Determining the life history strategy of the cryptobenthic reef gobies *Coryphopterus hyalinus* and *C. personatus*

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ABSTRACT: Understanding the life history strategy of species can clarify their functional role, and contribution to the productivity and resilience of an ecosystem. We use otolith microstructure analysis to study the life history of 2 widespread and abundant Caribbean reef fishes, genetically identified here as the glass goby *Coryphopterus hyalinus* and masked goby *C. personatus.* Our analysis reveals that these species exhibit an extreme life history relative to other vertebrates due to their short lifespan, small adult body size, early maturity, and continuous growth in body length throughout reproductive age. We find that pelagic larval duration (PLD) varies widely, and average larval growth influences PLD where faster-growing larvae have shorter PLDs. We show that average daily growth substantially decreases during the settlement transition to reef habitat, approximately coinciding with reproductive maturity. Continuous somatic growth throughout reproductive age can serve to support greater fecundity in older, larger-bodied females and enhance survivorship. Several features of the ecology (i.e. broad depth range, planktivorous diet) and life history (i.e. small adult body size, quick generational turnover, short lifespan) of *C. hyalinus* and *C. personatus* indicate that they play a key trophic role in transferring nutrients from pelagic plankton to Caribbean reef predators and the reef benthos. Our analyses highlight why life history traits related to survival, reproduction, and population dynamics can enhance our understanding of ecosystem-scale processes and functioning on coral reefs.

KEY WORDS: Life history · Functional ecology · Coral reef fish · Lifespan · Body size · Conservation biology · Cryptobenthic · Otolith microstructure

1. INTRODUCTION

Variable extrinsic mortality directly influences age at maturity and lifespan of terrestrial vertebrates where higher mortality rates result in earlier maturation and shorter lifespans (Ricklefs 2010). For fishes, high extrinsic mortality is expected to select for small adult body size, short lifespan, and short generation time (Winemiller 2005). Fishes of the smallest size classes that inhabit benthic reef habitats are collectively known as cryptobenthic reef fishes, and they constitute a significant portion of reef fish biodiversity

and biomass production (Brandl et al. 2018). Field, mesocosm, and otolith studies indicate that cryptobenthic reef fishes, such as gobies, experience high predation mortality on coral reefs (Hernaman & Munday 2005b, Depczynski & Bellwood 2006, Goatley & Bellwood 2016, Goatley et al. 2017). Understanding the life history strategy of species can clarify their functional role, and contribution to the productivity and resilience of an ecosystem (Winemiller 2005).

The glass goby *Coryphopterus hyalinus* (Böhlke & Robins 1962) and masked goby *C. personatus* (Jordan & Thompson 1905) are both abundant and widespread

in the Caribbean (Pezold et al. 2015); moreover, they are often the most numerically abundant gobies on shallow Caribbean reefs (Luckhurst & Luckhurst 1978, Greenfield & Johnson 1999, Dominici-Arosemena & Wolff 2005). Like most reef fishes, *C. hyalinus* and *C. personatus* disperse as pelagic larvae and then undergo a morpho-physiological transition to benthic reef habitat known as settlement (Leis & McCormick 2002). These gobies form large social aggregations of 10s to 1000s of individuals (Luckhurst & Luckhurst 1978, Robertson & Justines 1982), and these shoals hover in the water column above the edges and drop-off slopes of coral reefs (Cole & Robertson 1988, Thacker & Cole 2002). *C. hyalinus* and *C. personatus* exhibit protogynous hermaphroditism in which all individuals begin life as females and some transition to males after settlement in as little as 9 d; however, this ability is regulated by social hierarchy dynamics within the population (Cole & Robertson 1988, Cole & Shapiro 1990, Allsop & West 2004). Based on gonad histology, post-settlement *C. hyalinus* and *C. personatus* are reproductively mature at a small size of 17–19 mm total length (TL); however, some males develop from immature females, and as a result, these primary males can mature at a smaller size of 13–15 mm TL (Cole & Robertson 1988).

C. hyalinus and *C. personatus* feed on plankton, and they are found at a broad depth range (2–52 and 1–70 m respectively, Baldwin & Robertson 2015). Larger reef fishes such as lionfish and grouper feed on these gobies (Randall 1967, Morris & Akins 2009, Côté & Maljković 2010), and their small adult body size indicates that they are highly vulnerable to predation (Sogard 1997, Goatley & Bellwood 2016, Goatley et al. 2017). Along with their high numerical abundance and widespread distribution, these ecological characteristics indicate that *C. hyalinus* and *C. personatus* likely play a key trophic role in transferring nutrients from pelagic plankton to reef predators and the reef benthos (Winterbottom & Southcott 2008).

The life history traits of fishes can be used to predict features of their ecology and population dynamics (Bjørkvoll et al. 2012). For example, pelagic larval duration (PLD) can be used to estimate dispersal potential (Lester & Ruttenberg 2005). Larval growth and body size at settlement have implications for recruitment success and survivorship (Wilson & Meekan 2002, Rankin & Sponaugle 2014). We are also interested in age at maturity, maximum body size, and lifespan because these life history traits can serve as indicators of predation risk where high predation risk likely results in early maturation and

short lifespan (Reznick & Endler 1982, Depczynski & Bellwood 2006, Walsh & Reznick 2008).

We seek to test if *C. hyalinus* and *C. personatus* exhibit extreme life history traits similar to those described in a few other cryptobenthic reef fishes with small adult body sizes and highly abundant populations. Specifically, we aim to (1) quantify and describe the life history traits (i.e. PLD, TL at settlement, maximum TL at capture, age at maturity, lifespan, and growth patterns) of *C. hyalinus* and *C. personatus* and (2) explore the implications of this life history on the evolution and functional role of these species in coral reef ecosystems.

2. MATERIALS AND METHODS

2.1. Study site and sample collection

Coryphopterus hyalinus and *C. personatus* specimens were collected by divers on SCUBA using hand nets and anesthetic clove oil at sites on the windward side of Turneffe Islands Atoll, Belize in early January 2017. Turneffe Atoll is located on the Belize Barrier Reef, and it is a bank reef consisting of mangrove islands, patch reefs, and fringing reefs partially encircling a shallow lagoon (Gibson & Carter 2003). Post-settlement specimens were collected from fore-reef sites at depths between 11 and 17 m. Individual specimens were photographed shortly after collection and before preservation in 95% ethanol to retain their body size before shrinking occurred. Body size was measured as TL and standard length (SL) at capture (precision: 0.001 mm) on calibrated images using ImageJ software.

2.2. Species identification

To determine species identity, we used a 2-step process with restriction site-associated DNA (RAD) sequencing. RAD libraries consisting of ~35 000 DNA fragments were generated following a modified RAD-tag procedure (Peterson et al. 2012). Genomic DNA was fragmented using 2 restriction endonucleases (*Msp*I and *Eco*RI) and size-selected for fragments between 450 and 575 bp in our university's Genomics Core laboratory. As no reference genome is available for *Coryphopterus*, 6 samples were sequenced on a MiSeq platform (unidirectional read length of 300 bp) to ensure overlapping coverage for a more accurate reference assembly. All samples were then sequenced using the NovaSeq 6000 S4

sequencing lane with a unidirectional read length of 150 bp. MiSeq and NovaSeq sequencing was performed by New York University (NYU) Langone Genome Technology Center. After trimming to remove low-quality sequences with TRIMMOMATIC (Bolger et al. 2014), dDocent (Puritz et al. 2014) was used to de novo assemble MiSeq reads into 1 metagenome to which NovaSeq sequences were mapped. Single-nucleotide polymorphisms (SNPs) were filtered to retain only loci with 2 alleles, no insertions/deletions (indels), have a minimum Phred quality of 94, a minimum mean depth of coverage of 43, and be present in >85% of individuals before contigs were randomly sampled for a single SNP. To identify species, NovaSeq sequences were mapped to the mitochondrial genome of *Bathygobius cocosensis* (Evans et al. 2018). Sequences that successfully mapped were BLASTed in GenBank (Altschul et al. 1990), and any sequence with >99% similarity to either *C. hyalinus* or *C. personatus* were assigned these identities. For individuals that did not map to the reference mitochondrial genome, we used *k*-means clustering of principal components to identify nuclear multi-locus DNA clusters (Jombart et al. 2010), with the number of clusters chosen based on minimization of the Bayesian information criterion (BIC) value, using both the reference samples for which we had species IDs from BLAST and the unknown specimens. The 2 resulting clusters aligned with the BLAST-based reference species identity and were used to identify individuals from the unknown dataset.

2.3. Otolith microstructure

Life history parameters, including PLD, back-calculated TL at settlement, pre- and post-settlement growth patterns, and total age at capture, were estimated using otolith microstructure techniques and analysis. We assumed that 1 otolith increment corresponded to 1 d, since several gobies, including those ecologically similar to *C. hyalinus* and *C. personatus*, deposit otolith increments consisting of a dark and light band on a daily basis (Hernaman et al. 2000, Shafer 2000, Depczynski & Bellwood 2006, Wilson et al. 2008). Similarly, we assumed that the first otolith increment found near the primordium is deposited at or near hatching (Thorrold & Hare 2002). We recognized a settlement mark, corresponding to the transition from a pelagic to benthic environment (Wilson & McCormick 1997, Shafer 2000, Hogan et al. 2017), as a particularly contrasting increment.

2.4. Otolith preparation and microstructure analysis

Sagittal otoliths were extracted from a subset of collected individuals. Once cleaned of residual tissue with MilliQ water and dried, whole otoliths were mounted sulcus-down to petrographic slides with thermoplastic Crystalbond™, leaving the otolith surface exposed. Otoliths were viewed using Type B immersion oil and transmitted light at 500× magnification with a Nikon Eclipse LV100ND compound microscope to assess how much polishing was needed. Oil was blotted dry, and otoliths were hand-polished with 3M imperial diamond lapping films (15, 6, 3, 1, 0.5 μm) until a continuous sequence of growth increments were visible from the otolith primordium to the edge (Fig. 1). Otoliths were imaged at 500× magnification with a Nikon Digital Sight DS-fi2 camera. All otolith measurements were made from calibrated images using NIS-Elements computer imaging software and were performed by 1 reader. Otolith radius at capture, a measure of total otolith size, was measured as the longest linear distance from core to edge. PLD was estimated as the number of daily increments between the otolith primordium and the settlement mark (our Fig. 1; Thorrold & Hare 2002). Age at capture (days) and daily growth were estimated simultaneously by counting increments and measuring their widths (μm) respectively along the otolith radius. Increment widths or otolith growth rates were standardized as a percentage of the larval or post-larval component of the radius at capture. This approach reduces bias in estimating otolith growth rates from the radius chosen for measurement and allows comparison of otolith growth rates within and between life history stages. Otoliths were re-aged on a separate occasion, blind to sample information, and the coefficient of variation (CV) was used as a measure of precision between the 2 estimates (Campana 2001) where individuals with CV <10% were retained for analyses (Walker & McCormick 2004, Hernaman & Munday 2005a, Depczynski & Bellwood 2006).

2.5. Back-calculated TL at settlement

Individual TL at settlement (mm) was estimated using the experimental Modified Fry back-calculation model (Eq. (1) in Box 1; Vigliola & Meekan 2009) in the R package RFISHBC (Ogle 2018) for comparison with TL at reproductive maturity and to determine the percentage of maximum TL attained

Fig. 1. Sagittal otolith radius of *Coryphopterus hyalinus/personatus* imaged at 500× magnification indicating key features. Estimated age at capture: 95 d; pelagic larval duration: 28 d. The sagittal otoliths of both gobies are very similar in appearance. P: primordium; S: settlement mark; E: edge. The black line from 'P' to 'S' indicates the larval component of the radius at capture while the black line from 'S' to 'E' indicates the post-larval component of the radius at capture.

at settlement. This specific model performs well in ecologically similar gobies (Wilson et al. 2008). Body length at hatch was set at 2 mm based on a breeding study of *C. personatus* (Gardner 2000), and otolith radius at hatch was averaged across individuals to obtain a mean (±SD) of 6.73 ± 1.74 μm (n = 66) for *C. hyalinus* and 6.77 ± 1.59 μm (n =13) for *C. personatus.* These measurements at hatch for *C. hyalinus* and *C. personatus* are comparable to other ecologically similar gobies (Wilson et al. 2008), including congeners (Kramer & Patzner 2008). We evaluated linearity in a set of confirmatory tests to establish that otolith measures are reliable proxies of back-calculated TL, growth, and age for *C. hyalinus* and *C. personatus.* The equation (Eq. (1)) is shown in Box 1, where TL_s is the TL at settlement, 0.75L0p is the body length at otolith formation, L0p is the body length at hatch, Lcap is the TL at capture, Ri is the otolith radius at settlement, R0p is the mean otolith radius at hatch, and Rcap is the otolith radius at capture.

2.6. Statistical analysis

To test the hypothesis that *C. hyalinus* and *C. personatus* attain small adult body sizes, we measured a broad size range of several post-settlement individuals to determine the frequency distribution of TLs. To test for short lifespan (<1 yr), we aged individuals of both species that spanned their TL range to determine the frequency distribution of estimated age at capture. We performed a linear regression on estimated age and TL at capture to test for continuous post-settlement growth. We estimated age at reproductive maturity from known estimates of TL at reproductive maturity. We performed a spline smooth on average larval growth and PLD to determine if and how larval growth influences PLD. These individual growth averages were calculated by summing daily larval growth rates and dividing by PLD. We used a 1-way ANOVA to test for significant differences in average daily growth between growth stages (larval, 10 d pre-settlement, and 10 d post-settlement). General linear

Box 1

$$TL_s\,(mm) = 0.75L0p + exp\left(log(L0p - 0.75L0p) + \frac{[log(Lcap - 0.75L0p) - \, log(L0p - 0.75L0p)]^{\bullet}[log(Ri) - log(R0p)]}{log(Rcap) - log(R0p)}\right) \quad (1)$$

hypothesis testing was performed using planned post hoc comparisons to test for significant differences in average daily growth between (1) larval stage and 10 d post-settlement, and (2) 10 d pre- and post-settlement with free adjustment of p-values. Model assumptions of normality and homogeneity of variances were evaluated against Shapiro-Wilk α = 0.01 and Breusch-Pagan or Brown-Forsythe-Levene α = 0.05, respectively. Both assumptions were met in most analyses; however, departures from normality in the *C. hyalinus* spline smooth and ANOVA were generally robust given the adequate sample size specified by the central limit theorem and ability to interpret untransformed raw data. All statistical analyses used α = 0.05 to determine statistical significance and were performed in R v.3.4.1 (R Core Team 2017) using the following packages: multcomp (Hothorn et al. 2008), ggplot2 (Wickham 2009), mgcv (Wood 2011), gridExtra (Auguie 2017), dplyr (Wickham et al. 2018), and tidyr (Wickham & Henry 2019).
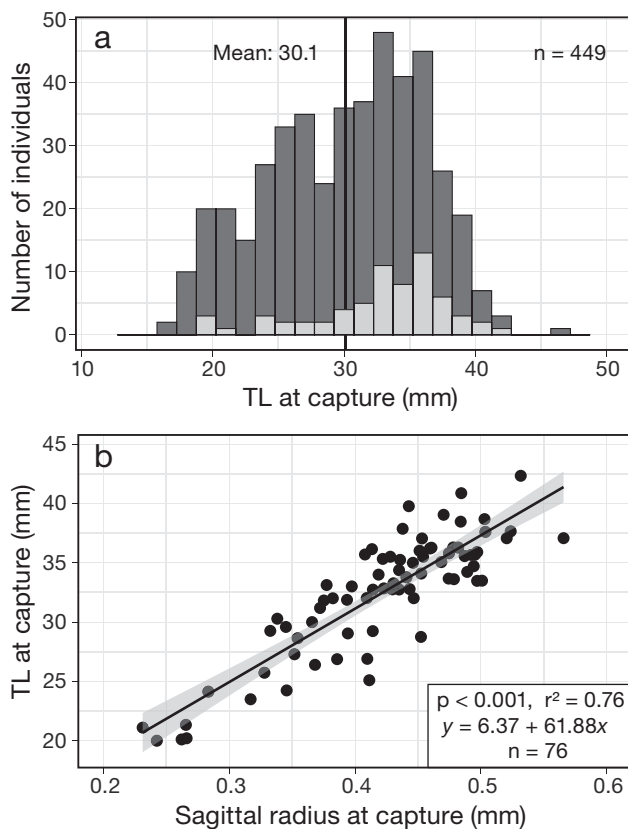

Fig. 2. (a) Frequency distribution of *Coryphopterus hyalinus* total length (TL) at capture. Lighter-shaded region: the subset of individuals (n = 66) with an estimated age at capture. Binwidth: 1.5 mm. (b) Relationship between *C. hyalinus* otolith radius and TL at capture modeled by a linear regression. Shaded area: 95% confidence interval

3. RESULTS

3.1. Species identification

We collected a total of 729 individuals. A total of 1.9 billion NovaSeq reads were sequenced, with a median of 1.5 million reads per individual. The final filtered dataset consisted of 1446 SNPs, with mean individual depth of coverage of 127 (median: 35) in 729 individuals. Mapping of raw NovaSeq reads to the *Bathygobius cocosensis* mitochondrial genome followed by using BLAST to identify species and resulted in the identification of 166 *Coryphopterus hyalinus* and 67 *C. personatus*. The *k*-means clustering of principal components resulted in 2 clear groupings with each aligning well with the BLAST results (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m659p161_supp.pdf). Five individuals showed disagreement between nuclear cluster assignment and BLAST identity suggesting potential introgression (Selwyn et al. unpubl.). After species assignment, there were a total of 595 *C. hyalinus* and 134 *C. personatus* which were used in subsequent analyses.

3.2. TL at capture, otolith radii, and back-calculated TL at settlement

We had a total of 449 *C. hyalinus* and 93 *C. personatus* with measurements of TL at capture. Of these, 66 *C. hyalinus* (CV: 2.80 ± 2.29%, mean ± SD) and 13 *C. personatus* (CV: 3.37 ± 2.30%) were processed for the full suite of otolith microstructure measurements. This subset of samples for both species spanned their TL at capture range (Fig. 2a, Fig. S2a in the Supplement) from 16.80 to 45.84 mm with a mean (±SD) of 30.09 ± 5.90 mm for *C. hyalinus* (n = 449, Fig. 2a), and from 18.37 to 57.88 mm with a mean of 38.87 ± 8.83 mm for *C. personatus* (n = 93, Fig. S2a). For 13 additional *C. hyalinus*, otolith radius at settlement, larval duration (CV: 3.58 ± 2.76%, mean ± SD), and growth could be estimated, with 10 of these also having estimates for otolith radius at capture, and hence, back-calculated TL at settlement. Otolith radius at settlement ranged from 141.0 to 292.1 μm with a mean (±SD) of 187.1 ± 22.66 μm for *C. hyalinus* (n = 79), and from 152.2 to 211.1 μm with a mean of 179.0 ± 19.39 μm for *C. personatus* (n = 13). Otolith radius at capture ranged from 231.2 to 565.8 μm with a mean of 421.7 ± 71.51 μm for *C. hyalinus* (n = 76), and from 301.8 to 737.5 μm with a mean of 502.0 ± 141.97 μm

for *C. personatus* (n = 13). Otolith radius at capture was positively correlated with TL at capture for *C. hyalinus* (p < 0.001, r^2 = 0.76, Fig. 2b) and *C. personatus* (p < 0.001, r^2 = 0.87, Fig. S2b). This indicates that daily otolith growth is proportional to daily somatic growth (Campana & Neilson 1985, Thorrold & Hare 2002) and supports back-calculation of TL at settlement (Vigliola & Meekan 2009). Back-calculated TL at settlement ranged from 11.59 to 21.86 mm with a mean (±SD) of 15.27 ± 1.50 mm for *C. hyalinus* (n = 76, Fig. S3 in the Supplement), and from 12.52 to 18.14 mm with a mean of 15.52 ± 1.58 mm for *C. personatus* (n = 13, Fig. S3).

3.3. Age at capture and PLD

Age at capture ranged from 51 to 136 d with a mean (±SD) of 97 ± 19.87 d (n = 66, Fig. 3a) for *C. hyalinus*, and from 62 to 195 d with a mean of 112 ± 37.37 d (n = 13) for *C. personatus*. Otolith radius at capture was positively correlated with age at capture for *C. hyalinus* (p < 0.001, r^2 = 0.70, Fig. 3b) and *C. personatus* (p < 0.001, r^2 = 0.91, Fig. S4a in the Supplement). This makes otolith size a useful predictor of age and indicates that otolith increments are continually deposited as individuals age, which reduces bias in age underestimations (Green et al. 2009). Age at capture was positively correlated with TL at capture for *C. hyalinus* (p < 0.001, r^2 = 0.59, Fig. 4) and *C. personatus* (p < 0.001, r^2 = 0.81, Fig. S4b). PLDs ranged widely from 21 to 50 d with a mean (±SD) of 32 ± 5.36 d for *C. hyalinus* (n = 79, Fig. 5), and from 30 to 46 d with a mean of 35 ± 5.02 d for *C. personatus* (n = 13).

3.4. Pre- and post-settlement growth

Overall, both gobies grew fastest during the larval stage, starting slow at first, then rapidly accelerating before peaking during the ~25 d prior to settlement (Fig. 6a, Fig. S5a in the Supplement). Further, growth declined immediately upon settlement and continued to decline slowly thereafter (Figs. 6a & S5a). Average growth of both gobies was faster during the larval stage relative to 10 d post-settlement (both p < 0.01, Table 1, Figs. 6a & S5a). For *C. hyalinus*, average daily growth abruptly decreased by 25% from the pre-settlement zone (average ± SE of 10 d pre-settlement: 3.25 ± 0.10%) to the post-settlement zone (average of 10 d post-settlement: 2.43 ± 0.12%) (p < 0.001, Table 1, Fig. 6b). For *C. person-*
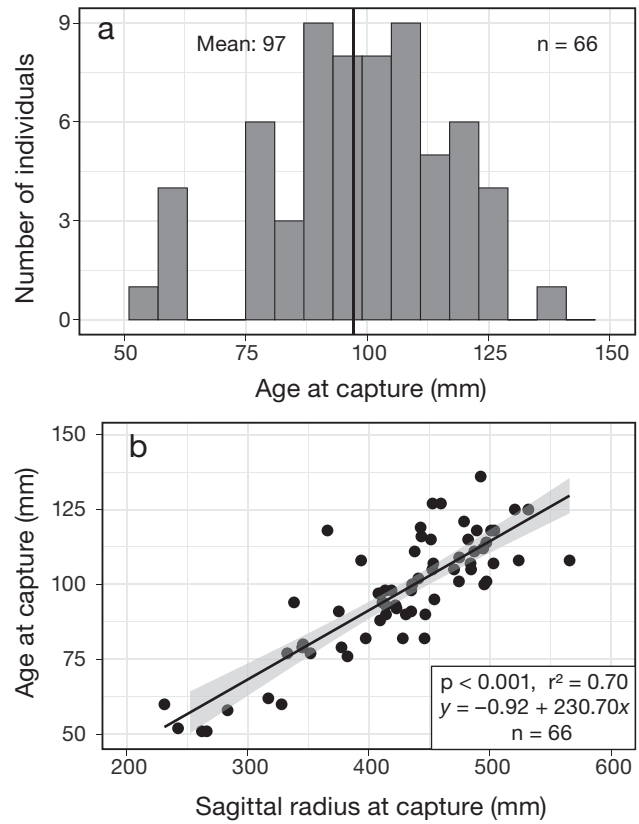

Fig. 3. (a) Frequency distribution of *Coryphopterus hyalinus* estimated age at capture. Binwidth: 6 d. (b) Relationship between *C. hyalinus* otolith radius and estimated age at capture modeled by a linear regression. Shaded area: 95% confidence interval
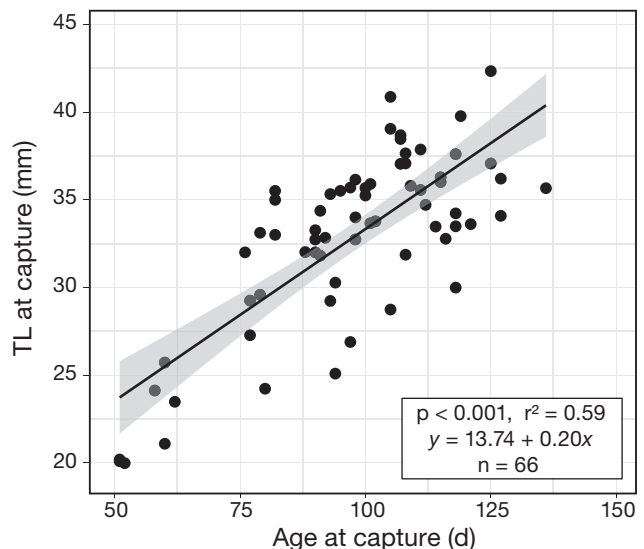

Fig. 4. Relationship between *Coryphopterus hyalinus* estimated age and total length (TL) at capture modeled by a linear regression. Shaded area: 95% confidence interval. The linear regression equation to predict age, given TL: $y = -0.85 + 2.99x$, p < 0.001, r^2 = 0.59
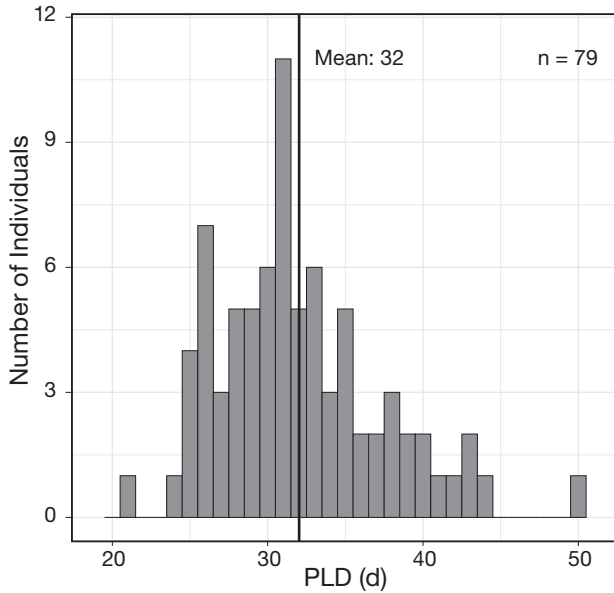
Fig. 5. Frequency distribution of *Coryphopterus hyalinus* pelagic larval duration (PLD). Binwidth: 1 d
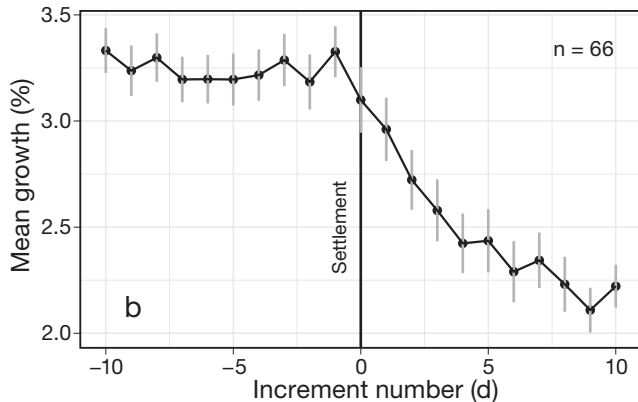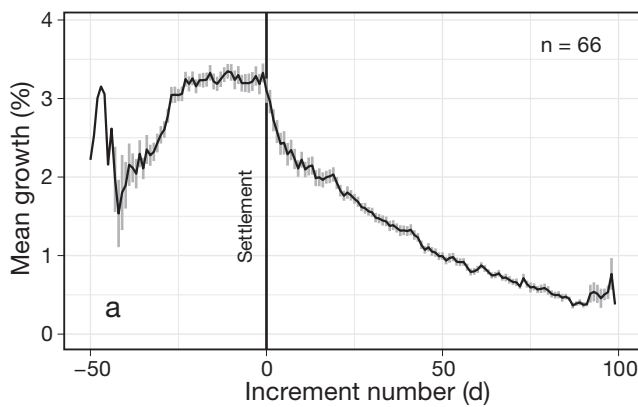

Fig. 6. Average daily growth (±1 SE) profile of *Coryphopterus hyalinus*: (a) entire life history profile; (b) close-up profile of the settlement transition, 10 d pre- and post-settlement. Increment numbers are centered around the settlement mark at 0. Negative increment numbers: larval increments; positive increment numbers: post-settlement increments

Table 1. *Coryphopterus hyalinus* and *C. personatus* 1-way ANOVA (average daily growth ~ growth stage) summary. Planned post hoc comparisons resulted in significant differences in average daily growth between larval stage and 10 d post-settlement, and between 10 d pre- and post-settlement

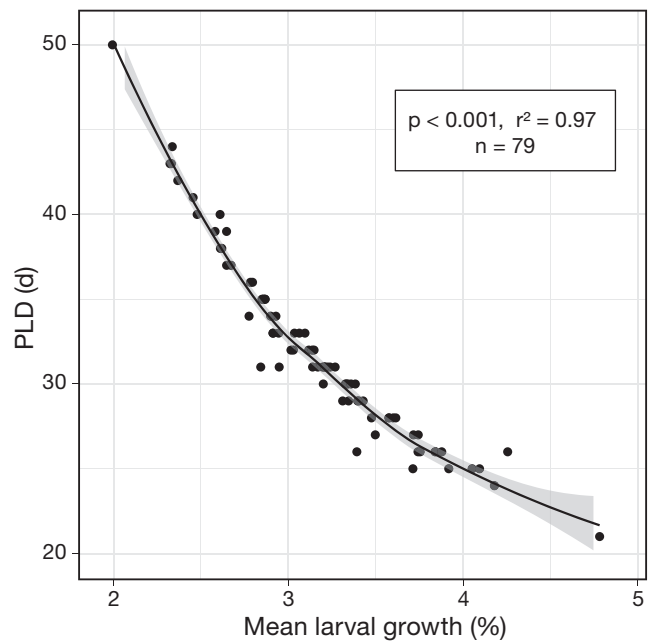| Species	n	df (growth stage)	df (residuals)	*F*	p
C. hyalinus	66	2	195	21.16	<0.001
C. personatus	13	2	36	8.26	0.001

Fig. 7. Inverse relationship between *Coryphopterus hyalinus* average larval growth and pelagic larval duration (PLD) modeled by a spline smooth. Shaded area: 95% confidence interval

atus, average daily growth abruptly decreased by 33% from the pre-settlement zone (average of 10 d pre-settlement: 2.95 ± 0.21%) to the post-settlement zone (average of 10 d post-settlement: 1.97 ± 0.24%) (p < 0.01, Table 1, Fig. S5b). Individuals with longer PLDs grew slower for a longer period early in the larval stage, and then their growth increased rapidly, ultimately peaking to similar larval growth rates of individuals with shorter PLDs (Figs. 6a & S5a). Consequently, average larval growth (%) was inversely related to PLD for *C. hyalinus* (p < 0.001, r^2 = 0.97, Fig. 7) and *C. personatus* (p < 0.001, r^2 = 0.96, Fig. S6 in the Supplement).

4. DISCUSSION

We used otolith microstructure analysis of 2 widespread and abundant Caribbean reef gobies *Coryphopterus hyalinus* and *C. personatus* to quantitatively describe their life history traits. We found that these species exhibit remarkably short lifespans, with 95% of individuals (n = 75) living at most 130 d. Although PLDs of these species varied widely, 75% (n = 69) of individuals had PLDs of at most 35 d. Interestingly, average larval growth influences PLD, where faster larval growth led to shorter PLDs. Notably, these fishes may immediately transition to reproductive growth after their settlement on the reef. The small adult body size, quick generational turnover, and short lifespan of these species are among the most extreme life history traits recorded for coral reef fishes (Table 2) and all vertebrates. We explore the implications of this life history on the evolution and functional role of these species in coral reef ecosystems.

Faster larval growth can reduce size-selective predation risk by producing larger size-at-age individuals that abbreviate their high-mortality larval stage by reaching developmental competence sooner (Fontes et al. 2011). Moreover, fitness of individuals that grew faster as larvae may be considerably higher than their slower-growing counterparts (Shima & Findlay 2002, Wilson & Meekan 2002). Although slower-growing larvae spend more time in the pelagic environment, this can increase their potential to disperse farther and colonize relatively isolated reef habitats (Lester & Ruttenberg 2005). However, we find that the distribution of PLDs in *C. hyalinus* and *C. personatus* contains a modal PLD that is less than the average PLD and right-skewness with very few long PLDs (Fig. 5). This indicates that *C. hyalinus* and *C. personatus* larvae may remain relatively close to natal reefs, since close relatives inhabit the same reefs (Selwyn et al. 2016). This is further supported by cryptobenthic fish larvae being more abundant in near-reef environments compared to offshore pelagic environments dominated by larvae of larger reef fishes (Brandl et al. 2019). Larval retention near reefs, concordant with our result of a higher portion of faster-growing larvae with shorter PLDs, may be a key mechanism by which cryptobenthic reef fishes like *C. hyalinus* and *C. personatus* sustain their local populations and compensate for high predation mortality on coral reefs (Brandl et al. 2019).

C. hyalinus and *C. personatus* attain small adult body sizes (max.: 46 and 58 mm TL respectively, Figs. 2a & S2a) and settle at comparatively large body sizes (mean: ~15 mm TL for both fishes). Here, back-calculated lengths at settlement were comparable to lengths obtained from field collections of recently settled *C. hyalinus* (6.9–8.4 mm SL, Victor 2015) and *C. personatus* (7.8–8.6 mm SL, Victor 2015), once corrected for the average length (±SD) of

Table 2. Life history traits of representative reef fishes from published studies that highly contrast and in turn emphasize the extreme life histories of the reef gobies in our study. Body size and age at reproductive maturity are combined for males and females excluding *Thalassoma lunare* (only female data available, data on early-maturing males is na). Lifespan and max. body size are the maximum reported for the species and were typically obtained from males (i.e. *Pomacentrus amboinensis*, *Thalassoma lunare*, and *Asteropteryx semipunctatus*). na: not available; PLD: pelagic larval duration; SL: standard length; TL: total length. Some cells include references for the data presented in that specific cell. The source column specifies the reference(s) for data in the remaining cells of that row

Family	Representative species	PLD (d)	Body size at settlement (mm)	Body size (mm) and/or age at reproductive maturity	Max. body size (mm)	Lifespan	Source
Pomacentridae	*Pomacentrus moluccensis*	14–23 (Wellington & Victor 1989, Bay et al. 2006)	10 SL (Beukers & Jones 1998)	33–52 SL (Mapstone 1988)	70 SL	14–18 yr	Fowler & Doherty (1992), Doherty & Fowler (1994)
	P. amboinensis	15–32 (Bay et al. 2006)	10–15 SL (Kerrigan 1996)	34 SL (30 SL for early-maturing males); 2 yr	78 SL	6 yr	McCormick (2016)
Labridae	*Thalassoma lunare*	39–55 (Victor 1986)	na	70 SL; 1 yr	184 SL	7 yr	Ackerman (2004)
Gobiidae	*Asteropteryx semipunctatus*	na	Average of 7.5 TL (Hernaman 2003)	18–30 TL; 5–7 mo	56 TL	1.3 yr (16 mo)	Hernaman & Munday (2005a,b)
	Coryphopterus hyalinus	21–50	Average of 15 TL (back-calculated)	17–19 TL (13–15 TL for early-maturing males) (Cole & Robertson 1988); 22–51 d	46 TL	0.37 yr (136 d)	Present study

the caudal fin (TL minus SL) for *C. hyalinus* (5.19 ± 1.33 mm, n = 446) and *C. personatus* (7.12 ± 2.01 mm, n = 92) of the present study. These sizes at settlement are not unusual for coral reef fishes (Kerrigan 1996, Juncker et al. 2006); however, attaining 26 and 33% of the maximum body length (*C. personatus* and *C. hyalinus* respectively) prior to settlement is unusual. For example, longer-lived reef fishes such as the damselfish *Pomacentrus moluccensis* and the ocean surgeonfish *Acanthurus bahianus* attain 14 (Table 2) and 12% of their maximum body length at settlement, respectively (Robertson et al. 2005). A congener of *C. hyalinus* and *C. personatus*, *C. kuna*, shows a similar, albeit more extreme pattern (Victor et al. 2010). This may be a characteristic of the genus or perhaps more broadly of cryptobenthic reef fishes in general.

Back-calculated TL at settlement for *C. hyalinus* (11.59 to 21.86 mm) and *C. personatus* (12.52 to 18.14 mm) roughly corresponds with TL at reproductive maturity (Fig. S3) for males (13 to 15 mm) and females (17 to 19 mm) (Cole & Robertson 1988), which indicates that some individuals mature immediately upon or shortly after settlement. Based on our age-at-length linear regression model for *C. hyalinus*, we estimate that a 20 mm TL individual matures at a total age of 59 d (including PLD). However, maturity most likely occurs earlier, because using the upper estimate for TL at maturity provides the upper estimate for age at maturity. By using age at settlement to interpret age at maturity, we estimate that total age at maturity occurs between 22 and 51 d for *C. hyalinus* and between 31 and 47 d for *C. personatus*. The mean age at settlement of 33 d for *C. hyalinus* and 36 d for *C. personatus* can be used as relative estimates of mean total age at maturity. In addition, *C. hyalinus* and *C. personatus* change sex from female to male at a mean TL (±SD) of 24.1 ± 2.3 mm (Cole & Robertson 1988), which corresponds to a mean total age of 71 and 61 d respectively, based on our age-at-length linear regression models. However, the body size at maturity for males being well below the body size at sex change from female to male indicates that some of the males of both species are primary males, having matured first as males (Cole & Robertson 1988, Allsop & West 2004). Average daily growth abruptly decreases immediately after settlement (Figs. 6b & S5b), which may indicate a shift in energy being allocated to reproduction instead of somatic growth (Cole & Robertson 1988, Winemiller 2005), further supporting our conclusion that reproductive maturation occurs at or shortly after settlement.

C. hyalinus and *C. personatus* show continuous post-settlement growth where they do not appear to reach an asymptotic or maximum body length given their length-at-age relationship (Figs. 4 & S4b). Asymptotic size in fishes is caused predominantly by a shift in energy resources from somatic growth to reproduction (Stamps et al. 1998). However, selection may favor continuous somatic growth throughout reproductive age, particularly for small-bodied fishes. The short reproductive lifespans of individuals of both species (95% had post-settlement lifespans of at most 99 d, n = 75) indicate that continuous growth, and consequently larger body size, can confer an increasing fitness advantage with age, since fecundity usually increases with body size (Wootton 1990, Heino & Kaitala 1999). Some cryptobenthic reef fishes, including *C. hyalinus* and *C. personatus*, exhibit protogynous hermaphroditism where larger body length allows successful mate and nest site monopolization in haremic males and can induce sex change in females (Cole & Robertson 1988, Warner 1988, Brandl et al. 2018). Sex change from female to male can alleviate mate competition (Allsop & West 2004) and enhance reproductive output in *C. hyalinus* and *C. personatus* which exhibit small home ranges (Dominici-Arosemena & Wolff 2005) and a sex ratio skewed toward females of about 4:1 (Cole & Robertson 1988).

Along with reproductive advantages, continuous growth can also provide advantages associated with species survivorship and competitive dominance. Natural mortality rates of juvenile and adult cryptobenthic reef fishes can decline rapidly with increasing body size where small increases in TL can result in notable increases in lifespan (estimated 11 d per 1 mm increase in TL for post-settlement fishes <43 mm TL, Goatley & Bellwood 2016). Interestingly, the majority of *C. hyalinus* and *C. personatus* individuals measured here are smaller than this body size threshold (Figs. 2a & S2a). Also, small differences in body length (i.e. a mean difference of 12 mm TL) can drive whether a cryptobenthic reef fish will be predator or prey (Goatley et al. 2017). Reef fishes, including gobies, are aggressive most often with conspecifics, where larger individuals generally initiate and win competitive interactions for food and shelter (Shulman 1985, Munday & Jones 1998, Forrester et al. 2006). Notably, competitively dominant individuals influence the growth, maturity, and habitat use along with mortality of subordinate individuals, which can regulate population distribution and abundance (Shulman 1985, Munday & Jones 1998, Forrester et al. 2006).

Several features of the ecology (i.e. broad depth range, planktivorous diet) and life history (i.e. small adult body size, continuous growth, quick generational turnover rate, short lifespan) of *C. hyalinus* and *C. personatus* indicate that they play a key trophic role in transferring nutrients to Caribbean reef predators and the reef benthos (Brandl et al. 2019). Faster rates of biomass accumulation, generational turnover, and energy transfer to other trophic levels through predation can indicate that a species is more prevalent within a food web (Thillainath et al. 2016). High predation pressure (i.e. measured as presence/absence, predation intensity, or predator abundance) likely imposes time constraints on reproduction, which can select for faster growth and earlier maturity in fishes (Reznick & Endler 1982, Heibo & Magnhagen 2005, Walsh & Reznick 2008), reducing the risk of predation occurring before reproduction. In captivity, *C. personatus* can reproduce at 1 yr of age and attains a considerably longer lifespan up to 4 yr of age (Oceans Reefs and Aquariums [Fort Pierce, FL] pers. comm.) which suggests high risk of extrinsic mortality in the wild (Randall & Delbeek 2009, Ricklefs 2010). On the IUCN Red List, *C. hyalinus* and *C. personatus* are listed as Vulnerable (Pezold et al. 2015), due to invasive, predatory lionfish and decreasing quality and extent of coral reef habitat in the Caribbean (59% decline from 1970 to 2011, Jackson et al. 2014). However, the quick generational turnover of some cryptobenthic reef fishes, such as *C. hyalinus* and *C. personatus*, can enable greater population resilience to these and other ecosystem threats (Lefèvre et al. 2016). Lifespans of <1 yr, described here for *C. hyalinus* and *C. personatus*, are relatively rare among both terrestrial and aquatic vertebrates (3 of 3761 species with lifespan estimates in the AnAge database, De Magalhaes & Costa 2009, Eckhardt et al. 2017). However, the life histories of fishes are understudied relative to terrestrial vertebrates, comprising only 25% of lifespan estimates in the AnAge database (De Magalhaes & Costa 2009).

Small adult body size, quick generational turnover, and short lifespan are a suite of life history traits that closely characterizes other cryptobenthic reef fishes (Sponaugle & Cowen 1994, Wilson 2004, Depczynski & Bellwood 2006, Longenecker & Langston 2006, Winterbottom & Southcott 2008, Victor et al. 2010). Because of these life history traits, *C. hyalinus* and *C. personatus* populations are highly productive and widespread in the Caribbean, constituting a considerable amount of biomass on coral reef habitats (Pezold et al. 2015). Further, cryptobenthic reef fishes such as gobies and blennies make substantial contri-

butions to biomass productivity (g m^{-2} wk^{-1}) that match or exceed those of larger, abundant reef fishes such as surgeonfishes and wrasses (Depczynski et al. 2007). Notably, a recent study indicates that cryptobenthic reef fishes like *C. personatus* and *C. hyalinus* constitute the majority of fish biomass consumed on coral reefs (Brandl et al. 2019). As a result, fast-growing and short-lived cryptobenthic reef fishes as a guild can serve as key forage species or trophic intermediates between basal food levels (i.e. plankton, detritus, algae) and piscivorous predators (Depczynski et al. 2007, Brandl et al. 2018).

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