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Early-life history traits of *Thalassoma bifasciatum* in Culebra, Puerto Rico

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ABSTRACT

Introduction: The study of labrid otoliths has contributed significantly to our understanding of life histories of tropical reef fish. Life history theory is based on the effect on lifetime reproductive success (i.e., fitness), growth, mortality rates, age at maturity, reproductive output, and particularly for reef fish age and size at settlement of pelagic larvae to benthic juveniles.

Objective: Quantify age and larval growth at settlement, subsequent length, and body condition of *Thalassoma bifasciatum*.

Methods: Two hundred *T. bifasciatum* individuals were collected from Punta Maguey, in Culebra, Puerto Rico. One hundred individuals were euthanized for otolith dissection.

Results: Otolith analyses revealed settlement ages ranging from 10 to 37 days and estimated standard length of 9–20 mm at settlement. Growth analyses demonstrated a significant positive relationship between age and length, while length – weight regression revealed a negative allometric growth, where length increases at a faster rate than body mass ($b < 3$). Additionally, Fulton's condition factor declined with the increasing length.

Conclusions: This study highlights early life history and growth patterns in *T. bifasciatum* in Culebra, PR and underscores the need for further exploration of life history traits to better understand population dynamics of tropical reef fishes. The rapid settlement observed in our study may be attributed to elevated water temperatures, suggesting that environmental drivers play a critical role in shaping recruitment and growth. This emphasizes the importance of incorporating environmental drivers when evaluating recruitment and population structure.

Key words: coral reef; otolith; aging; condition factor.

RESUMEN

Aspectos de la historia de vida temprana de *Thalassoma bifasciatum* en Culebra, Puerto Rico

Introducción: El estudio de los otolitos de lábridos ha contribuido significativamente a nuestra comprensión de las historias de vida de los peces arrecifales tropicales. La teoría de la historia de vida se basa en el efecto sobre



el éxito reproductivo a lo largo de la vida (es decir, la aptitud biológica), el crecimiento, las tasas de mortalidad, la edad de madurez, la producción reproductiva y, particularmente en los peces arrecifales, la edad y el tamaño al momento del asentamiento de larvas pelágicas a juveniles bentónicos.

Objetivo: Cuantificar la edad y el crecimiento larval al momento del asentamiento, así como la longitud y condición corporal posteriores de *Thalassoma bifasciatum*.

Métodos: Se colectaron doscientos individuos de *T. bifasciatum* en Punta Maguey, Culebra, Puerto Rico. Cien individuos fueron eutanasiados para la disección de otolitos.

Resultados: Los análisis de otolitos revelaron edades de asentamiento que oscilaron entre 10 y 37 días y una longitud estándar estimada de 9–20 mm al momento del asentamiento. Los análisis de crecimiento mostraron una relación positiva significativa entre edad y longitud, mientras que la regresión longitud-peso reveló un crecimiento alométrico negativo, donde aumenta en longitud de cuerpo más rápido que la masa corporal ($b < 3$). Además, el factor de condición de Fulton disminuyó con el incremento en longitud.

Conclusiones: Este estudio resalta la historia de vida temprana y los patrones de crecimiento de *T. bifasciatum* en Culebra, PR, y subraya la necesidad de explorar más a fondo los rasgos de la historia de vida para comprender mejor la dinámica poblacional de los peces arrecifales tropicales. El rápido asentamiento observado en nuestro estudio podría atribuirse a las elevadas temperaturas del agua, sugiriendo que los factores ambientales juegan un papel crítico en la configuración del reclutamiento y crecimiento. Esto enfatiza la importancia de incorporar los factores ambientales al evaluar el reclutamiento y la estructura poblacional.

Palabras clave: arrecife coralino; otolito; factor de condición; envejecimiento.

INTRODUCTION

Life history theory examines how growth, age and size at maturity, mortality rates, and reproductive output influence an organism's lifetime fitness (Campana & Thorrold, 2001). Teleost fish are particularly useful for studying these traits since much of this information is recorded in calcified structures such as scales, bones, and otoliths (Ackerman, 2004; Choat et al., 2003; Sponaugle & Grorud-Colvert, 2006; Victor, 1982). Otoliths are crystallized calcium carbonate structures of the inner ear surrounded by endolymph fluid (Victor, 1982), considered the most reliable structure for age determination (Campana & Thorrold, 2001; Jones, 1992; Victor, 1982). For instance, opaque rings are deposited daily, providing information on spawning time, age at settlement, and growth through the various life stages (Sponaugle & Grorud-Colvert, 2006; Victor, 1986). Thus, the relationship between a fish's body length and otolith length can be used to calculate the size at which a fish transitioned from a free-swimming pelagic larval to a juvenile stage established on the reef, i.e. settlement (Masterson et al., 1997).

Otoliths record not only age and growth but also environmental and physiological influences that shape life-history traits. Variations

in otolith growth patterns, such as irregular or widened daily rings, can reflect changes in water temperature, food availability, or other environmental stressors (e.g., predation), providing insight into the conditions experienced by individuals throughout their life (Hamilton & Warner, 2009; Victor, 1982, Victor 1986; Walker & McCormick, 2004; Wilson & McCormick, 1997). These records can help infer key life-history events, including settlement timing, growth rates, and shifts in reproductive strategies. However, the ability of otoliths to accurately reflect settlement age, size at settlement, and individual condition may be limited in some species or under certain environmental conditions (McCormick & Molony, 1995; Searcy & Sponaugle, 2000). Further research is therefore needed to clarify how otolith microstructure can best be used to reconstruct growth, recruitment, and early life-history variation. This need is particularly relevant given the limited understanding of how growth of small individuals, such as pre-settlement reef fishes, responds to climate change (Huang et al., 2021).

This study examines the relationship between age and estimated size at settlement, subsequent growth, age structure, and body condition (i.e., size-mass relationship)

of *Thalassoma bifasciatum* in Culebra Island, Puerto Rico. In particular, we evaluate whether otolith growth is proportional to somatic growth (i.e., standard length) and evaluate the reliability of otolith structures for early life-history trajectories of this species.

Thalassoma bifasciatum (family Labridae; bluehead wrasse) possesses several biological traits that are ideal for examining early life-history dynamics. This species exhibits a relatively short lifespan, continuous spawning and rapid juvenile growth. Indeed, *T. bifasciatum* has been widely used as a model species for studying otoliths due to their distinguishable daily growth increments (e.g. ring markings) and a clear settlement mark (Hoffman et al., 1985; Schultz & Warner, 1989; Schultz & Warner, 1991). Settlement marks show a critical transition of individuals' life history as a consequence, for example, of having an abrupt shift in habitat (from pelagic larval phase to benthic juvenile stage), behavior, diet, predation risk and survival patterns. High mortality rates are typical during this transition, where settlement strongly influences recruitment success and subsequent population dynamics (Sponaugle & Pinkard, 2004). Thus, analysis of settlement marks can provide key information on age and body length at settlement, reconstruction of growth trajectories, and inference of larval dispersal timing and recruitment patterns. In turn, this provides insight into the community dynamics and structure of reef fish assemblages and ecological processes (Sponaugle & Grorud-Colvert, 2006; Victor, 1986).

We hypothesize that variation in age at settlement in *Thalassoma bifasciatum* is associated with differences in body length, such that older individuals will be larger at settlement than younger ones. We further hypothesize that otolith growth is proportional to somatic growth (i.e., standard length), allowing reliable reconstruction of early life-history trajectories. Because slower somatic growth may correspond to lower body condition, otolith increments can serve as an indirect indicator of early growth performance and overall growth potential. By examining daily otolith growth increments and

overall otolith development, this study will evaluate the usefulness and limitations of otoliths as proxies for growth, settlement patterns, and variation in early life-history traits. The findings will provide valuable insights into *T. bifasciatum* population dynamics and help clarify variation in key life-history traits in Culebra, Puerto Rico.

Despite its abundance and wide distribution on Caribbean reefs, life-history traits in *Thalassoma bifasciatum* show considerable variation among populations and environmental conditions, highlighting the need for further research to better understand how this species responds to environmental variation and potential adaptive strategies. For example, settlement age, size at settlement, and condition factors do not necessarily follow consistent spatial patterns. Similar variability has been observed in related species, such as *Thalassoma lunare* (Ackerman, 2004). Among the many environmental variables that can have an effect on *T. bifasciatum* life history, Sponaugle & Grorud-Colvert (2006) found that water temperature was able to account for 78 % of larval growth variability. Because temperature anomalies will become more common under current climatic conditions (Hernández-Delgado & Rodríguez-González, 2025) it is crucial to further investigate how life history of fishes changes with respect to thermal variability. Findings will help predict their resilience, vulnerabilities and potential adaptations to habitat change.

Improving our understanding of larval development and recruitment dynamics is critical for interpreting the processes that influence coral reef fish communities. As well, understanding settlement patterns may provide key insight on the processes that shape recruitment dynamics to reef environments. The approach of analyzing daily growth patterns, enables comparisons of growth and survival across habitats and among species, providing valuable insights into ecological interactions such as competition, predation, and habitat selection in reef environments (Victor, 1986).



MATERIALS AND METHODS

Study Species: *Thalassoma bifasciatum* stands out as one of the most extensively studied tropical fish species. Its abundance, daily spawning capability, and protogynous hermaphroditic mating system have positioned it as a model species for age-based life history research (Shea et al., 2010; Victor, 1982). As juveniles, both male and female individuals are morphologically identical, however, as they progress into the terminal phase, males undergo changes in body coloration. Some individuals may undergo female-to-male sex change (i.e. protogynous hermaphroditism) and become a terminal phase male (Warner, 1984; Warner & Robertson, 1978). Sex change is socially mediated. Typically occurs when there is the absent dominant male allowing reproductive advantage. *T. bifasciatum* social system is centered on large terminal-phase males that defend aggressively spawning territories. Terminal phase males develop a striking blue head and exhibit a distinctive color pattern, setting them apart from both females and their initial phase male counterparts. The Caribbean *T. bifasciatum* has been reported to have a pelagic larval duration of 30 to 70 days and live not more than 3 years (Hoffman et al. 1985; Victor, 1986; Warner, 1998). There are reports of significant variation in age-based demographic parameters among populations within the same region, even within similar habitats (Ackerman, 2004)

Aside from serving as parasite cleaners for other fish, their primary dietary sources are zooplankton and small benthic organisms (Warner & Hoffman, 1980). There are no known major threats for this species other than predation. Yet due to their high site fidelity, habitat destruction may pose a local threat (Shea et al., 2010).

Sample locations: Sampling of *Thalassoma bifasciatum* was carried out from October 2022 through August of 2023 in 10 coral reef sites located along the coast of “Punta Maguey”, Culebra, Puerto Rico (Fig. 1). Structural complexity

(rugosity) varied notably among sites. Certain patch reefs exhibited minimal rugosity, consisting primarily of sand and degraded coral framework, whereas others displayed pronounced structural relief formed by large reef boulders. Coral cover was generally higher in areas of greater structural density, while some sites remained largely barren. Depth also varied among sites, ranging from ~ 3.7 – 7.6 m. These locations were selected specifically for their high structural variability within a relatively small geographic area. Twenty individuals from each site were captured arbitrarily using a mesh cage. Daily water-temperature was obtained from HOBOT-data loggers placed at the studied locations).

Specimen traits: All specimens (20 per site; total n = 200) were weighed (g) and measured for body length to the nearest 1mm using both standard length and fork length (SL and FL, respectively). Body condition was assessed using Fulton’s condition factor (K) which provides an index of the relative robustness of individual fish. K was calculated following the standard formula:

$$K = W / L^3 \times 100000$$

where W is the body weight (g) and L is the standard length (mm). This index allows comparison of the well-being of individuals across sites and treatments, with higher values indicating relatively heavier fish for a given length. The length–weight relationship and Fulton’s condition factor were evaluated using a subset of 48 males.

Otolith processing: A daily historical record of age, transitional events (i.e., settlement), growth and condition during life stages may be found in otoliths. As well, otolith structures provide valuable information on environmental and physiological influences that shape a fish’s life history. The deposited opaque rings are used for aging, where each ring represents a day of growth in their life (Victor, 1982; Victor, 1986). Ring markings are used to calculate age

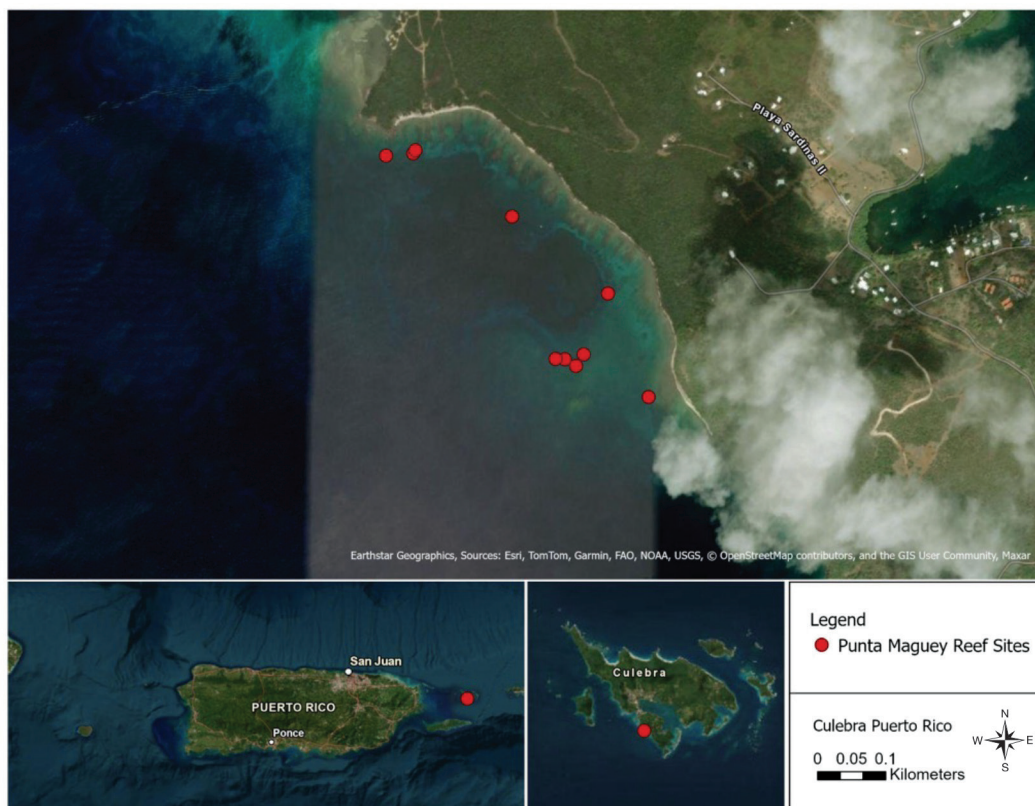


Fig. 1. Geographic locations of sampling sites.

at settlement and age at capture. As well, the distance from the center (nucleus) to the settlement mark is used to calculate the length of the individual at settlement.

For otolith dissection, a subsample of 100 individuals were euthanized by cold shock (IACUC protocol 2022-08-02 IPCM). Individuals were labeled and stored at -20°C until processed. Ten specimens were selected per site to ensure representation across sites. Following the National Oceanic and Atmospheric Administration protocol, asterisci were removed (Chittaro et al., 2020; Sponaugle & Pinkard, 2004; Victor, 1982) (Fig. 2). Seventy-eight (78) of 100 individuals dissected were used for otolith analyses. Of the 78 otoliths, daily increments of 76 were confidently readable to the otolith margin. The remaining specimens were omitted due to broken, lost, or unreliable daily ring count.

Even though sagittal, asteriscus, and lapillus structures were obtained, only asterisci were used for daily ring counts. When considering

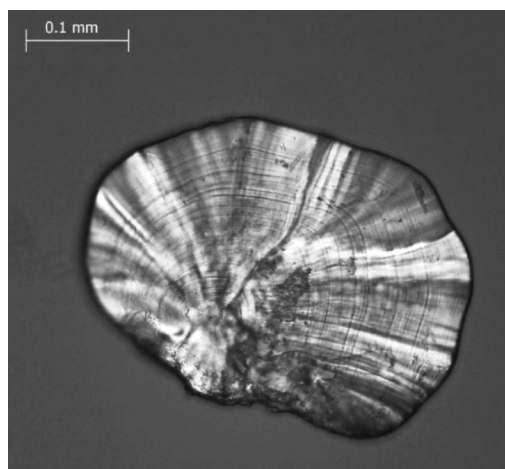


Fig. 2. Asteriscus otolith of *Thalassoma bifasciatum*.

only males, age patterns were evaluated for 35 terminal phase males.

Membranes surrounding otoliths were carefully removed, and otoliths were stored in 95 % ethanol until processed. While working under a Unitron Z10 stereo microscope with reflected light, otoliths were deposited individually on depression slides, immersed in food grade mineral oil to facilitate reading of daily ring patterns, cover slipped, and allowed to clear for at least 72 hours.

Cleared otoliths were examined under transmitted light using a Leica CME compound microscope equipped with a Leica EC3 digital camera (Leica Application Suite 3.4 software) and an adjustable polarizing filter. For each asteriscus, a series of photos in various focal planes were taken. Daily opaque ring increments were counted along the longest axis from the primordium (nucleus or otolith center) to the transitional mark (including the bands within the transition mark). This allowed for aging individuals from drifting larvae up to metamorphosis (before settlement). For aging at capture, ring increments were counted from the transitional (settlement) mark to the edge of the otolith (Ackerman, 2004; Victor, 1982; Victor, 1986). The transitional mark, or settlement mark, is defined as the significant decrease between daily increment width where there is an abrupt disappearance of ring markings (Fig. 3) (Sponaugle & Cowen, 1997; Victor, 1982). This mark corresponds to the planktonic larva settlement onto the reef (Victor, 1982). Daily increments for each asteriscus were counted two to three times, the average count was used for analysis. The distance from the center to the settlement mark is used to calculate the length of the individual at settlement. Measurements were done using ImageJ software (Masterson et al., 1997; Schneider et al., 2012; Sun & Lobel, 2023).

Statistical analysis: Spearman's rank correlation test was carried out to examine whether otolith growth was proportional to individuals' somatic growth, because data did not meet the assumption of normality. For growth patterns,

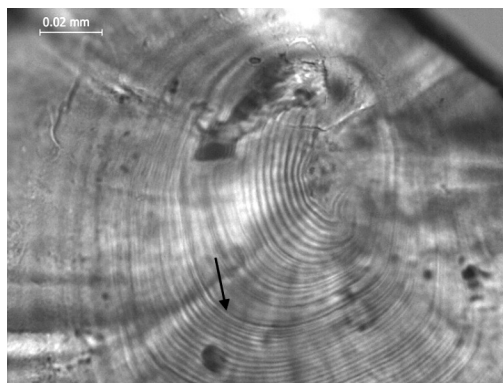


Fig. 3. Settlement mark of asteriscus otolith of *Thalassoma bifasciatum*.

a linear regression model was used to quantify the relationship between standard length (SL) and age. This model examined the significance of the relationship that exists between body growth and age, which is biologically expected for fish individuals that generally grow in body length as they age. A modified direct proportion method was used to estimate SL at settlement. This method uses the regression of fish length while adjusting for somatic growth that may be gained prior to otolith growth. For each regression, we evaluated the significance of the relationship. Linear regression model was used to evaluate the relationship between length and age. Length and weight relationship was also tested using linear regression on log-transformed data, to meet assumptions of linearity and normality. The slope of regression (β) was used for allometric growth exponent interpretation. Fulton's condition factor (K), and its relationship with SL was tested utilizing linear regression.

For the purposes of this study, we have consolidated the low sample size of transitional (i.e., in the process of sex change) individuals, and terminal phase males into a single group to augment our male sample size for analysis. Pooling male individuals, regardless of their current phase, allowed us to increase statistical robustness and estimate the general male body condition of our sample, while avoiding bias associated with small sample size. All

statistical analyses were conducted using R Studio Team (2024).

RESULTS

The number of ring markings from the nucleus (center) of the otolith to the settlement mark, also known as age at settlement, ranged from 10 to 37 days (Fig. 4). Utilizing otolith radius measurements, a modified direct proportion method was done to estimate SL at settlement. Individuals' estimated SL at

settlement measurements ranged from 9 to 20mm, 13.5 ± 2.13 (mean $\pm$ SD), (Fig. 5). Spearman's rank correlation revealed a significant positive association between age and estimated SL at settlement ($\rho = 0.446$, $p < 0.001$), indicating that individuals that settle at an older age tended to be longer.

Daily opaque ring increments were counted from the nucleus of the otolith along the longest axis to the edge of the otolith. For the 76 individuals that were used in otolith analysis, age at capture ranged from 78 to 159

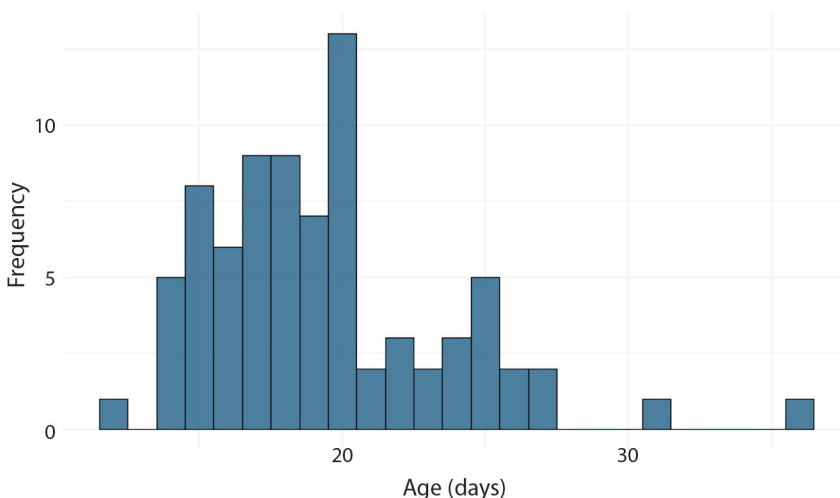


Fig. 4. Age at settlement distribution of collected *Thalassoma bifasciatum*.

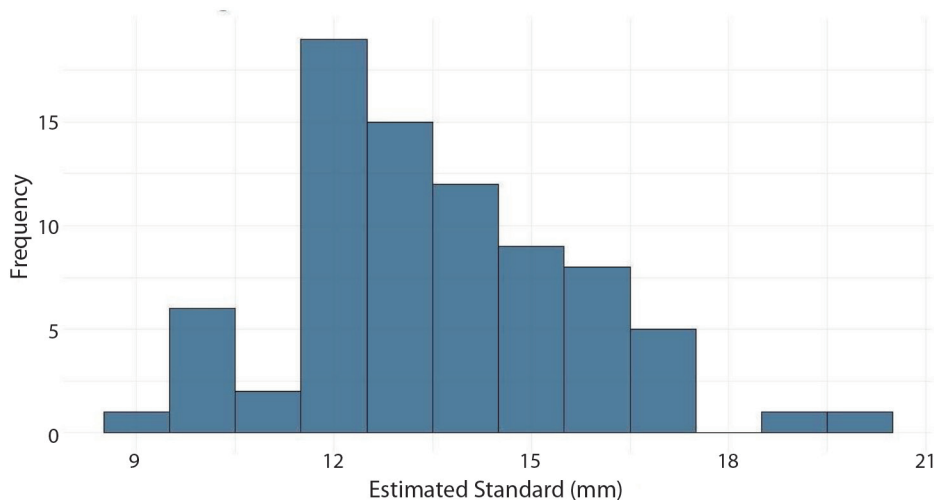


Fig. 5. Estimated length at settlement distribution of *Thalassoma bifasciatum*.

days (Fig. 6). A linear regression revealed a significant positive relationship of age and SL ($\beta = 0.44$, $SE = 0.06$; $R^2 = 0.43$, $F_{1,74} = 55.89$, $p < 0.001$), which quantifies the expected increase in body length as they age. Standard length of the 200 *T. bifasciatum* specimens at capture ranged from 39.8 to 86.6 mm (Fig. 7). The largest and oldest male was 86.6 mm long and 159 days old, whereas the smallest individual was 42.2 mm long and 102 days old.

The length and weight data of *T. bifasciatum* was log-transformed to meet assumptions of linearity and normality. Length-weight

relationships revealed strong positive relationships ($\beta = 2.89$, $SE = 0.09$; $R^2 = 0.096$, $p < 0.001$). Slope parameter ($\beta = 2.887$) was slightly under the isometric value of 3 ($t = 2.88$, $df = 204$, $p < 0.001$), indicating a lower than allometric growth. Suggesting that individuals in this study grow slightly faster in length than in weight, even though weight increases with length (Fig. 8).

Fulton's Condition Factor (K) was correlated to specimens' length. Our findings indicate a negative slope when all our specimens ($n = 200$) are combined, where body condition decreases

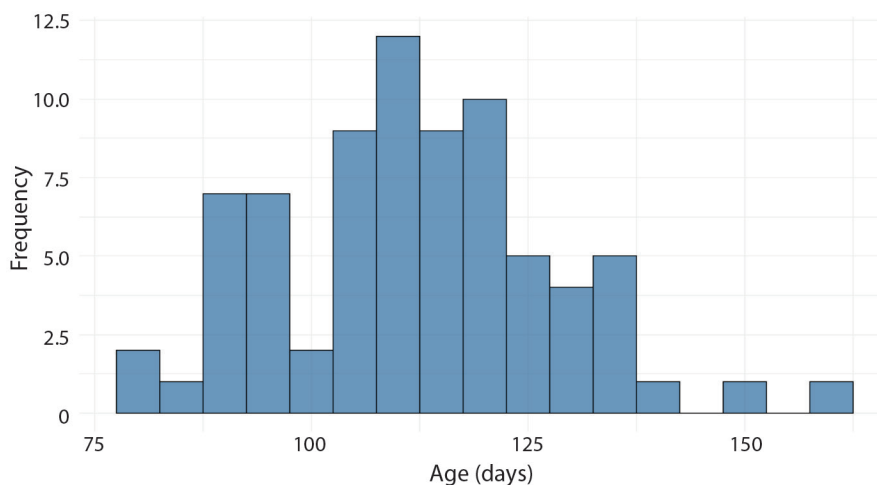


Fig. 6. Age distribution of *Thalassoma bifasciatum*.

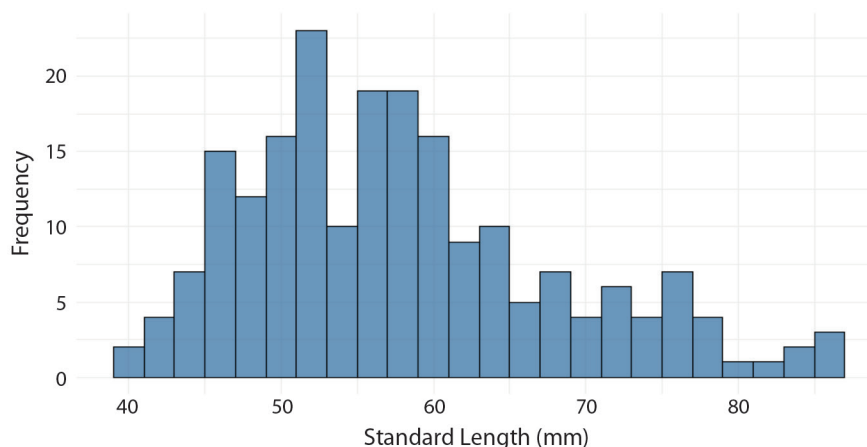


Fig. 7. Length distribution of *Thalassoma bifasciatum*.

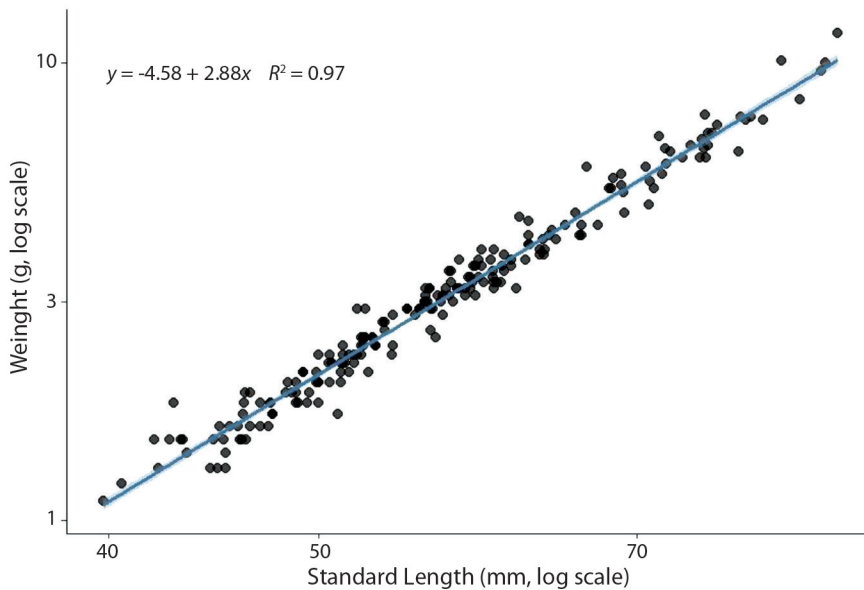


Fig. 8. Linear regression of length and weight in *Thalassoma bifasciatum*.

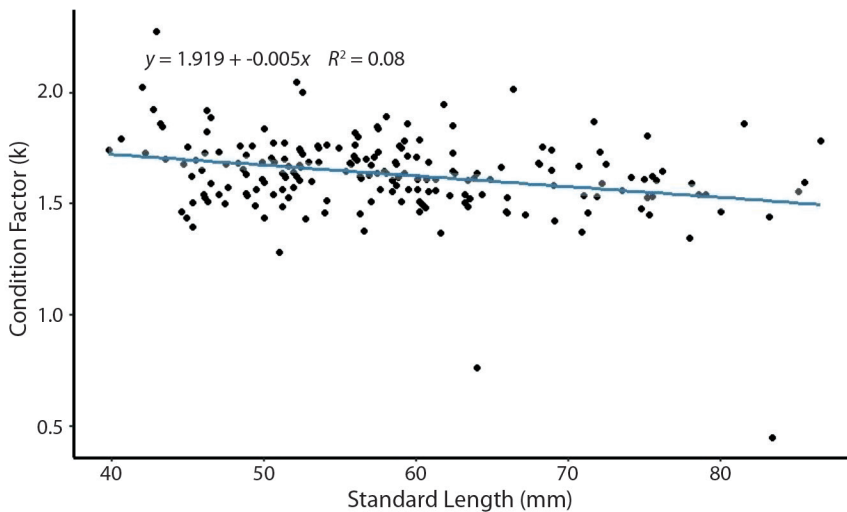


Fig. 9. Relationship between Fulton's condition factor (K) and length in *Thalassoma bifasciatum*. Blue line represents the fitted linear regression, and the lightly shaded grey area indicates the 95 % confidence interval of the model.

with the increase of SL (Fig. 9). Indicating that smaller *T. bifasciatum* individuals were proportionally more robust than larger individuals.

Furthermore, Male-only analyses followed a similar trend where there was significant relationship between age and length ($y = 0.443x + 11.791$, $R^2 = 0.43$, $p = 1.26e-10$) and between

length and weight ($b = 3.046$, $p < 0.001$, $R^2 = 0.92$). The length - weight relationship of males showed positive allometric growth, indicating that males increase in weight slightly faster than predicted by isometric growth. However, Fulton's condition factor was not correlated with length ($p = 0.601$, $R^2 = 0.08$).



DISCUSSION

Otolith analysis plays a crucial role in the study of life history in many fishes. The calcium carbonate structures provide the basis for obtaining knowledge on the individual's growth, mortality, age, and other fundamental parameters with a high degree of precision (Pawson, 1990; Rodríguez Mendoza, 2006; Victor, 1982). Otolith ring markings of short-lived species, like *Thalassoma bifasciatum*, have been confirmed to be a permanent record of an individual's daily growth, due to otolith ring increments remaining sufficiently distinct for accurate validation (Victor, 1982; Victor, 1986). In contrast, in longer-lived reef fishes, daily otolith ring markings often become compressed and difficult to distinct, therefore age determination typically relies on annual otolith markings. This study focused on otolith formation, daily-ring counts, settlement and growth patterns of *T. bifasciatum* in Culebra, Puerto Rico.

Age and length at settlement: Pelagic larvae duration is estimated to be the time from hatching up to metamorphosis, before individuals are integrated into near-reef aggregations alongside similarly sized juveniles (Sponaugle & Cowen, 1997; Sponaugle & Grorud-Colvert, 2006; Victor, 1982; Victor, 1986; Warner, 1995). This process may start approximately 2 days after fertilization. *T. bifasciatum* are reported to spend from 30 to 70 days drifting pelagically before settling onto reefs (Philibotte, 2002; Sponaugle & Cowen, 1997; Victor, 1986). Previous research found that *T. bifasciatum* planktonic life ranged from 40 to 72 days, an average of 48 days, in San Blas Panamá (Victor, 1982). However, age at settlement of our sample specimens ranged from 10 to 26 days with an outlier of 36 days. Such a finding may indicate that spatial dispersal in our study sites is limited. A study conducted on the San Cristóbal Platform in the southwest of Puerto Rico (Hensley et al., 1994) disclosed that although *T. bifasciatum* eggs spawned over the reef platform are dispersed by currents, even several hundred meters, the majority remain close,

thereby limiting excessive loss and making local retention more substantial. This dispersal limitation may potentially favor strategies that shorten early-life vulnerability.

Structural complexity of reefs has been often related with coral reef fish density, abundance and species richness, in part due to its association with shelter availability (Ménard et al., 2012). In a parallel study conducted with the same sample individuals, we found that reef rugosity did not influence our findings when comparing fish collected from areas of low rugosity to those from areas of high rugosity (unpublished data). Therefore, we suggest that habitat availability, specifically in high rugosity areas with numerous holes and crevices that could provide shelter (Ackerman, 2004), does not necessarily play a role in the life history of *T. bifasciatum* in the study areas.

Compared to other labrids, previous work on *T. bifasciatum* indicates a longer time to settle and relatively low growth rate during pelagic period (Houde & Zastrow, 1993). Previously reported lengths at settlement were around 12 mm in San Blas Islands of Panamá (Robertson, 1992; Victor, 1991). However, Sponaugle & Cowen (1997) found that *T. bifasciatum* settled at much smaller sizes in Barbados (7.9–8.8 mm). Our specimens' estimated average length at settlement was 13.5 mm. Readiness to settle once certain minimum environmental conditions are available can influence *T. bifasciatum* age and length at settlement which could happen more quickly in individuals that grow faster (Searcy & Sponaugle, 2000; Sponaugle & Grorud-Colvert, 2006; Sponaugle et al., 2009). Yet minimal conditions for settlement of this species have not been identified. However, length alone does not appear to influence survival of *T. bifasciatum* (Grorud-Colvert & Sponaugle, 2006; Searcy & Sponaugle, 2001). In fact, length differences at settlement became obscured after a few days spent as juveniles on the reef: fast-growing, high condition settlers continued to grow fast and caught up to those individuals that were larger at settlement and of lower condition (Grorud-Colvert & Sponaugle, 2006).

A key contributing factor that influences larval growth and condition is food availability. Thus, diet and prey composition variations may play a role in driving the time of settlement and larval performance. Sponaugle et al. (2009) reported a direct relationship between gut fullness and larval growth yet suggested that availability of specific prey composition may also be influencing larval growth trajectories and conditions. Nonetheless, it is important to recognize that other environmental variations may have a deeper influence on the development of these individuals. Water temperature is of particular interest given its observed influence on larval growth and the pelagic stage duration (Sponaugle & Grorud-Colvert, 2006).

The ability of *T. bifasciatum* recruits to alter physical traits or behaviors in response to environmental fluctuations is an adaptive response especially for the unpredictable environmental challenges that can be found on coral reef ecosystems (Sultan & Spencer, 2002). Specifically, changes in temperature have been reported to manifest in various ways in fish's growth, development, and survival (Ackerman, 2004; Huang et al., 2021; Mazumder et al., 2015; Thunell et al., 2023). Notably, over the past decades in tropical seas, marine heat waves have surged (Hernández-Delgado & Rodríguez-González, 2025). Including 2023, the year during which this study was conducted, and 2024 setting numerous temperature records, which may further explain the accelerated settlement in our sample. For instance, Sponaugle & Grorud-Colvert (2006) found that pelagic larval duration varied inversely with water temperature, where cold-water larvae remained more time in their plankton phase before settlement, whereas larvae in warm-water grew more rapidly yet settled at smaller size. Similarly, in a controlled laboratory setting, *Amphiprion melanopus* larvae reared at 25 °C exhibited a longer pelagic larval duration than those larvae reared at 28°C (Green & Fisher, 2004). These findings highlight how a relatively small change in temperature can strongly influence larval growth and development.

Temperature recorded by HOBO loggers across sampling sites ranged from 25.7 to 30.4 °C, with a mean of 27.3 ± 0.8 °C. These thermal conditions experienced by larvae and early juveniles within the study area were comparable to the warm-water conditions described by Sponaugle & Grorud-Colvert (2006) study. Thus, our findings improve our understanding of how environmental variables influence settlement and suggest that rapid settlement observed may have been associated with elevated water temperatures. A multi-year study would be needed to firmly evaluate temperature influences on life-history patterns, enabling us to obtain and compare samples in warmer and colder than average temperatures; however, this would require a separate research effort.

Otolith growth proportional to somatic growth: A pattern of wide daily growth rings on otoliths during the “pre-settlement” stage indicated rapid growth and development (Victor, 1982). Our results showed a significant decrease in daily ring width following settlement marks, suggesting a slowdown in growth after settlement. This decline likely reflects the energetic costs associated with habitat transition, behavioral shifts, and the need to adapt to new benthic conditions. Such a finding aligns with previous findings that otolith growth rate diminishes progressively during early juvenile stages (Searcy & Sponaugle, 2000). Because otolith deposition continues throughout these transitions, changes in increment width provide a reliable record of such physiological shifts. The strong correlation we found between otolith radius and standard length further supports the notion that otolith microstructure faithfully tracks somatic growth rates (Rodríguez Mendoza, 2006; Pawson, 1990). Moreover, our findings are consistent with Victor's (1982) work, which demonstrated that daily increment widths in *T. bifasciatum* closely mirror changes in somatic growth. Collectively, these results underscore the sensitivity of otolith microstructure as an indicator of physiological and ecological transitions associated with reef settlement.



Body Condition Factor: Phenotypic plasticity refers to variation in an organism's phenotype arising from environmental influences and individual responses to those conditions. Such variability can affect key life-history traits, including fecundity, growth, and survival (Schultz & Warner, 1991; Thunell et al., 2023). Because organisms operate under energetic constraints, investment in one biological function often reduces the energy available for others. For example, increased reproductive investment may occur at the expense of somatic growth, generating potential trade-offs between fecundity and growth. Phenotypic variation may also reflect differences in the availability of environmental resources that influence multiple physiological functions simultaneously (Schultz & Warner, 1991).

The physiological condition of fishes, particularly newly settled recruits, is strongly shaped by these energetic trade-offs and survival strategies. Their ability to compete for food and avoid predation can influence feeding behavior and nutritional intake, potentially resulting in reduced body condition (Booth & Beretta, 2004). Grorud-Colvert & Sponaugle (2006) found that recruits with a high body condition exhibited a decrease in foraging behavior in the presence of predators, while displaying enhanced swimming capabilities, and more effective predator evasion. Given that swimming demands considerable energy expenditure, individuals maintain a substantial energetic reserve, affording them a competitive edge against predators (Booth & Beretta, 2004; Grorud-Colvert & Sponaugle, 2006). Conversely, mortality rates may rise among individuals in poor condition due to an increased risk of predation, potentially leading to starvation (Searcy & Sponaugle, 2000).

This study observed an inverse relationship, wherein K values decrease as specimen length increases. This pattern may reflect reduction in energy allocated to foraging, allowing energy resources to be redirected towards alternative survival strategies. Our findings could also be related to reproductive dynamics (e.g., constant reproduction), where

higher energy investment towards reproductive output leads to a relative decrease in body mass (Thunell et al., 2023). Similar trade-offs has been studied in *Larimichthys polyactis*, where a model parameter resulting in higher population fecundity was associated with a shorter lifespan (Su et al., 2024).

Limitations: While environmental challenges may influence early development, predation exerts another layer of selective pressure on individuals. *T. bifasciatum* is reported to live up to 3 years on reefs (Prescod, 2015; Warner, 1987). However, the individuals in our study did not exceed half a year at the time of collection. Field observations revealed predation on *T. bifasciatum* by groupers (Haemulidae), lizardfish (Synodontidae), and snappers (Lutjanus), suggesting that constant predation pressure likely limits the likelihood of individuals reaching older ages in these habitats. Moreover, a study on fish assemblages at our study sites determined that in 2023 there was an increase in the presence of these predators, further supporting predation's role in shaping the population structure of this species (Hernández-Delgado et al., 2025). Warner (1998) suggested that in the presence of a reward, males of this species are inclined to take risks, even in the presence of potential predators, such as groupers and snappers. Studies have also reported a change in courtship behaviors and coloration in response to predator presence (Warner, 2000). In contrast other short-lived labrids, like *T. lunare*, may be less likely to take risks where a potential threat is evident (Ackerman, 2004; Depczynski & Bellwood, 2006). Thus, it could be suggested that predation may influence individuals through maturity. Future research should integrate predator presence to continue to clarify its role in shaping the survival and life-history traits of *Thalassoma bifasciatum*.

To conclude, our study found rapid settlement of *Thalassoma bifasciatum* in this region, which may be allocated to minimizing the most vulnerable stage of life and be potentially influenced by increased water temperatures in the tropics. The observed correlation between

otolith radius and standard length, along with the inverse relationship between condition factor and length, highlights important growth and energetic trade-offs. Integration of otolith analyses is essential for the continued understanding of how environmental variability influences life history and population dynamics of species. Such knowledge is fundamental not only for predicting population responses to future climate scenarios, but also for guiding reef management and conservation strategies aimed at mitigating the long-term consequences of ocean warming on tropical reef fish.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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