to expose daily growth increments. We evaluated a single otolith for each fish, and took a series of photos along the postrostral axis using a Canon D3-50 camera affixed to a Leica compound microscope. Images were then aligned in a common focal plane, using natural imperfections in the otoliths as reference points, to obtain a complete and uninterrupted record of daily otolith increments. We used image analysis software (ImagePro Premier 9.2) to process images, and to count daily increments. We did not obtain estimates of individual otolith increment widths because we were unable to resolve these along a common growth axis for most sampled individuals. We identified a 'hatch check' as an approximate doubling in increment width near the centre of the otolith (after Shima & Swearer 2009). For each fish, we estimated cumulative 'age' as the number of increments from the hatch check to the otolith edge. We calculated a 'hatch date' as the difference between the 'collection date' (date fish was sacrificed) and 'age'. We estimated 'mean growth rate' over the lifetime of the fish as SL divided by 'age'.

Statistical analyses

Males collected over 15 sampling dates were pooled for all analyses. We used a general linear model ('stats' package, R version 3.2.2; R Core Team 2015) to independently evaluate the hypotheses that males of differing breeding status (i.e. floaters, territory holders without eggs or territory holders with eggs) varied in: (1) size (SL), (2) body condition (Fulton's K) and (3) hatch date.

We evaluated variation in growth rate (response variable) as a function of hatch date (modelled as a continuous variable), breeding status and the interaction between hatch date and breeding status. Additionally, for a subset of hatch dates (March and April 2014), we investigated differences in growth rate between males of different reproductive status, after statistically accounting for variation in hatch date between males (using 'least square' [LS] means). We evaluated variation in these adjusted growth rates among males of differing reproductive status using Tukey tests. Assumptions of statistical tests were satisfactorily met for all statistical analyses. We used the packages 'LSmeans' (Lenth 2016) to evalu-

ate differences between adjusted growth rates, 'CAR' (Fox & Weisberg 2011) to assess the assumption of linearity in our general linear models and 'stats' (R version 3.2.2; R Core Team 2015) to perform ANOVAs and our general linear model.

RESULTS

We sampled 141 adults, and of these, 55 (39%) were identified as floater males and 86 (61%) were identified as territorial males. Eggs were present in 47 of the 86 territories and absent in the remaining 39. We were not able to reconstruct hatch dates and/or growth rates for all sampled fish due to imperfections in otoliths. We successfully resolved daily otolith increments for the entire postrostral axis for a subset of 51 males (20 floater males, 18 territorial males without eggs and 13 males with eggs present), which facilitated estimates of 'hatch date' and 'growth rate' for these individuals.

Effects of body size and condition on breeding status

Size (SL) of males ranged from 33.90 to 53.07 mm, and varied significantly with breeding status ($F_{2,138} = 22.566$, $p < 0.001$; Fig. 1a). Territorial males were ~4 mm (or roughly 10%) larger than non-territorial males, but the sizes of territorial males did not vary with presence or absence of eggs (Fig. 1a). Body condition (g mm^{-3}) of males ranged from 8.54×10^{-6} to 2.05×10^{-5} and varied significantly with reproductive status ($F_{2,138} = 9.886$, $p < 0.001$; Fig. 1b). Body condition did not differ between floater males and territorial males without eggs. However, territorial males with eggs had a condition index that was 6.1% greater than the other 2 groups (Fig. 1b).

Effect of hatch date on breeding status

Life-history reconstructions from otoliths suggest that sampled males hatched over a 9 mo period, from 11 October 2013 to 15 June 2014, with a median hatch date of 9 March 2014. Hatch dates differed among males of different breeding status ($F_{2,49} = 44.284$, $p < 0.001$, Fig. 2). Floater males hatched significantly later than both territorial males with eggs (Tukey: $p < 0.001$) and without eggs ($p < 0.001$). For territorial males, hatch date was earlier for males with eggs compared to males without eggs ($p = 0.00957$).

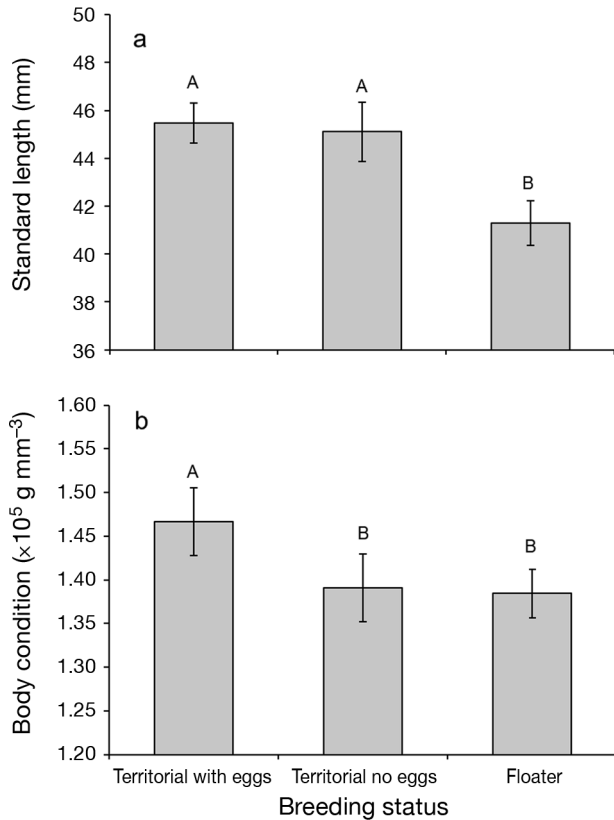


Fig. 1. Variation in (a) size (mean standard length, $\pm 95\%$ CI) and (b) body condition (mean Fulton's K , $\pm 95\%$ CI) of adult male common triplefin *Forsterygion lapillum* of different breeding status: territorial with eggs, territorial without eggs and floaters. Different letters above bars indicate significant differences among groups based on post hoc Tukey tests ($\alpha = 0.05$). Response axes are offset from 0 for graphical presentation

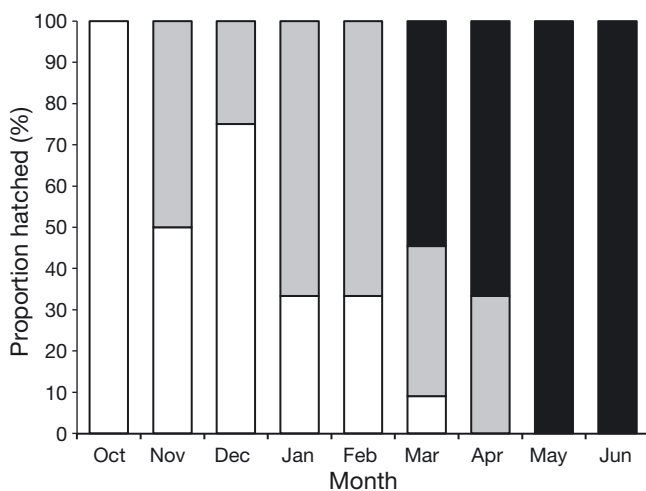


Fig. 2. Breeding status varies with hatch date. Given are proportions of male common triplefin of differing breeding status (white: territorial with eggs; grey: territorial without eggs; black: floaters; sampled August to November 2014) that hatched in a given month (from October 2013 to June 2014)

Relationship between growth rate, hatch date and breeding status

Growth rates for sampled males increased with hatch date irrespective of their breeding status ($F_{1,48} = 262.99$, $p < 0.001$, Fig. 3). However, the relationship between growth rate and hatch date varied with male reproductive status (interaction term: $F_{2,46} = 14.087$, $p < 0.001$). Fig. 3 illustrates the significant interaction between hatch date and growth that is most likely attributable to the steeper relationship between growth rate and hatch date for floaters. Given the minimal overlap in hatch dates between floaters and territorial males, we performed 2 further analyses to investigate the relationship between hatch date, growth rate and reproductive status.

Firstly, we conducted a secondary ANCOVA without floaters to evaluate differences in growth between territorial males with eggs and without eggs. For the subset of males that were territorial, individuals with eggs had faster growth rates than individuals without eggs regardless of hatch date ($F_{1,27} = 13.21$, $p = 0.001$). Secondly, we graphically compared adjusted mean growth rates (LS means) among floaters and territorial males (with and without eggs), for the 2 mo where there was an overlap in hatch date (i.e. March and April 2014, from Fig. 2). Estimates of LS means ($\pm 95\%$ CI) suggest that growth rates (corrected for variation in hatch dates) did not differ between floater males and territorial males that had not received eggs. However, estimated 95% CI for territorial males with eggs did not include mean val-

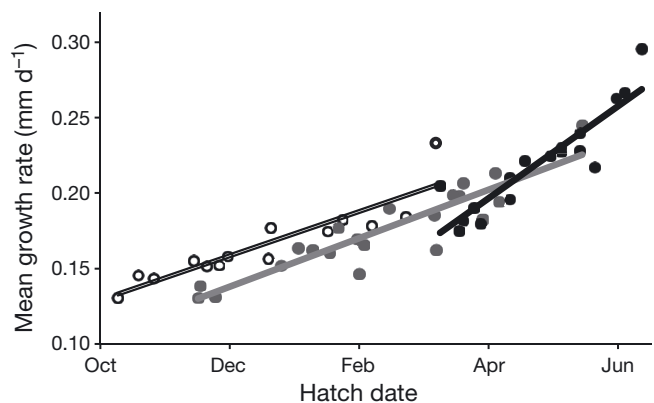


Fig. 3. Relationship between growth rate (GR) and hatch date (HD) (from October 2013 to June 2014) for male common triplefin of differing breeding status: territorial with eggs (open circles, double line), territorial without eggs (grey circles, grey line) and floaters (black circles, black line). $\text{GR}_{\text{territorial with eggs}} = 0.0005 \times \text{HD} - 19.83$, $R^2 = 0.8194$. $\text{GR}_{\text{territorial without eggs}} = 0.0005 \times \text{HD} - 21.78$, $R^2 = 0.8292$. $\text{GR}_{\text{floaters}} = 0.001 \times \text{HD} - 41.59$, $R^2 = 0.8148$. Response axis is offset from 0 for graphical presentation

ues of either territorial males without eggs or floater males (and vice versa), suggesting that growth rates of males with eggs are faster than both males without eggs, regardless of territoriality and independent of hatch dates (Fig. 4).

DISCUSSION

Identifying determinants of reproductive success has been a focus of investigation for many species, spanning a diversity of mating systems (Clutton-Brock 1988). In species with male parental care, body size and condition have been identified as important indicators of male fitness, and these traits have been the subject of many studies (e.g. Lindström & Hellström 1993, Uusi-Heikkilä et al. 2012). Variation in body size and/or condition is likely to be influenced by birth date and/or growth rate (Taborsky 1998, Michel et al. 2018); however, the latter traits are less commonly considered as underlying drivers of reproductive success (but see Fagundes et al. 2015, Michel et al. 2018). Our results suggest that reproductive status of males is predicted by differences in size and condition, but also by hatch date and growth rate (and the 2 sets of traits may be decoupled from one another, because late hatching individuals appear to experience compensatory growth). Collectively, these results suggest that triplefin breeding populations comprise mixtures of individuals that differ in a range of traits and have corresponding differences in reproductive success. Our results also imply that

different tactics (e.g. tortoise or hare tactics, sensu Michel et al. 2018) may be employed by common triplefin to maximise individual reproductive success.

Phenotype

Reproductive status was predicted by differences in body size. Territory holders were larger than floaters. Associations between body size and territoriality are common among fishes (e.g. Magnhagen & Kvarnemo 1989) and other taxa (O'Neill 1983, Candolin & Voigt 2001). Male body size can influence competitive ability (Järvi 1990, McElligott et al. 2001) as well as successful acquisition and defence of a territory or nesting site (Cole 1982).

Differences in body size did not predict the presence or absence of eggs between territorial males (i.e. putatively, female mate choice) as is suggested in other fish species such as the closely related mottled triplefin *Forsterygion varium* (Thompson 1986) or the sand goby *Pomatoschistus minutus* (Lindström & Hellström 1993). Our results also appear to contradict a recent study on the common triplefin by Mensink et al. (2014), who found a significant effect of male body size on the probability of acquiring eggs.

Differences in body condition, however, did predict presence/absence of eggs for territorial males. Females may favour males in better condition for several reasons; elevated condition could indicate greater energetic reserves that equate to improved parental care (increasing the quality of care and/or reducing the risk of egg predation by caregiving males; Hanson & Cooke 2009). Indeed, Mensink (2014) found that *F. lapillum* egg size was significantly correlated to male condition, which may suggest assortative (i.e. size-matched) mating between larger (or better conditioned) females and males.

Conversely, the correlation between increased body condition and presence of eggs may have been driven by another mechanism. Females may lay eggs indiscriminately with respect to male condition, and the elevated condition of males with eggs could simply arise from filial cannibalism (i.e. males with eggs routinely consume a portion of their clutch). Alternatively, the apparent absence of eggs associated with males in poorer condition could be the result of filial cannibalism. Males that practice paternal care often decrease in body condition when caring for young (Lindström & Hellström 1993), and some species may exhibit filial cannibalism (i.e. egg consumption) as a mechanism to maintain body condition during this

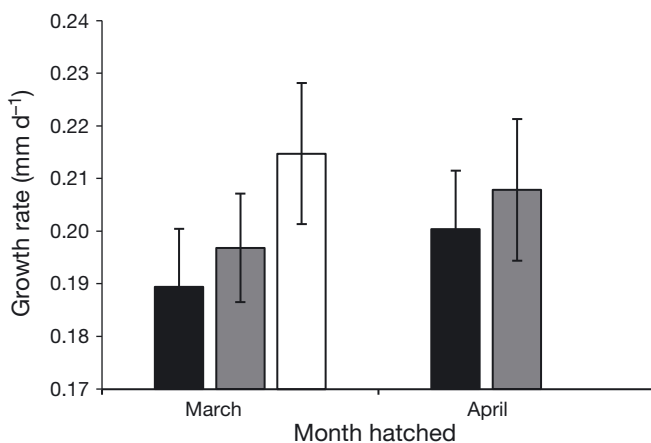


Fig. 4. Adjusted mean growth rates ($\pm 95\%$ CI) estimated for male common triplefin of different reproductive status that hatched during the same months (March and April 2014). White: territorial with eggs, grey: territorial without eggs, black: floaters. Response axis is offset from 0 for graphical presentation

period (FitzGerald 1992, Vinyoles et al. 1999, Gomanogano & Kohda 2008). Further work would be required to determine the drivers and implications of these patterns.

Life history

We found that reproductive status of males is also predicted by differences in hatch dates. All sampled males that hatched earlier than March 2014 had acquired territories, and all males that hatched earlier than mid-November 2013 successfully obtained eggs (Fig. 2). Admittedly, this is simply another way to describe age-dependent effects, but an explicit evaluation of hatch date (as opposed to age) focusses attention on the important link between a potential parental strategy (i.e. timing of reproduction) and its consequences for the fitness of offspring (e.g. Shima et al. 2018). Early hatching dates may have granted the territorial males a longer growing period before the onset of the breeding season in August 2014, and may have driven the observed differences in body size and condition. Additionally, the wide range in hatch dates (~9 mo, from October 2013 to June 2014) suggests that later-hatching males may have developed in very different environmental conditions, with possible consequences for individual growth (e.g. Brett et al. 1969, Angilletta et al. 2004) and phenotype (Monaghan 2008, Shima & Swearer 2009).

Males with early hatch dates were more likely to be territorial, and their territories were more likely to contain eggs, suggesting that order of arrival (i.e. priority effects) probably influences male reproductive success in the common triplefin. Priority effects have been described for many species: e.g. Geange & Stier (2010) demonstrated how earlier-arriving reef fish are subject to less aggression and are less likely to be displaced from their habitat by competitors, even if they would otherwise be considered subordinate in a cross-species dominance hierarchy. Similarly, subordinate salmon may acquire, and successfully maintain, preferred feeding sites when they arrive before more dominant individuals (Harwood et al. 2003). Likewise, brown trout fry that obtain territories early are able to successfully defend their territory against competitors up to 30% larger in size (Johnsson et al. 1999).

If earlier-hatching male triplefin are the first to arrive to a rocky reef, they may be more likely to acquire and defend better territories relative to their later-arriving conspecifics. In addition, earlier-arriving males may mature at an earlier date than later-

arriving males, potentially allowing the earlier-hatching males to begin mating earlier in the breeding season, when males typically receive more eggs (Mensink 2014). Moreover, if females exhibit a preference for males with eggs (e.g. Alonzo 2008), then early successful mating could result in feedbacks that propagate increased reproductive success for males over a protracted mating season.

Later-hatching males appear to have faster growth rates than earlier-hatching males (Fig. 3). The significant interaction between growth rate and hatch date was likely due to accelerated growth rates of the floater males (Fig. 3). Floater males were younger and smaller than territorial males and may not have reached asymptotic size. Alternatively, floaters could have experienced faster growth rates because they hatched and developed in very different environmental conditions compared to males that were identified as territorial. However, this would require the colder, rougher sea conditions in which the floaters hatched and developed to promote faster growth than the relatively warm and calm conditions that the territorial males experienced, which seems unlikely given the evidence to the contrary (Friedland et al. 2000, MacKenzie & Kjørboe 2000, Neuheimer et al. 2011). Individuals hatching later in the season may simply adopt a strategy of hyperphagia (e.g. Ali et al. 2003) to achieve faster growth rates.

Regardless of hatch date, territorial males with eggs grew faster than territory holders without eggs. This supports a hypothesis that a faster growth rate may give males an additional fitness advantage independent of hatch date. We speculate that faster growth rates may result in more attractive male phenotypes, and/or may enable males to attain a more attractive territory. However, we note that support for this hypothesis is merely correlative, and we cannot rule out the possibility that a causal relationship does not exist (or that causality is reversed; e.g. filial cannibalism could drive this relationship, as discussed above). Additionally, because we have only crude estimates of reproductive success (e.g. presence/absence of eggs), we cannot evaluate multiple paternity, and therefore, true fitness differences among putative alternative reproductive tactics. Further studies would be required to determine the drivers and consequences of these patterns.

Our results suggest the existence of multiple pathways to success for male common triplefin. Reproductive success may be maximised by hatching early. However, if males fail to hatch early, then a faster growth rate may enable individuals to overcome an inauspicious birth date (i.e. a tortoise versus hare tac-

tic, sensu Michel et al. 2018). Males born later in a season (after March in this study) could be adopting an alternative growth and/or reproductive tactic. Conceivably, these younger males may forego territorial behaviours in favour of a 'sneaker male' strategy (e.g. Alonzo & Warner 2000a,b, Fagundes et al. 2015). Although we can only speculate, young/small males may effectively parasitize mating events between females and larger males. However, we also note that sneaker males might be expected to divert energetic resources from somatic growth towards reproductive development (i.e. have slower somatic growth rates at smaller sizes; Jennings & Philipp 1992). In our study, floater males appeared to show the opposite pattern (i.e. they grew faster), suggesting that these individuals may be investing disproportionately in growth at the expense of any reproduction (although this does not discount the possibility that they may still achieve faster growth rates than males engaged in territorial defence and/or nest guarding). As an alternative hypothesis, these late-hatching males forego reproductive attempts in the present season and then attempt to breed in the following season. Further research would be needed to test these hypotheses.

Our work on the common triplefin complements an important body of work conducted on other reef fishes (in particular, the work on *Symphodus ocellatus*, e.g. Alonzo & Warner 2000a,b, Alonzo et al. 2000, Alonzo & Heckman 2010, Alonzo 2012; and the work on *Salarias pavo*, e.g. Goncalves et al. 1996, Fagundes et al. 2015). Both of these systems have been extensively studied and have made important contributions to our understanding of the evolution of alternative reproductive tactics. For the common triplefin, we do not yet have confirmation of alternative reproductive tactics, but our ability to precisely estimate birth dates and to demonstrate relationships between birth dates and other traits linked to reproductive success motivate questions related to the link between reproductive strategies of adults and the fitness consequences for offspring (Shima et al. 2018). These effects may be of particular importance for the common triplefin, a comparatively short-lived species, possibly with more limited opportunities for individuals to shift between reproductive tactics over the course of their lifespan.

Conclusion

Overall, our study suggests that life history traits (hatch dates and growth rates) could constitute important determinants of male reproductive success, particularly in systems with male parental care.

Correlated phenotypic variation (e.g. variation in body size and/or territory quality) may be the proximate variables upon which females make their choice, but explicit consideration of birthdate effects (Taborsky 1998) focusses attention on intergenerational links that may, through important eco-evolutionary feedback, drive the evolution of alternative reproductive tactics (e.g. Shima et al. 2018). Correct attribution of the life-history determinants of fitness has important implications for both population dynamics and evolutionary ecology in systems with male parental care.

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