ECOLOGICAL IMPLICATIONS OF ABUNDANT CRYPTOBENTHIC REEF FISHES:
ESTIMATING PREVIOUSLY UNKNOWN LIFE HISTORY TRAITS OF THE
MASKED/GLASS GOBY *CORYPHOPTERUS PERSONATUS/HYALINUS* COMPLEX

A Thesis

by

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This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

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. However, for many cryptobenthic reef fishes such as gobies, much is unknown about their life history. Understanding the demographics of a species can clarify its functional role, productivity, and resilience to disturbances in an ecosystem. The masked/glass goby *Coryphopterus personatus/hyalinus* is an understudied Caribbean reef goby complex that is common and abundant. Otolith microstructure techniques reveal that *C. personatus/hyalinus* exhibits an extreme life history relative to other vertebrates due to its short lifespan, fast larval growth, and early maturity with linear growth in body length throughout reproductive age. Average daily larval growth largely determines pelagic larval duration where faster-growing individuals complete the larval stage in less time. The back-calculation of body length at settlement indicates that individuals with slower average larval growth had longer larval durations, and they compensate by attaining larger body lengths at settlement. Average daily growth substantially decreases over the settlement transition zone which approximately corresponds to sexual maturity. Notably, linear growth in body length may serve to support greater fecundity in older, larger-bodied females and enhance survivorship. The quick generational turnover, high abundance/productivity, broad depth range, and planktivorous diet of *C. personatus/hyalinus* indicates that it plays an important trophic role in transferring nutrients from pelagic plankton to reef predators and the reef benthos. Estimating life history traits related to survival, reproduction, and population size has useful applications in conservation biology and resource management.

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INTRODUCTION

In part, life history theory aims to describe the diversity of life history strategies and understand the ecological mechanisms and consequences of such strategies. Across a broad range of terrestrial vertebrate taxa, age at maturity is correlated with lifespan where earlier-maturing families have shorter lifespans (Ricklefs, 2010). Similarly, variable extrinsic mortality appears to directly influence age at maturity and lifespan where higher mortality rates result in earlier maturation and shorter lifespans (Ricklefs, 2010). Understanding the demographics of a species can clarify its functional role, productivity, and resilience to disturbances in an ecosystem (Winemiller, 2005). As a result, life history theory and establishing baseline estimates of life history traits for species of interest has applications in conservation of coral reef ecosystems.

Coral reefs are one of the most diverse and productive marine ecosystems (Coker *et al.,* 2014). Cryptobenthic reef fishes make up a significant portion of reef fish biodiversity and biomass production (Brandl *et al.,* 2018). These reef fishes are morphologically/behaviorally cryptic, and they are recognized for their small adult size (typically < 50 mm total body length, Depczynski & Bellwood, 2003) and close association with reef habitat (Coker *et al.,* 2014; Brandl *et al.,* 2018). In particular, about half of all currently valid goby species (over 1,700 total, Hastings *et al.,* 2014) are associated with reef habitats (Patzner *et al.,* 2011; Brandl *et al.,* 2019), comprising a large portion of the cryptobenthic reef fish assemblage (Winterbottom & Southcott, 2008). Although gobies are the most diverse family of tropical marine fishes (Patzner *et al.,* 2011; Tornabene *et al.,* 2016) and among some of the smallest vertebrates (Depczynski & Bellwood, 2006), much of their life history is unknown (Ackerman & Bellwood, 2000; Hernaman *et al.,* 2000).

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The masked/glass goby *Coryphopterus personatus* (Jordan & Thompson 1905)/*hyalinus* Böhlke & Robins 1962 is an understudied Caribbean reef goby complex. Prior studies had suggested that these were sister species that existed separately on the basis of morphological (number of anterior interorbital pores) and mitochondrial genetic data (Baldwin *et al.,* 2009). However, more recent genetic analyses appear to refute this hypothesis, finding mismatches between morphotypes and genetic types using both nuclear and mitochondrial markers (Selwyn *et al., unpubl.data*). *Coryphopterus personatus/hyalinus* is both common and abundant throughout the Caribbean (Pezold *et al.,* 2015); moreover, it is frequently the most numerically abundant goby on shallow Caribbean reefs (Luckhurst & Luckhurst, 1978; Greenfield & Johnson, 1999; Dominici-Arosemena & Wolff, 2005). This species complex forms large social aggregations or shoals of 10s to 100s of individuals (Luckhurst & Luckhurst, 1978; Robertson & Justines, 1982; Selwyn *et al.,* in prep.). These groups hover in the water column above the edges and drop-off slopes of coral reefs (Cole & Robertson, 1988; Thacker & Cole, 2002). *Coryphopterus personatus/hyalinus* exhibit protogynous hermaphroditism in which all individuals begin life as females and some transition to males after settlement in as little as 9 days; however, this ability is regulated by social hierarchy dynamics within the population (Cole & Robertson, 1988; Cole & Shapiro, 1990; Allsop & West, 2004).

In order to make some inferences on the functional role of *C. personatus/hyalinus*, it is necessary to consider what is known on the ecology of this reef goby complex. It has a planktivorous diet (Baldwin & Robertson, 2015), and it is probably highly susceptible to predation due to its small adult body size (Sogard, 1997; Depczynski & Bellwood, 2006; Goatley & Bellwood, 2016; Goatley *et al.,* 2017). *Coryphopterus personatus/hyalinus* are prey of larger reef fishes such as lionfish (Morris & Akins, 2009; Côté & Maljković, 2010), wrasse (Steele &

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Forrester, 2002) and grouper (Randall, 1967). Notably, this species complex is found at a broad depth range of 1-70 m (Baldwin & Robertson, 2015). Along with its high numerical abundance, these characteristics indicate that *C. personatus/hyalinus* plays an important trophic role in transferring nutrients from pelagic plankton to reef predators and the reef benthos. Examining both the ecology and life history (age structure, growth) of *C. personatus/hyalinus* and other cryptobenthic reef fishes can provide a better understanding of their functional role, productivity, and resilience in coral reef ecosystems.

Otolith microstructure is used to estimate daily age and growth of individual fish with lifespans less than one year (Campana, 1992). Otoliths, or ear stones, are calcium carbonate structures in the inner ear of teleost fish that assist in balance, orientation, and hearing (Popper *et al.,* 2005). The daily deposition of otolith increments, consisting of a dark and light band, has been validated for several gobies (Hernaman *et al.,* 2000; Shafer, 2000; Depczynski & Bellwood, 2006; Wilson *et al.,* 2008) so here it was assumed that one otolith increment corresponds to one day. Similarly, the deposition of the first otolith increment near the primordium has been shown to occur at or near hatching in coral reef fishes (Thorrold & Hare, 2002). In addition, otolith settlement marks recognized by changes in increment width and contrast have been described and validated for coral reef fishes including gobies (Radtke *et al.,* 1988; Shafer, 2000; Hogan *et al.,* 2017) transitioning from a pelagic to benthic environment (Victor, 1982; Wilson & McCormick, 1997).

A recent study indicates that cryptobenthic reef fishes like *C. personatus/hyalinus* constitute the majority of fish biomass consumed on coral reefs (Brandl *et al.,* 2019). I hypothesize that the high risk of predation mortality selects for an opportunistic life history strategy (i.e., short lifespan) in *C. personatus/hyalinus* which is currently recognized for its small

adult body size and highly abundant populations (typical traits of opportunistic life history strategists, Winemiller, 2005).

The objectives of this study:

1. Estimate pelagic larval duration, previous body size at settlement, body size structure (i.e., maximum body size), age structure (i.e., lifespan), and growth patterns of the *C. personatus/ hyalinus* complex.

2. Provide inferences and interpretations on the functional role, productivity, and resilience of *C. personatus/hyalinus* populations.

3. Enhance our understanding of the biology, ecology, and evolution of cryptobenthic reef fishes along with their trophic contribution in coral reef ecosystems.

METHODS

Coryphopterus personatus/hyalinus 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 (Fig. 1) in early January 2017. Water temperature ranged from 26-28°C. Turneffe Atoll is located on the Belize Barrier Reef, the second largest barrier reef system in the world (Gibson & Carter, 2003), and it was officially established as Belize's largest Marine Protected Area (MPA) on November 22nd, 2012 (Belize Fisheries Department, 2015). The largest atoll (531 km^2) in the area, Turneffe Islands is a bank reef consisting of mangrove islands, patch reefs, and fringing reefs partially encircling a shallow lagoon (Gibson & Carter, 2003). Specimens were collected from forereef sites at depths between 36 and 57 ft. Individual specimens were photographed shortly after collection and before preservation in 95% ethanol. Somatic size at capture (standard length, SL; total length, TL) of post-larval individuals was measured (precision 0.001 mm) on calibrated images using ImageJ software.
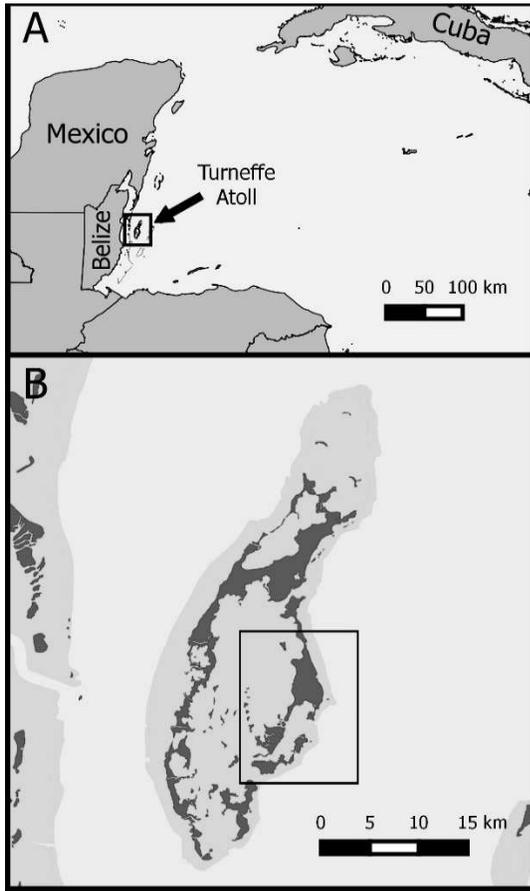

Figure 1: (A) Map of Mesoamerica indicating the location of Turneffe Atoll, Belize (box). (B) Map of Turneffe Atoll indicating the location of the sampling area (box). Samples were collected from multiple forereef sites on the windward side of Turneffe Islands Atoll, Belize. The Belize Barrier Reef is the string of small islands (running north–south) west of the atoll.

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Sagittal otoliths were prepared for daily age and growth estimation. First, the sagittal otoliths were extracted from a subset of collected individuals since this pair is generally the largest, formed the earliest (Green *et al.,* 2009) and has been examined for tropical reef gobies (Sponaugle & Cowen, 1994; Depczynski & Bellwood, 2006). Once cleaned of residual material with MilliQ water and dried, whole otoliths were mounted flat or 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 500X 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 along the longest otolith radius from core to edge. Otoliths were imaged at 500X magnification with a Nikon Digital Sight DS-fi2 camera, and measurements were made from calibrated images using NIS-Elements computer imaging software. Otolith radius, a measure of otolith size, was estimated by summing the measurements of the longest larval and post-larval linear radii. Specifically, the larval radius was measured as the linear distance from the start of the first increment that bounds the core to the start of the settlement mark (Fig. 2). Subsequently, pelagic larval duration (PLD) was estimated as the number of daily increments between the otolith primordium (Fig. 2) which is oval-shaped in gobiiforms (Brothers, 1984) and the settlement mark (Thorrold & Hare, 2002). Post-larval radius was measured as the linear distance from the start of the settlement mark to the otolith edge (Fig. 2). Age at capture (in days) and daily growth were measured simultaneously by counting increments and measuring their widths (µm) respectively along the otolith radius. Increment widths or otolith growth rates were standardized as a proportion (%) of the larval or post-larval radius they were measured along. 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 second, separate occasion

blind to sample identity. The coefficient of variation was used as a measure of precision between

the two age at capture estimates (Campana, 2001) in which individuals with CV > 10% were

excluded from analyses (Walker & McCormick, 2004; Hernaman & Munday, 2005a;

Depczynski & Bellwood, 2006). Only five individuals met this criterion, so a total of 87

individuals with a mean CV of 2.87% ±2.31 SD were retained for further analyses. For 14

additional individuals, post-settlement increments were unresolved for measurement; however,

these individuals were retained for their larval duration (mean CV of 3.52% ±2.66 SD) and larval

growth estimates. Coefficient of variation was estimated as follows:

$$\text{CV (\%)} = \frac{\text{SD}}{\text{mean}} * 100,$$

where SD is the standard deviation.

To estimate individual body size (TL in mm) at settlement, the experimental Modified

Fry back-calculation model (Vigliola & Meekan, 2009) was employed in R package RFISHBC

(Ogle, 2018). This specific model was chosen because it produced the most precise and accurate

estimates of previous body length at age for individual reef-associated gobies compared to other

back-calculation models and the use of otolith radius at age (Wilson *et al.,* 2008). Body length at

hatch was set at 2 mm (Kramer & Patzner, 2008; T. Gardner, pers. com.), and sagittal radius at

hatch was averaged across individuals to obtain a mean value of 6.73 μm ±1.68 SD (n = 87).

These values obtained for *C. personatus/hyalinus* are comparable to other reef-associated gobies

(Wilson *et al.,* 2008) and congeners (Kramer & Patzner, 2008). Estimated total length at

settlement was modeled by the following equation:

$$TL_s \text{ (mm)} = 0.75L0p + \exp\Bigg(\log(L0p - 0.75L0p) +$$

$$\frac{\big(\log(Lcap - 0.75L0p) - \log(L0p - 0.75L0p)\big) * \big(\log(Ri) - \log(R0p)\big)}{\log(Rcap) - \log(R0p)}\Bigg),$$

where *TL_s* is the total length at settlement, *0.75L0p* is the body length at otolith formation, *L0p* is the body length at hatch, *Lcap* is the total length at capture, *Ri* is the sagittal radius at settlement, *R0p* is the mean sagittal radius at hatch, and *Rcap* is the sagittal radius at capture.

Model quality and fit were evaluated using statistical measures of probability and power. Simple linear regressions were determined as the best fit between x and y variables according to (1) linearity of the relationship ($p > 0.1$; linear model is more appropriate than a curved model), (2) homoscedasticity of the residuals across x values ($p > 0.01$), (3) model significance ($p < 0.001$), (4) Explanatory power or r^2. A spline smooth was fit to larval data according to (1) linearity of the relationship ($p < 0.001$; curved model is more appropriate than a linear model), (2) homoscedasticity of the residuals across x values ($p > 0.01$), (3) Significance of the smooth term or x variable ($p < 0.001$), (4) Explanatory power or r^2, (5) number of knots is appropriate ($p > 0.1$). General linear hypothesis testing was performed using planned post-hoc comparisons to test for significant ($p < 0.001$) differences in average otolith growth between (1) Larval stage and 10 days post-settlement and between (2) 10 days pre- and post-settlement with free adjustment of p-values.
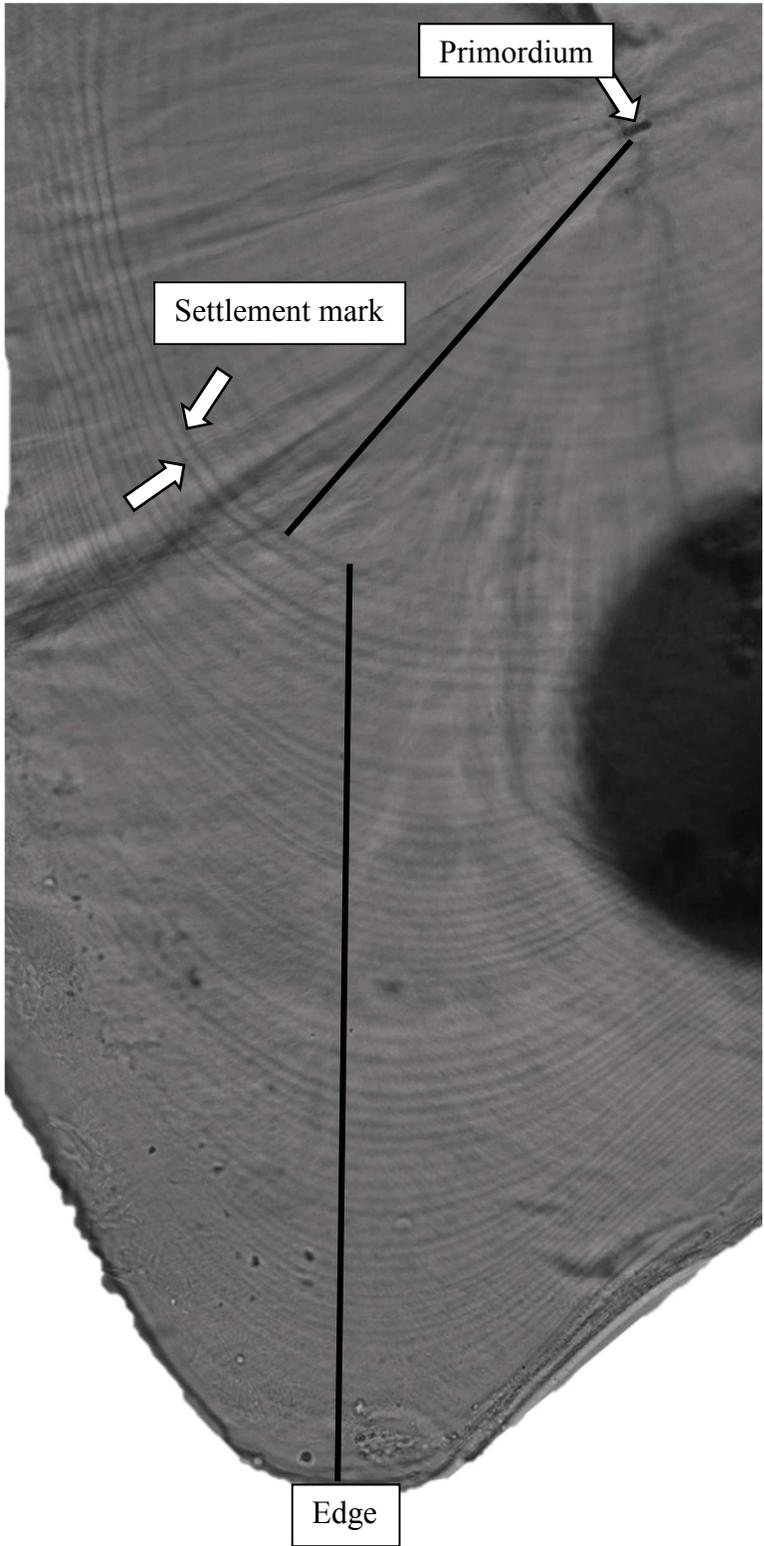
Figure 2: Sagittal otolith radius of *Coryphopterus personatus/hyalinus* imaged at 500X magnification indicating important features.

RESULTS

Total length at capture ranged from 16.8 to 57.9 mm with a mean of 31.5 mm (n = 596; Fig. 3). For a subset of individuals spanning the total length range (Fig. 3), estimated age at capture ranged from 51 to 195 days with a mean of 100 days (n = 87; Fig. 4). There was a strong linear correlation between sagittal radius and estimated age at capture (p < 0.001; Fig. 5a). Similarly, there was a strong linear correlation between sagittal radius and total length at capture (p < 0.001; Fig. 5b). Across individuals, estimated age at capture was approximately correlated with total length at capture so a linear model fit well to the data (p < 0.001; Fig. 6).
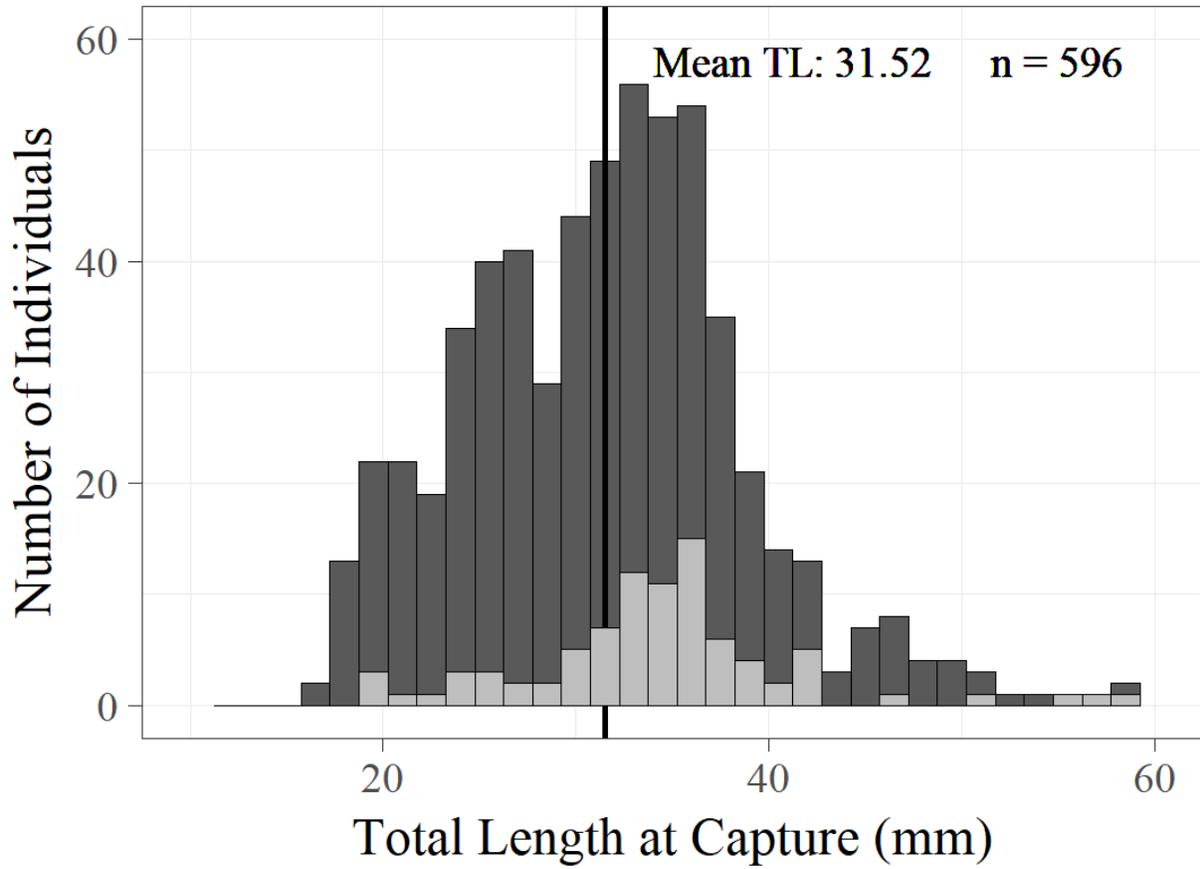
Figure 3: Frequency distribution of *Coryphopterus personatus/hyalinus* total length at capture. Binwidth = 1.5 mm. Gray-shaded region indicates the subset (n = 87) of individuals used for aging.
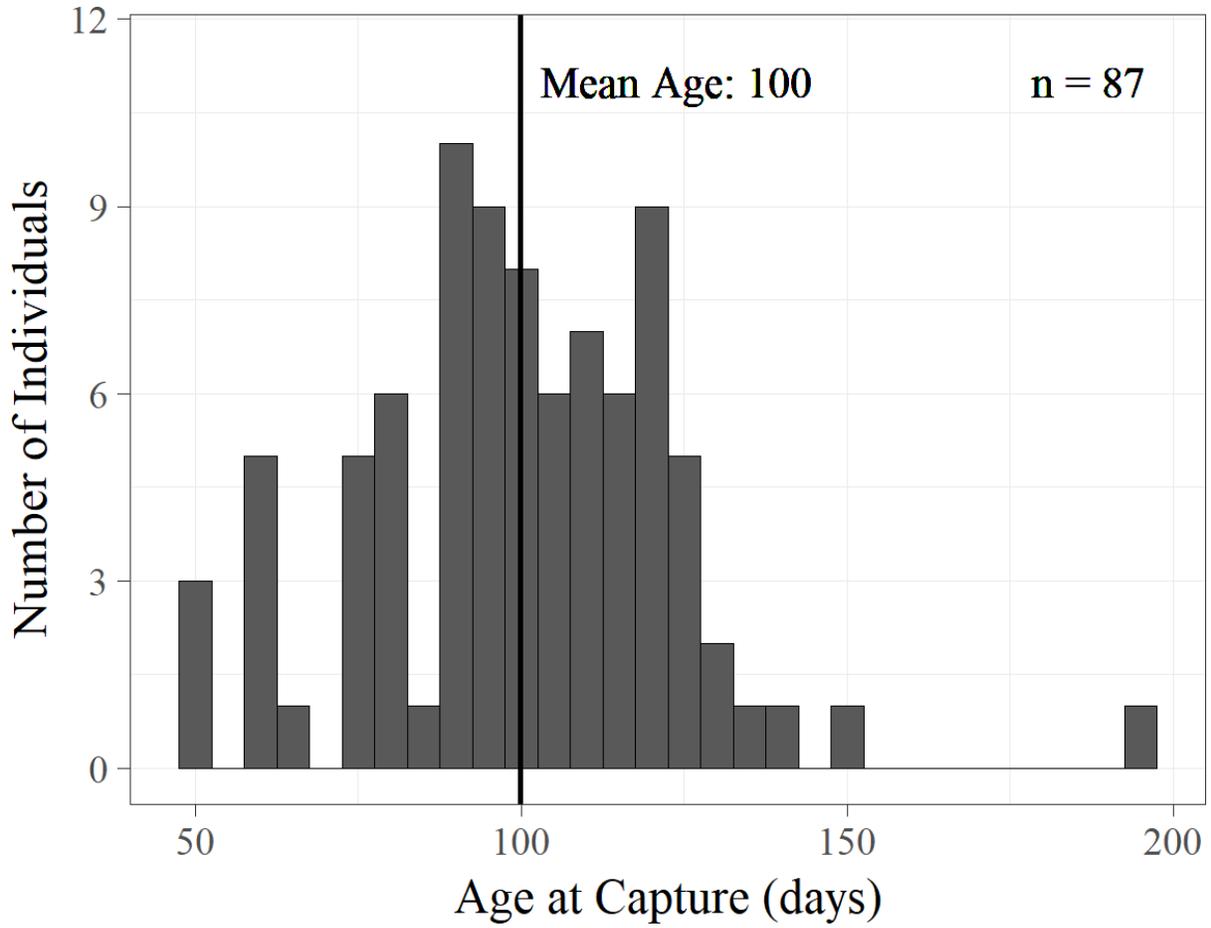
Figure 4: Frequency distribution of *Coryphopterus personatus/hyalinus* estimated age at capture. Binwidth = 5 days.
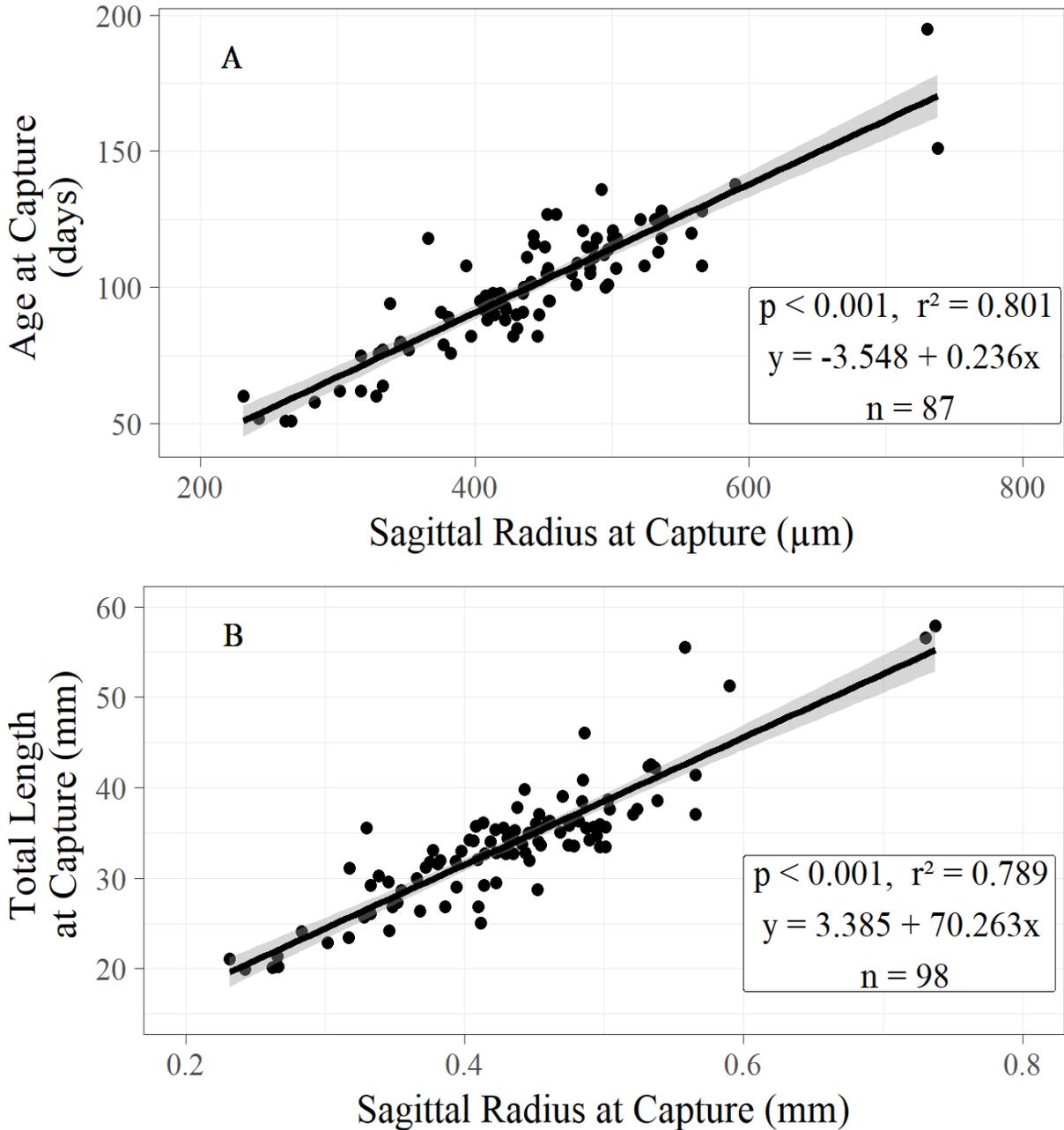
Figure 5: (A) Relationship between *Coryphopterus personatus/hyalinus* sagittal radius and estimated age at capture modeled by a linear regression. (B) Relationship between *Coryphopterus personatus/hyalinus* sagittal radius and total body length at capture modeled by a linear regression. Shaded area is 95% CI.
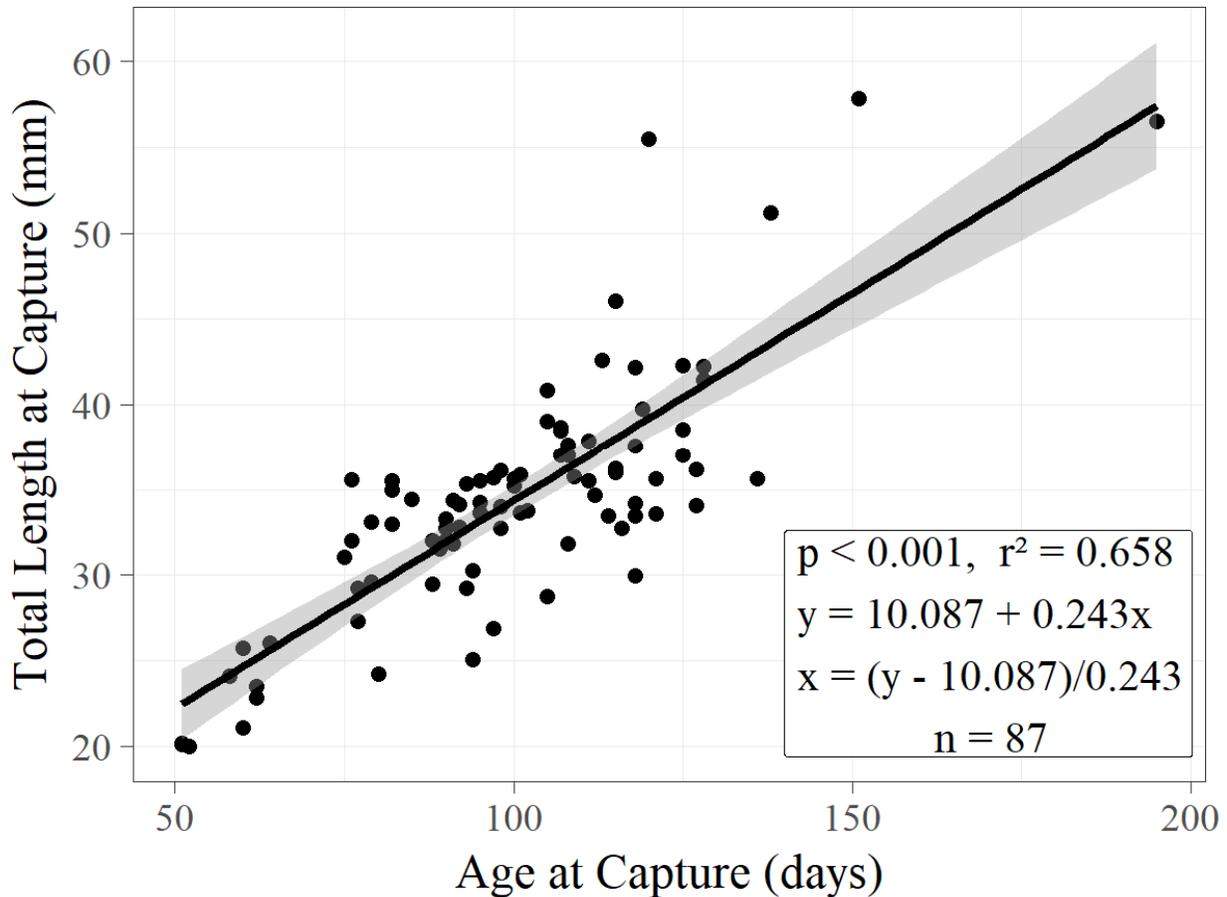
Figure 6: Relationship between *Coryphopterus personatus/hyalinus* estimated age and total body length at capture modeled by a linear regression. The equation to predict age from TL is also provided. Shaded area is 95% CI.

Pelagic larval duration ranged widely from 21 to 50 days with a mean of 33 days (n = 101; Fig. 7). Also, there was a strong inverse relationship between average daily larval otolith growth and larval duration ($p < 0.001$; Fig. 8). Most of the individuals (98/101) with larval duration and larval growth estimates, also had all of the estimates needed to back-calculate body size at settlement. Estimates of total body length at settlement ranged from 11.6 to 21.9 mm with a mean of 15.3 mm ±1.5 SD (n = 98; Fig. 9). Individuals with slower average larval growth and longer larval durations compensated by attaining larger total body lengths at settlement (Fig. 9).

Larval duration explained 25.5% of the variation in total body length at settlement (p < 0.001; Fig. 9a), while average daily larval otolith growth explained 26.9% of the variation in total body length at settlement (p < 0.001; Fig. 9b). Average daily otolith growth was fastest during the larval phase relative to post-settlement (p < 0.001; Fig. 10a & 11). Average daily otolith growth decreased 28% from the pre-settlement zone (average of 10 days before settlement = 3.2% ±0.79 SD; n = 87) to the post-settlement zone (average of 10 days after settlement = 2.3% ±0.93 SD; n = 87) (p < 0.001; Fig. 10b & 11).
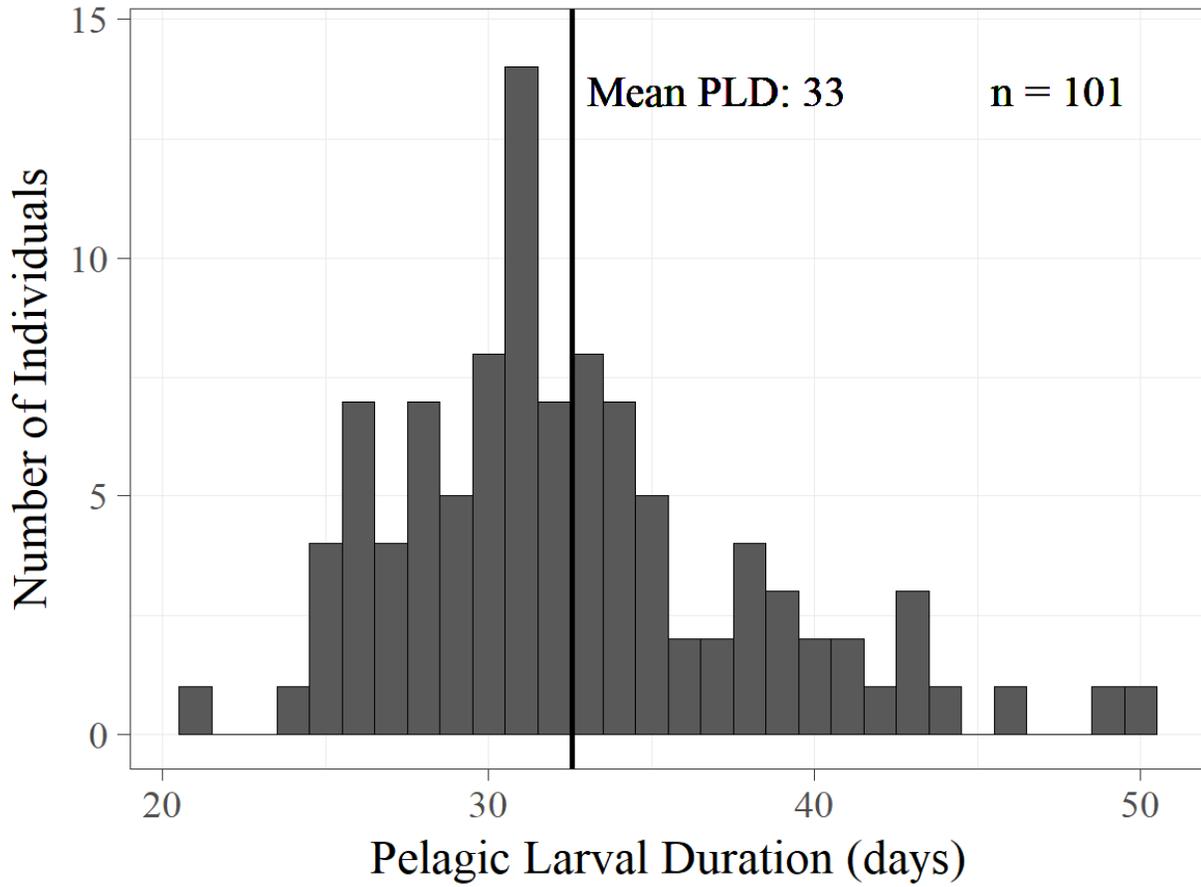
Figure 7: Frequency distribution of *Coryphopterus personatus/hyalinus* pelagic larval duration. Binwidth = 1 day. Modal PLD is 31 days.
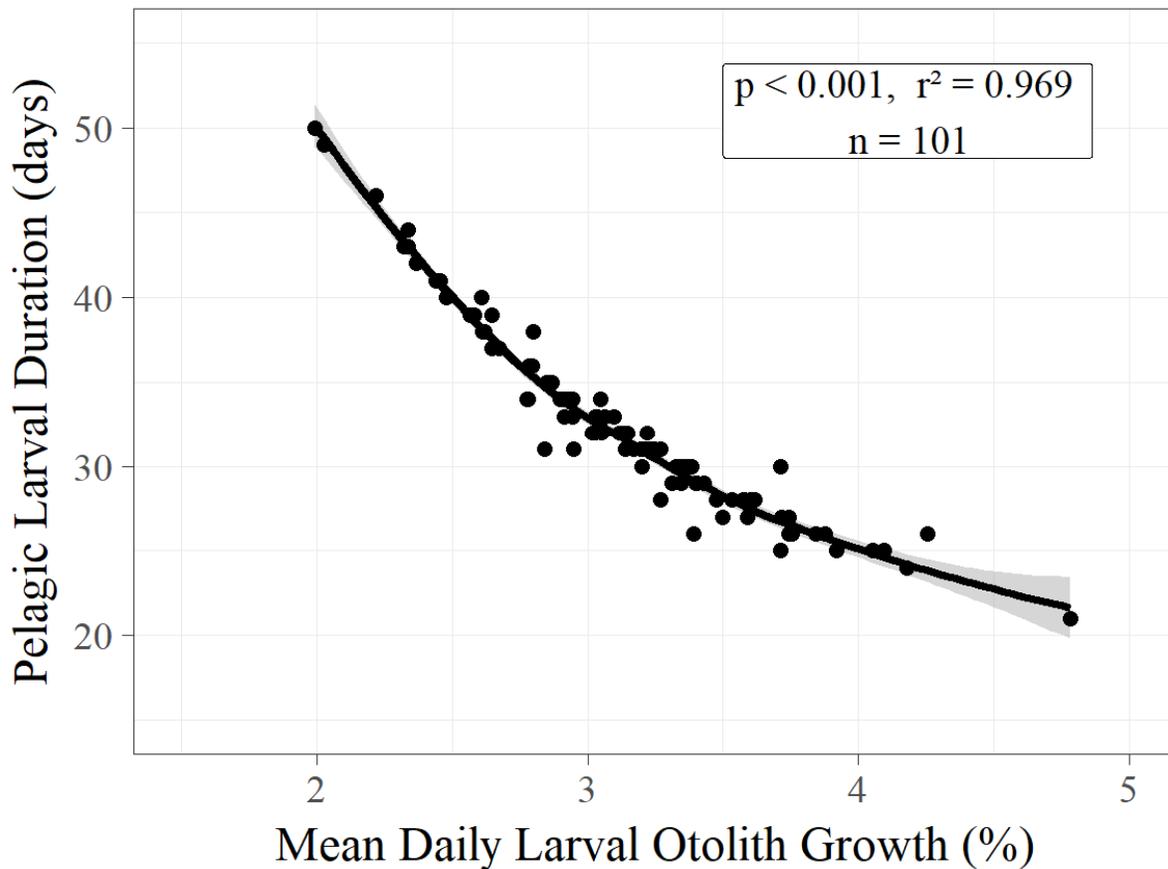
Figure 8: Inverse trend between *Coryphopterus personatus/hyalinus* average daily larval otolith growth and pelagic larval duration modeled by a spline smooth. Daily larval otolith growth rates were standardized as a proportion (%) of the larval radius they were measured along. Means were calculated by summing daily larval otolith growth rates and dividing by PLD for each individual. Shaded area is 95% CI.
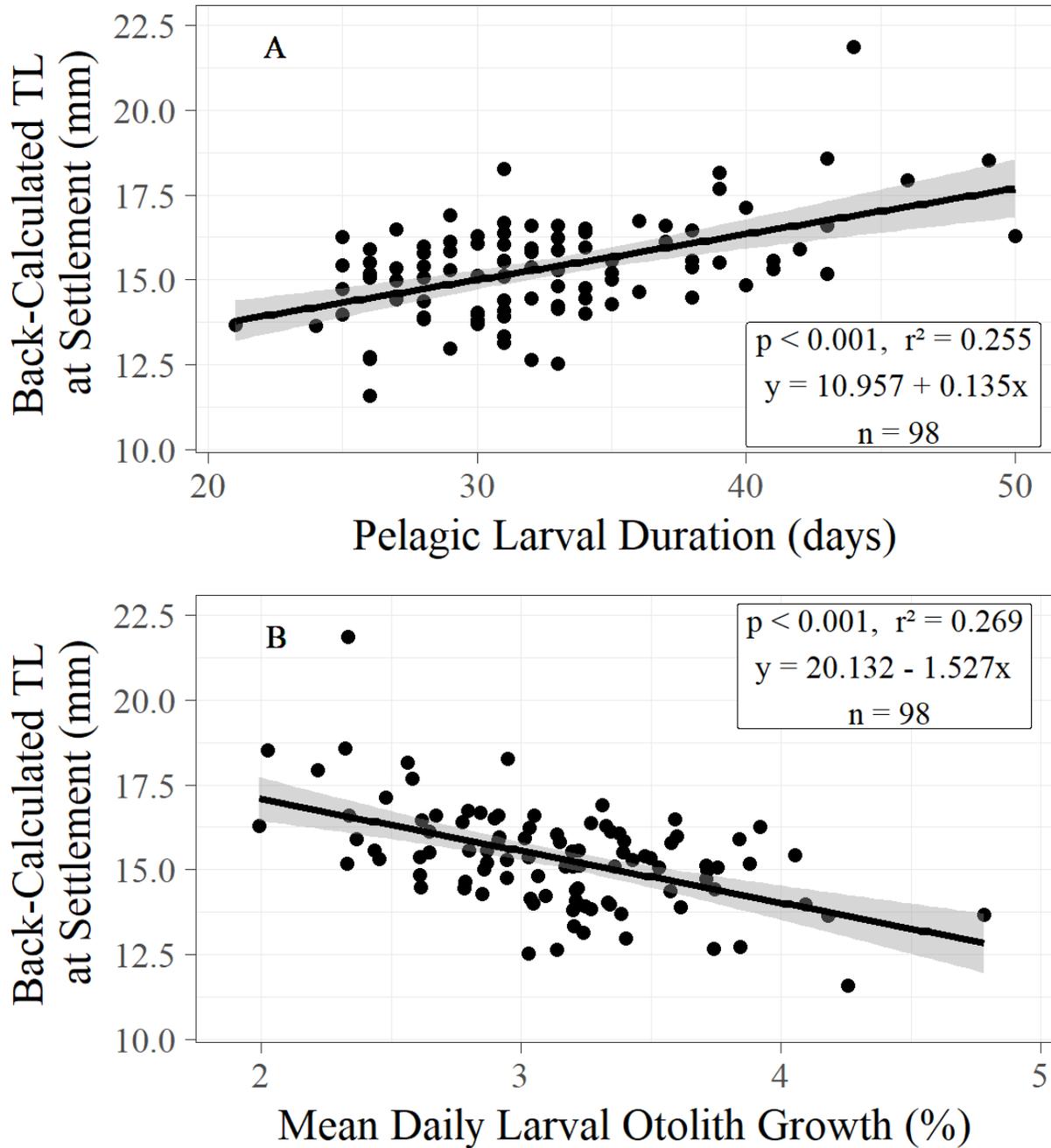
Figure 9: (A) Relationship between *Coryphopterus personatus/hyalinus* pelagic larval duration and back-calculated total body length at settlement modeled by a linear regression. (B) Relationship between *Coryphopterus personatus/hyalinus* average daily larval otolith growth and back-calculated total body length at settlement modeled by a linear regression. Shaded area is 95% CI.
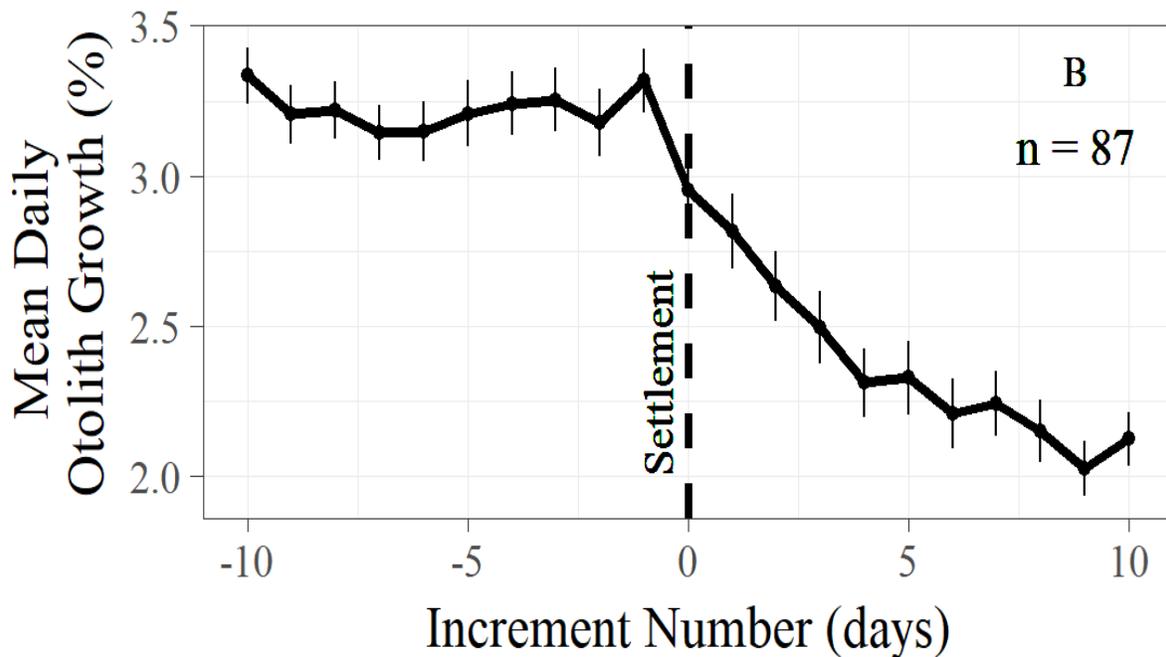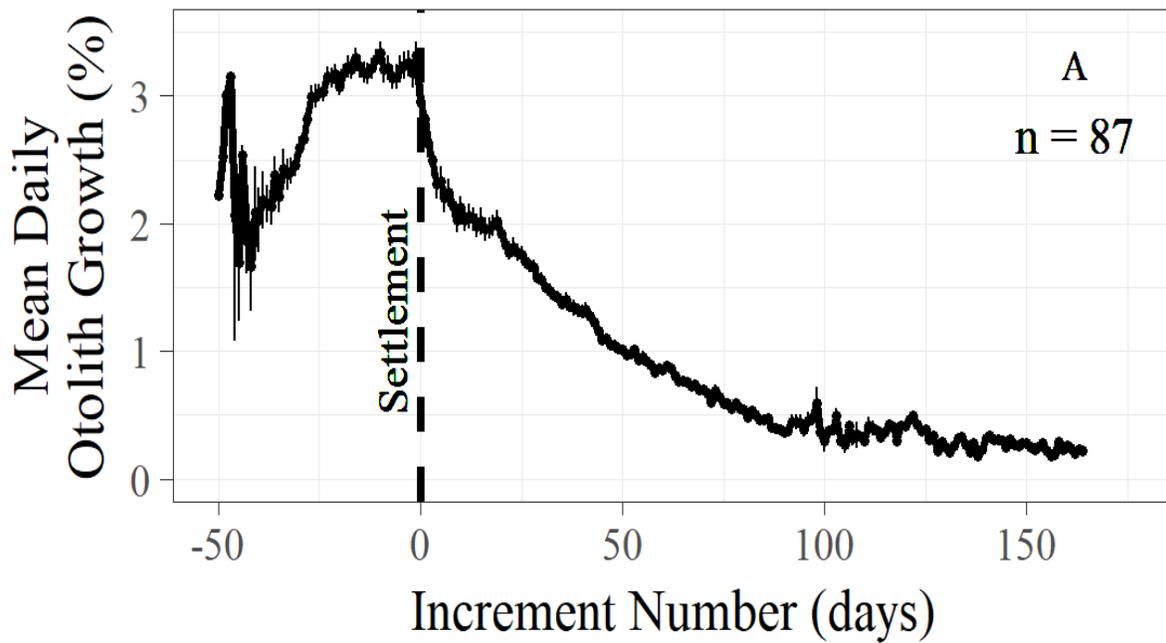
Figure 10: Average daily otolith growth (±1 SE, %) profile of *Coryphopterus personatus/hyalinus*. Increment numbers are centered around the settlement mark at 0. Negative increment numbers indicate larval increments while positive increment numbers indicate post-settlement increments. (A) Entire life history profile where only 3 individuals had post-settlement ages ≥ 99 days. (B) Close-up profile of the settlement transition, 10 days pre- and post-settlement.
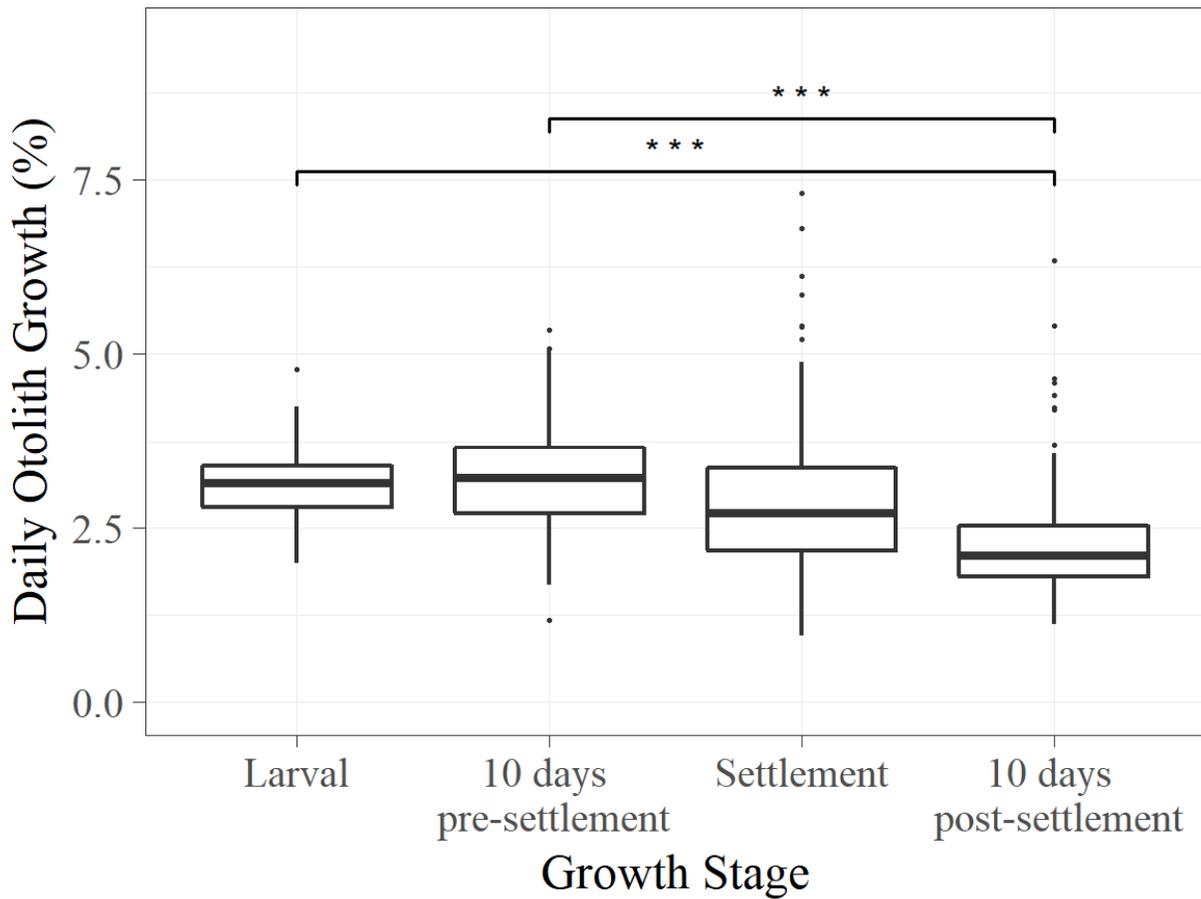
Figure 11: Distribution of *Coryphopterus personatus/hyalinus* average daily otolith growth between growth stages. n = 87 for each factor level. The larval, 10 days pre-settlement, and 10 days post-settlement levels are distributions of individual mean values. The settlement level is not a distribution of means since it represents 1 day of otolith growth or measurement for each individual. These boxplots indicate the min, 25% quartile, median (bold bar), 75% quartile and max where outliers are plotted as individual points. ***: $p < 0.001$.

DISCUSSION

Here I found that otolith microstructure analysis is a reliable and useful technique for estimating life history traits of *C. personatus/hyalinus.* Sagittal radius at capture is strongly proportional to both age and total length at capture (Fig. 5a & b). The former makes otolith size (measured as a radius) a useful predictor of age and indicates that otolith increments are continually deposited in older individuals which reduces bias in age underestimations. The latter indicates that daily otolith growth is proportional to daily somatic growth and supports back-calculation of previous body length at settlement (Campana & Neilson, 1985; Thorrold & Hare, 2002; Vigliola & Meekan, 2009).

Coryphopterus personatus/hyalinus have an abbreviated life cycle with life history traits consistent with those of other cryptobenthic reef fishes (Depczynski & Bellwood, 2006). This species complex attains small maximum body sizes (max = 58 mm TL; Fig. 3), and their reproductive lifespans are short (max post-settlement age = 164 days; however, 95% of individuals had post-settlement ages of ≤ 98 days, n = 84). Notably, these individuals maintain linear growth in body length throughout reproductive age which makes body size a useful predictor of age (Fig. 6). Interestingly, growth rate during the larval phase largely determines larval duration (Fig. 8) and to a lesser extent total body length at settlement (Fig. 9b), indicating that the environment experienced during the larval stage can drive demographic patterns in these populations (Hogan *et al.,* 2017). Average daily growth was fastest during the pelagic larval phase (Fig. 10a & 11) and decreased substantially during the settlement transition to benthic reef habitat (Fig. 10b & 11), possibly due to a shift from somatic growth to reproduction early post-settlement.

Individuals that grew faster during the pelagic larval phase spent less time in the pelagic environment. This may be beneficial if it allows these individuals to settle onto quality reef habitats and reach reproductive maturity sooner with less time constraints post-settlement. Accordingly, faster larval growth may reduce 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). In contrast, individuals that grew slower during the pelagic larval phase spent more time in the pelagic environment which may increase their ability to disperse and colonize relatively isolated reef habitats (Victor, 1986c; Wellington & Victor, 1989). Given a relatively long larval duration, accumulated larval growth can produce individuals with larger body lengths at settlement. In this study, variation in back-calculated settlement size (CV = 9.76%) was less than variation in larval duration (CV = 17.01%) which suggests selection for a settlement size threshold required to survive in reef habitats. Here, back-calculated estimates of total length at settlement are comparable to measurements obtained from field collections of recently settled *C. personatus/hyalinus* (8-8.5 mm SL, Victor, 2015) given the average length of the caudal fin (5.5 mm ±1.64 SD, TL - SL, n = 592) for individuals of this study.

Similar correlations between larval growth, larval duration, and body length at settlement have been found for other common Caribbean reef fishes (Sponaugle & Cowen, 1994; Bergenius *et al.,* 2005; Sponaugle & Grorud-Covert, 2006; Rankin & Sponaugle, 2014). Gobies, like many reef fishes, are aggressive most frequently with conspecifics, where larger individuals generally initiate and win competitive interactions for food and shelter (Shulman, 1985; Munday & Jones, 1998; Forrester *et al.*, 2006, Potter *et al.,* 2019). Further, larger body size at settlement could be advantageous in competitive interactions between individuals for reef resources at settlement or

shortly afterwards (Rankin & Sponaugle, 2014). Notably, competitively dominant individuals influence the growth, maturity, and mortality along with habitat use of subordinate individuals, which can regulate population distribution and abundance (Shulman, 1985; Munday & Jones, 1998; Forrester *et al.*, 2006).

Settlement is a very stressful period in a fish's life in which there are major morphological and physiological changes that coincide with the transition from the pelagic environment to the benthos. Otoliths often record this transition as a change in growth rate and/or particularly large increment (Wilson & McCormick, 1999). The settlement mark of *C. personatus/hyalinus* can be best described as Type 1a, which is characterized by an abrupt decrease in average otolith growth over settlement. This is the most common settlement pattern reported for coral reef fishes (Wilson & McCormick, 1999). Contrasting other coral reef fishes with a Type 1a settlement pattern, *C. personatus/hyalinus* appear to settle during their peak otolith growth which may represent developmental "competence" to settle (Wilson & McCormick, 1999).

Post-settlement *C. personatus/hyalinus* mature at a small size of 17-19 mm TL; however, males appear to mature at a smaller size of 13-15 mm TL based on gonad histology (Cole & Robertson, 1988). Interestingly, body length at maturity for males (13-15 mm TL) and females (17-19 mm TL) roughly coincides with body length at settlement calculated here (12-22 mm TL; Fig. 9) or shortly afterwards indicating a very abbreviated juvenile phase. Based on my linear size-at-age model, I estimate that a 20 mm TL individual matures at 41 total days (including PLD). However, maturity probably occurs earlier, because using the upper estimate of total length at maturity inflates the estimate of age at maturity. By using age at settlement to interpret age at maturity, I estimate that age at maturity instead occurs earlier between 22-51 total days.

Moreover, the mean age at settlement of 34 days could be used as a relative estimate of mean total age at maturity which indicates that some individuals mature as soon as they settle. In addition, *C. personatus/hyalinus* has been shown to change sex from female to male at a mean TL of 24 mm (Cole & Robertson, 1988) which corresponds to 57 total days based on my linear size-at-age model. The abrupt decrease in daily growth immediately following settlement may result from energy being allocated to reproduction instead of somatic growth (Cole & Robertson, 1988; Winemiller, 2005).

Coryphopterus personatus/hyalinus show linear post-settlement growth, and individuals do not appear to reach an asymptotic or maximum body size based on the length-at-age relationship (Fig. 6). Natural selection may produce this pattern since larger body size is related to an increase in fecundity in older, larger-bodied females (Wootton, 1990; Heino & Kaitala, 1999). The short reproductive lifespans of this species complex indicate that constant growth and consequently larger body size can confer an increasing fitness advantage with age. For many sequential hermaphroditic species such as *C. personatus/hyalinus*, larger body size enables dominance in social groups and is often linked to the transition between female and male (Liu & Sadovy, 2004). Also, becoming a dominant male in a haremic system confers considerable fitness advantages for coral reef fishes (Warner, 1988). For *C. personatus/hyalinus*, larger body length allows successful mate and nest site monopolization in males and can induce sex-change in females (Cole & Robertson, 1988; Allsop & West, 2004). Sex-change from female to male may alleviate mate competition and enhance reproductive output in *C. personatus/hyalinus* which exhibits small home ranges (Forrester & Steele, 2004; Dominici-Arosemena & Wolff, 2005) and a sex ratio skewed toward females about 4:1 (Cole & Robertson, 1988). Along with reproductive advantages, constant growth may also provide advantages associated with an

individual's vulnerability to predation. Natural mortality rates of juvenile and small adult cryptobenthic reef fishes can decline rapidly with increasing body size where small increases in total length can result in notable increases in lifespan (estimated 11 days per 1 mm increase in TL for post-settlement fishes < 43 mm TL, Goatley & Bellwood, 2016). Interestingly, the majority of *C. personatus/hyalinus* individuals measured here are smaller than this body size threshold (Fig. 3).

Several features of the ecology (i.e., small adult body size, broad depth range, planktivorous diet) and life history (i.e., linear growth, quick generational turnover rates, short lifespan) of *C. personatus/hyalinus* indicate that it plays an important trophic role in transferring nutrients to Caribbean reef predators and the reef benthos. The rate of biomass accumulation, generational turnover, and energy transfer to other trophic levels through predation provides an indication of a species prevalence within a food web (Thillainath *et al.,* 2016). Predation pressure (i.e., presence/absence, predation intensity, or predator abundance) can select for faster growth and earlier maturity in fishes (Reznick & Endler, 1982; Heibo & Magnhagen, 2005; Walsh & Reznick, 2008). In captivity, *C. personatus/hyalinus* are capable of reproducing at 1 year of age and attain considerably longer lifespans up to 4 years of age (Oceans, Reefs & Aquariums, pers. com., 2018) which suggests high extrinsic risk of mortality in the wild (Ricklefs, 2010; Eckhardt *et al.,* 2017). Lifespans of less than 1 year described here for *C. personatus/hyalinus* are relatively rare among both terrestrial and aquatic vertebrates (3 of 3,761 vertebrate species with lifespan estimates in AnAge database, De Magalhaes & Costa, 2009). However, fishes represent only 25% of these lifespan estimates in AnAge partly because their life histories are understudied relative to terrestrial vertebrates. *Coryphopterus personatus/hyalinus* is best described as an opportunistic life history strategist selected for small maximum body size, high reproductive

effort or early maturity and short lifespan (Winemiller, 2005). Along with, and presumably a result of, high post-settlement predation mortality (indicated by field, lab and otolith studies: Steele & Forrester, 2002; Forrester & Steele, 2004; Hernaman & Munday, 2005b; Depczynski & Bellwood, 2006; Goatley & Bellwood, 2016; Goatley *et al.,* 2017), this suite of opportunistic life history traits seems to characterize cryptobenthic reef fishes (Sponaugle & Cowen, 1994; Wilson, 2004; Depczynski & Bellwood, 2006; Longenecker & Langston, 2006; Winterbottom & Southcott, 2008; Victor *et al.,* 2010; Kingsford *et al.,* 2017). As a consequence of these life history traits, *C. personatus/hyalinus* is widespread in the Caribbean, found in large numbers, and constitutes a considerable amount of biomass on coral reef habitats. Similarly, fast-growing and short-lived cryptobenthic reef fishes as a guild may serve as keystone 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). Further, cryptobenthic reef fishes such as gobies and blennies make substantial contributions to biomass productivity ($g/m^2 \cdot wk^{-1}$) that match or exceed those of larger reef fishes such as acanthurids and labrids (Depczynski *et al.*, 2007). Moreover, a third of reef fish growth production in length and mass available to predators is supported by cryptobenthic reef fishes (Depczynski *et al.*, 2007).

Generally, pelagic forage fish (i.e., abundant and planktivorous clupeids, engraulids, capelin) contribute to the catch and value of commercially harvested predators and serve as important prey for various non-harvested marine predators (Pikitch *et al.,* 2014). *Aphia minuta,* a pelagic neritic goby found in the Mediterranean, feeds on zooplankton and has been found in large numbers in the stomachs of Atlantic bluefin tuna (Iglesias *et al.,* 1997) which supports a high-valued commercial fishery (Collette *et al*., 2011). Cryptobenthic reef fishes may make similar trophic contributions to coral reef ecosystems and the fisheries they support. For

example, exploited predatory fishes of the Great Barrier Reef obtain the majority of their

biomass production from planktonic primary production possibly through planktivorous trophic

intermediates such as pomacentrids and labrids (Frisch *et al.,* 2014). Continually, planktivores

represent 43-70% of total fish biomass on forereefs of the Great Barrier Reef (Williams &

Hatcher, 1983). Biomass production of basal consumers can have important consequences for

predators of freshwater ecosystems as well. For instance, fishes from two New Zealand streams

fed primarily on invertebrate *primary* consumers (i.e., plant and detritus feeders) rather than

invertebrate secondary consumers (Hopkins, 1976). Greater production of primary consumers

7.6 -72.1 $g/m^2 \cdot y^{-1}$ relative to secondary consumers 0.8 -11.9 $g/m^2 \cdot y^{-1}$ may support exploitation

by both fish and invertebrate predators (Hopkins, 1976). Such studies including the current one,

highlight the important functional role of abundant basal consumers; that is, food web production

and nutrient transfer in various ecosystems such as coral reefs, coastal pelagic waters and

freshwater streams.

<div align="center">Future Directions</div>

Many fishes are dependent on coral reef habitats for prey, niche space, for settlement,

reproduction and refuge from predators among other parameters of survivorship (Coker *et al.,*

2014). Habitat quality can influence the early survivorship of individuals; moreover, it can affect

the abundance along with the somatic size and age structure of fish populations (Shulman, 1984;

Jones, 1988; Connell & Jones, 1991; Tupper & Boutilier, 1997; Beukers & Jones, 1998; Ross,

2003; Forrester & Steele, 2004). Small-bodied organisms like gobies may benefit from reef

characteristics that are inaccessible to larger organisms. Further, small cryptobenthic fishes can

exploit fine-scale reef microhabitats for abundant, nutrient-rich prey items and refuge from

predators (Depczynski & Bellwood, 2004; Ticzon *et al.,* 2012). As a result, these individuals

may reap life history advantages such as faster growth and higher survivorship. *Coryphopterus personatus/hyalinus* show extreme differences in density among microhabitats (Selwyn *unpubl. data*) which suggests that habitat may play an important role in the population dynamics of this species complex.

The International Union for the Conservation of Nature lists *C. personatus/hyalinus* as vulnerable (Pezold *et al.,* 2015) due to invasive, predatory lionfish and decreasing coral reef habitat in the Caribbean (59% from 1970-2011, Jackson *et al.,* 2014). The combined impacts of invasive species and habitat degradation are identified as the leading cause of extinction in fishes (Clavero & García-Berthou, 2005; Rocha *et al.,* 2015). The quick generational turnover of some cryptobenthic reef fishes such as *C. personatus/hyalinus,* could enable greater population resilience to ecosystem threats (i.e., invasive species, habitat degradation, environmental change, Lefèvre *et al.,* 2016). The ecology, life history, putative functional role and resilience of *C. personatus/hyalinus*, makes it an ideal model species complex for the guild of cryptobenthic reef fishes. Determining the effects of microhabitat use and quality on the demographics (i.e., age structure, growth) of *C. personatus/hyalinus* and other species can provide a better understanding of their population dynamics and in turn improve conservation and management strategies. DNA barcoding of gut contents can be used to identify specific predators (Valdez-Moreno *et al.,* 2012; Paquin *et al.,* 2014) of cryptobenthic reef fishes, which can clarify their trophic contribution in coral reef ecosystems. In addition, short-lived vertebrates can serve as model organisms for research on human senescence, age-related diseases and ultimately health (Harel *et al.,* 2015; Reuter *et al.,* 2019).

REFERENCES

Ackerman JL., & Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series*, 206:227–237.

Allsop, D. J. & West, S. A. (2004). Sex allocation in the sex-changing marine goby, *Coryphopterus personatus*, on atoll-fringing reefs. *Evolutionary Ecology Research, 6*(6), 843-855.

Andradi-Brown, D. A., Gress, E., Wright, G., Exton, D. A., & Rogers, A. D. (2016). Reef fish community biomass and trophic structure changes across shallow to upper-mesophotic reefs in the Mesoamerican barrier reef, Caribbean. *Plos One, 11*(6), e0156641. doi:10.1371/journal.pone.0156641.

Baldwin, C.C., Weigt, L.A., Smith, D.G., & Mounts, J.H. (2009). Reconciling genetic lineages with species in western Atlantic *Coryphopterus* (Teleostei: Gobiidae). In: Lang MA et al. (Eds). Proceedings of the Smithsonian Marine Science Network Symposium. Smithsonian Contributions to the Marine Sciences 38: 113–140.

Baldwin, C. C. & Robertson, D. R. (2015). A new, mesophotic Coryphopterus goby (Teleostei, Gobiidae) from the southern Caribbean, with comments on relationships and depth distributions within the genus. *ZooKeys, 513*(513), 123-142. 10.3897/zookeys.513.9998.

Belize Fisheries Department (2015). Turneffe Atoll Marine Reserve. Available at http://www.fisheries.gov.bz/turneffe-atoll-marine-reserve/

Bergenius, M. A. J., McCormick, M. I., Meekan, M. G., & Robertson, D. R. (2005). Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. *Marine Biology*, 147(2), 291-300.

Beukers, J. S., & Jones, G. P. (1998). Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia*, 114(1), 50-59.

Böhlke, J. E. & Robins, C.R. (1962). The taxonomic position of the West Atlantic goby, *Eviota personata*, with descriptions of two new related species. Proceedings of the Academy of Natural Sciences of Philadelphia 114(5), 175-189.

Brandl, S. J., Goatley, C. H. R., Bellwood, D. R., & Tornabene, L. (2018). The hidden half: Ecology and evolution of cryptobenthic fishes on coral reefs. *Biological Reviews of the Cambridge Philosophical Society, 93*(4), 1846-1873. doi:10.1111/brv.12423.

Brandl, S. J., Tornabene, L., Goatley, C. H. R., Casey, J. M., Morais, R. A., Côté, I. M., . . . Bellwood, D. R. (2019). Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning. *Science* (New York, N.Y.), eaav3384.

Brothers, E. B. (1984). Otolith studies. In *Ontogeny and Systematics of Fishes*. (Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W. & Richardson, S.L., eds), *Special Publication*, *1*, 50-57.

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Montevecchi, W. A. (2014). Bottom-up regulation of Capelin, a keystone forage species. *Plos One, 9*(2), e87589. doi:10.1371/journal.pone.0087589.

Campana, S. E. & Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences, 42*(5), 1014-1032. 10.1139/f85-127.

Campana, S. E. (1992). Ch.4: Measurement and interpretation of the microstructure of fish otoliths. In *Otolith Microstructure Examination and Analysis* (Stevenson, D.K. and Campana, S.E., eds), pp. 59-71. Ottawa, Canada: Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology, 59*(2), 197-242. 10.1006/jfbi.2001.1668.

Clavero, M., & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution, 20*(3), 110.

Coker, D., Wilson, S., & Pratchett, M. (2014). Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries, 24*(1), 89-126. 10.1007/s11160-013-9319-5.

Cole, K. S. & Robertson, R. D. (1988). Protogyny in the Caribbean reef goby*, Coryphopterus personatus*: Gonad ontogeny and social influences on sex-change. *Bulletin of Marine Science, 42*(2), 317-333.

Cole, K.S., & Shapiro, D.Y. (1990). Gonad structure and hermaphroditism in the gobiid genus *Coryphopterus* (Teleostei: Gobiidae). *Copeia*, (4), 996-1003.

Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., . . . Yáñez, E. (2011). High value and long Life—Double jeopardy for tunas and billfishes. *Science, 333*(6040), 291-292. doi:10.1126/science.1208730.

Connell, S. D., & Jones, G. P. (1991). The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology*, *151*(2), 271-294.

Côté, I. M. & Maljković, A. (2010). Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series, 404*, 219-225. 10.3354/meps08458.

De Magalhaes, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life□history traits. *Journal of Evolutionary Biology*, *22*(8), 1770-1774.

Depczynski, M. & Bellwood, D. R. (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series, 256*, 183-191.

Depczynski, M. & Bellwood, D.R. (2004). Microhabitat utilization patterns in cryptobenthic coral reef fish communities. *Marine Biology, 145*(3), 455-463.

Depczynski, M. & Bellwood, D.R. (2006). Extremes, plasticity, and invariance in vertebrate life history traits: Insights from coral reef fishes. *Ecology, 87*(12), 3119-3127.

Depczynski, M., Fulton, C. J., Marnane, M. J., & Bellwood, D. R. (2007). Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia, 153*(1), 111-120.

Dominici-Arosemena, A., & Wolff, M. (2005). Reef fish community structure in Bocas del Toro (Caribbean, Panama): Gradients in habitat complexity and exposure. *Caribbean Journal of Science, 41*(3), 613-637.

Eckhardt, F., Kappeler, P. M., & Kraus, C. (2017). Highly variable lifespan in an annual reptile, Labord's chameleon (*Furcifer labordi*). *Scientific reports*, *7*(1), 11397.

Espinoza, P., & Bertrand, A. (2008). Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt current system. *Progress in Oceanography, 79*(2), 215-227. doi:10.1016/j.pocean.2008.10.022.

Fontes, J., Santos, R. S., Afonso, P., & Caselle, J. E. (2011). Larval growth, size, stage duration and recruitment success of a temperate reef fish. *Journal of Sea Research*, 65(1), 1-7.

Forrester, G. E. & Steele, M.A. (2004). Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology, 85*(5), 1332-1342.

Forrester, G. E., Evans, B., Steele, M. A., & Vance, R. R. (2006). Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia, 148*(4), 632-640. doi:10.1007/s00442-006-0397-0.

Frisch, A., Ireland, M., & Baker, R. (2014). Trophic ecology of large predatory reef fishes: Energy pathways, trophic level, and implications for fisheries in a changing climate. *Marine Biology, 161*(1), 61-73.

Gibson, J. & Carter, J. (2003). The reefs of Belize. Latin American Coral Reefs. 171-202. 10.1016/B978-044451388-5/50009-6.

Greenfield, D. W., & Johnson, R. K. (1999). Assemblage structure and habitat associations of western Caribbean gobies (Teleostei: Gobiidae). *Copeia, 1999*(2), 251-266. doi:10.2307/1447470.

Green, B. S., Mapstone, B. D., Carlos, G., & Begg, G. A. (2009). Ch.1: Introduction to otoliths and fisheries in the tropics. In *Tropical Fish Otoliths: Information for Assessment, Management, and Ecology* (Green, B.S., Mapstone, B.D., Carlos, G., Begg, G.A., & Nielsen, J.L., eds), pp. 1-19. Springer.10.1007/978-1-4020-5775-5.

Goatley, C. H. R. & Bellwood, D. R. (2016). Body size and mortality rates in coral reef fishes: A three-phase relationship. *Proceedings of the Royal Society B-Biological Sciences, 283*(1841), 20161858.

Goatley, C. H. R., González-Cabello, A. & Bellwood, D. (2017). Small cryptopredators contribute to high predation rates on coral reefs. *Coral Reefs, 36*(1), 207-212.

Harel, I., Benayoun, B. A., Machado, B., Singh, P. P., Hu, C. K., Pech, M. F., ... & Brunet, A. (2015). A platform for rapid exploration of aging and diseases in a naturally short-lived vertebrate. *Cell*, *160*(5), 1013-1026.

Hastings, P.A., Walker, H.Jj, & Galland, G.R. (2014). Fishes a Guide to their Diversity. Oakland, Ca: University of California Press.

Heibo, E., & Magnhagen, C. (2005). Variation in age and size at maturity in perch (*Perca fluviatilis* L.), compared across lakes with different predation risk. *Ecology of Freshwater Fish*, *14*(4), 344-351.

Heino, M. & Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology, 12*(3), 423-429. doi:10.1046/j.1420-9101.1999.00044.x.

Hernaman, V., Munday, P. L., & Schläppy, M. L. (2000). Validation of otolith growth-increment periodicity in tropical gobies. *Marine Biology, 137*(4), 715-726. 10.1007/s002270000387.

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

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

Hogan, J. D., Kozdon, R., Blum, M. J., Gilliam, J. F., Valley, J. W., & McIntyre, P. B. (2017). Reconstructing larval growth and habitat use in an amphidromous goby using otolith increments and microchemistry. *Journal of fish biology*, 90(4), 1338-1355.

Hopkins, C. L. (1976). Estimate of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research, 10*(4), 629-640.

Iglesias, M., Brothers, E. B., & Morales-Nin, B. (1997). Validation of daily increment deposition in otoliths. Age and growth determination of *Aphia minuta* (pisces: Gobiidae) from the northwest Mediterranean. *Marine Biology, 129*(2), 279-287.

Jackson, J. Donovan, M.K., Cramer, K.L. and Lam, W. (eds). 2014. *Status and Trends for Caribbean Coral Reefs: 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.

Jones, G. P. (1988). Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology*, *123*(2), 115-126.

Jordan, D. S. & Thompson, J. C. (1905). The fish fauna of the Tortugas Archipelago. Bulletin of the Bureau of Fisheries. 24, 229-256.

Kingsford, M. J., O'Callaghan, M. D., Liggins, L., & Gerlach, G. (2017). The short‑lived neon damsel *Pomacentrus coelestis*: implications for population dynamics. *Journal of fish biology*, *90*(5), 2041-2059.

Kramer, A., & Patzner, R. A. (2008). Morphological and developmental studies on the eggs of four *Coryphopterus* species (Actinopterygii: Gobiidae) in the Caribbean Sea. *Acta Ichthyologica Et Piscatoria, 38*(2), 97-102. doi:10.3750/AIP2008.38.2.03.

Lefèvre, C. D., Nash, K. L., González-Cabello, A., & Bellwood, D. R. (2016). Consequences of extreme life history traits on population persistence: do short-lived gobies face demographic bottlenecks?. *Coral Reefs*, *35*(2), 399-409.

Liu, M., & Sadovy, Y. (2004). The influence of social factors on adult sex change and juvenile sexual differentiation in a diandric, protogynous epinepheline, *Cephalopholis boenak* (Pisces, Serranidae). *Journal of Zoology*, 264(3), 239-248.

Longenecker, K., & Langston, R. (2006). Life History Characteristics of a Small Cardinalfish, *Ostorhinchus rubrimacula* (Percoidei: Apogonidae), from Koro, Fiji. *Pacific Science*, *60*(2), 225-234.

Luckhurst, B. E., & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology, 49*(4), 317-323. doi:10.1007/BF00455026.

Morris, J. A., & Akins, J. L. (2009). Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes, 86*(3), 389-398. 10.1007/s10641-009-9538-8.

Munday, P. L., & Jones, G. P. (1998). The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology, 36*, 373-411.

Newman, M., Paredes, G. A., Sala, E., & Jackson, J. (2006). Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters, 9*(11), 1216-1227. doi:10.1111/j.1461-0248.2006.00976.x.

Ogle, D.H. (2018). RFishBC. R package version 0.1.1, http://derekogle.com/RFishBC.

Paquin, M. M., Buckley, T. W., Hibpshman, R. E., & Canino, M. F. (2014). DNA-based identification methods of prey fish from stomach contents of 12 species of eastern North Pacific groundfish. *Deep Sea Research Part I: Oceanographic Research Papers*, *85*, 110-117.

Patzner, R., Van Tassell, J. L., Kovacic, M., & Kapoor, B. G. (2011). *The Biology of Gobies*. Boca Raton, Fl: CRC Press.

Pezold, F., Van Tassell, J., Aiken, K.A., Tornabene, L. and Bouchereau, J.L. (2015). *Coryphopterus personatus*. The IUCN red list of threatened species 2015: e.T185960A1794928. http://dx.doi.org/10.2305/IUCN.UK.2015 2.RLTS.T185960A1794928.en.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., . . . Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries, 15*(1), 43-64.

Popper, A. N., Ramcharitar, J., & Campana, S. E. (2005). Why otoliths? Insights from inner ear physiology and fisheries biology. *Marine & Freshwater Research, 56*(5), 497-504. 10.1071/MF04267.

Potter, T., King, L., Travis, J., & Bassar, R. D. (2019). Competitive asymmetry and local adaptation in Trinidadian guppies. *Journal of Animal Ecology, 88*(2), 330-342.

Radtke, R. L., Kinzie, R. A., & Folsom, S. D. (1988). Age at recruitment of Hawaiian freshwater gobies. *Environmental Biology of Fishes, 23*(3), 205-213. 10.1007/BF00004911.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr., 5*, 665-847.

Rankin, T.L., & Sponaugle, S. (2014). Characteristics of settling coral reef fish are related to recruitment timing and success. *PLoS One, 9*(9), e108871.

Reuter, H., Krug, J., Singer, P., & Englert, C. (2019). The African turquoise killifish *Nothobranchius furzeri* as a model for aging research. *Drug Discovery Today: Disease Models*.

Reznick, D., & Endler, J. A. (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution, 36*(1), 160-177.

Ricklefs, R. E. (2010). Life-history connections to rates of aging in terrestrial vertebrates. *Proceedings of the National Academy of Sciences, 107*(22), 10314-10319.

Robertson, D. R., & Justines, G. (1982). Protogynous hermaphroditism and gonochorism in four Caribbean reef gobies. *Environmental Biology of Fishes, 7*(2), 137-142.

Robertson, D.R. & Kaufmann, K.W. (1998). Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: Accommodating variation in recruitment seasonality and longevity. *Australian Journal of Ecology, 23*, 226-233.

Robertson, D.R. & Van Tassell, J. (2015) Shorefishes of the Greater Caribbean: online information system. Version 1.0 Smithsonian Tropical Research Institute, Balboa, Panamá.

Rocha, L. A., Rocha, C. R., Baldwin, C. C., Weigt, L. A., & McField, M. (2015). Invasive lionfish preying on critically endangered reef fish. *Coral Reefs, 34*(3), 803-806.

Ross, S. W. (2003). The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. *Fishery Bulletin, 101*(2), 384-404.

Selwyn, J.D., Hogan, J.D., Downey-Wall, A.M., Gurski, L.M., Portnoy, D.S. & Heath, D.D. (2016). Kin-aggregations explain chaotic genetic patchiness, a commonly observed genetic pattern, in a marine fish. *PLoS One, 11*(4), e0153381.

Shafer, D. J. (2000). Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*. *Marine Ecology Progress Series, 199*, 217-229. 10.3354/meps199217.

Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology, 74*(1), 85-109.

Shulman, M.J. (1985). Coral reef fish assemblages- intraspecific and interspecific competition for shelter sites. *Environmental Biology of Fishes* 13, 81-92.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science, 60*(3), 1129-1157.

Sponaugle, S. & Cowen, R. K. (1994). Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): Contrasting early life histories in demersal spawners. *Marine Biology, 120*(1), 133-143.

Sponaugle, S., & Grorud-Covert, K. (2006). Environmental variability, early life-history traits, and survival of new coral reef fish recruits. *Integrative and Comparative Biology*, 46(5), 623-633. doi:10.1093/icb/ic1014.

Steele, M. A., & Forrester, G. E. (2002). Early postsettlement predation on three reef fishes: Effects on spatial patterns of recruitment. *Ecology, 83*(4), 1076.

Thacker, C. E. & Cole, K. S. (2002). Phylogeny and evolution of the gobiid genus *Coryphopterus*. *Bulletin of Marine Science, 70*(3), 837-850.

Thillainath, E. C., McIlwain, J. L., Wilson, S. K., & Depczynski, M. (2016). Estimating the role of three mesopredatory fishes in coral reef food webs at Ningaloo Reef, Western Australia. *Coral Reefs*, *35*(1), 261-269.

Thorrold, S. R. & Hare, J. A. (2002). Ch.11: Otolith applications in reef fish ecology. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (Sale, P.F., ed), pp. 243-264. San Diego, CA: Academic Press.10.1016/B978-012615185-5/50015-3.

Ticzon, V., Mumby, P., Samaniego, B., Bejarano-Chavarro, S., & David, L. (2012). Microhabitat use of juvenile coral reef fish in Palau. *Environmental Biology of Fishes, 95*(3), 355-370.

Tornabene, L., Van Tassell, J. L., Robertson, D. R., & Baldwin, C. C. (2016). Repeated invasions into the twilight zone: Evolutionary origins of a novel assemblage of fishes from deep Caribbean reefs. *Molecular Ecology, 25*(15), 3662-3682. doi:10.1111/mec.13704.

Tupper, M., & Boutilier, R. G. (1997). Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Marine Ecology Progress Series*, *151*, 225-236.

Valdez-Moreno, M., Quintal-Lizama, C., Gómez-Lozano, R., & del Carmen García-Rivas, M. (2012). Monitoring an alien invasion: DNA barcoding and the identification of lionfish and their prey on coral reefs of the Mexican Caribbean. *PloS one*, *7*(6), e36636.

Victor, B. C. (1982). Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Marine Biology, 71*(2), 203-208. 10.1007/BF00394631.

Victor, B. C. (1986c). Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology*, *90*(3), 317-326.

Victor, B. C., Vásquez-Yeomans, L., Valdez-Moreno, M., Wilk, L., Jones, D. L., Lara, M. R., ... & Shivji, M. (2010). The larval, juvenile, and adult stages of the Caribbean goby, *Coryphopterus kuna* (Teleostei: Gobiidae): a reef fish with a pelagic larval duration longer than the post-settlement lifespan. *Zootaxa, 2346*, 53-61.

Victor, B.C. (2015). Group 2: The short-fin gobies pt. 2 (six-spined, fused) *Coryphopterus* and *Lythrypnus*. In *A Photographic Guide to the Larvae of Coral Reef Fishes*. Available at http://www.coralreeffish.com/gobiidae2.html#coryphopterus.

Vigliola, L. & Meekan G. Mark. (2009). Ch.6: The back-calculation of fish growth from otoliths. In *Tropical Fish Otoliths: Information for Assessment, Management, and Ecology* (Bridget, G.S., Mapstone, B.D., Carlos, G., & Begg, G.A., eds), pp. 174-208. Springer.10.1007/978-1-4020-5775-5.

Walker, S.P.W. & McCormick, M. I. (2004). Otolith-check formation and accelerated growth associated with sex change in an annual protogynous tropical fish. *Marine Ecology Progress Series, 266*, 201-212.

Walsh, M. R., & Reznick, D. N. (2008). Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *Proceedings of the National Academy of Sciences*, *105*(2), 594-599.

Warner, R. R. (1988). Sex change and the size-advantage model. *Trends in Ecology & Evolution*, *3*(6), 133-136.

Wellington, G. M., & Victor, B. C. (1989). Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology*, *101*(4), 557-567.

Williams, D.M. & Hatcher, A.I. (1983). Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series*, 10, 239–250.

Wilson, D. T. & McCormick, M. I. (1997). Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Marine Ecology Progress Series, 153*, 259-271. 10.3354/meps153259.

Wilson, D. T. & McCormick, M. I. (1999). Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Marine Biology, 134*(1), 29-41. 10.1007/s002270050522.

Wilson, J. A., Vigliola, L., & Meekan, M. G. (2008). The back-calculation of size and growth from otoliths: Validation and comparison of models at an individual level. *Journal of Experimental Marine Biology and Ecology, 368*(1), 9-21. 10.1016/j.jembe.2008.09.005.

Wilson, S.K. (2004). Growth, mortality and turnover rates of a small detritivorous fish. *Marine Ecology Progress Series, 284*, 253-260.

Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management1. *Canadian Journal of Fisheries and Aquatic Sciences, 62*(4), 872-885.

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

Wootton, R. J. (1990). Ecology of teleost fishes. Chapman and Hall, London, UK.