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ORIGINAL PAPER

Age, growth, and reproductive biology of Achilles tang (*Acanthurus achilles*) around Hawai’i Island, USA

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Abstract A culturally important food fish in Hawai’i, Achilles tang (*Acanthurus achilles* Shaw), recently experienced sharp declines in biomass, density, and average length in west Hawai’i Island. In December 2022, State resource managers placed a 2-year moratorium on the Achilles tang fishery in west Hawai’i Island so that the cause of the collapse could be explored. The lack of life-history information for Achilles tang from Hawai’i, or elsewhere in its range, has been noted as an impediment to decision-making. Therefore, our objectives were to characterize this population’s age, growth, and reproductive biology. In working with community fishers, we collected 363 individuals ranging 69 – 264 mm in fork length (FL) and 0 – 39 years in age based on estimates from otoliths. Achilles tang in Hawai’i exhibit a high growth rate, reaching 138 ± 11 mm FL (mean ± SE) in their first year, and exhibit relatively little growth after their second year (<5 mm yr^{-1}). The majority of males (92.0% of n = 101) and females (73.6% of n = 159) were classified as spawning capable or actively spawning, without annual or lunar periodicity. Our study highlights that the basic biology of Achilles tang poses unique challenges to fisheries managers looking to ensure its sustainable harvest. Future research will aim to characterize the susceptibility of recruits’ habitat to local environmental stressors and the relative connectivity of juvenile and adult habitats.

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Introduction

Surgeonfishes (Acanthuridae) are important components of coral-reef fish assemblages worldwide. Most of the approximately 86 members of the family are typically herbivorous (Burkepile and Hay 2010; Marshell and Mumby 2015; Parata et al. 2020) and often represent a significant proportion of the fish biomass on reefs, especially in the Indo-Pacific (Friedlander and DeMartini 2002; Foo et al. 2020; Tebbett et al. 2022). As such, their feeding activity can serve as a check on the growth of algae which may otherwise overgrow corals (Marshell and Mumby 2012, 2015). Large schools of surgeonfishes act both to crop algal growth and cycle nutrients through reef food webs (Foster 1985; Lawson et al. 1999; Shantz et al. 2015; Guerra et al. 2023). Furthermore, surgeonfishes are heavily targeted in subsistence and recreational fisheries and contribute to the food security of coastal residents throughout the tropics (Robertson et al. 2005a, b; Craig et al. 2008). For example, Melanesians living in the Northern Province of New Caledonia consumed between approximately 300 – 900 g of surgeonfish per week, or 27 – 80% of the estimated average of 1.12 kg of fish consumed per week (Labrosse et al. 2006). Recreational fishing surveys in Hawai'i estimate the mean annual non-commercial catch of surgeonfishes to exceed 111 metric tons, with convict surgeonfish (*Acanthurus triostegus* Linnaeus), goldring bristletooth (*Ctenochaetus strigosus* Bennett), eyestripe surgeonfish (*Acanthurus dussumieri* Valenciennes) and bluespine unicornfish (*Naso unicornis* Forsskål) accounting for > 75% of the catch (Williams and Ma 2013). While surgeonfishes may contribute to local subsistence, recreational, and artisanal fisheries, they generally do not support large commercial fisheries. In Hawai'i for example, total commercial landings of all surgeonfish species combined was approximately 21 metric tons in 2021, with bluespine unicornfish and eyestripe surgeonfish accounting for approximately 79% of the landings (Akizuki et al. 2021). Commercial fisheries for surgeonfishes tend to be live capture for the aquarium trade as many species' bright colors and active nature make them popular (Randall 2001). While the impact of marine ornamental fisheries at broad spatial scales is unclear (Palmtag 2017), there are numerous examples of local populations being overfished (Shuman et al. 2004; Palmtag 2017; Dee et al. 2019). While most species are only targeted in ornamental or food fisheries, a number of species, such as goldring bristletooth and convict surgeonfish, are targeted both in commercial marine ornamental fisheries as juveniles and in non-commercial fisheries as adults.

Despite their ecological and economic importance, the basic biology and life history of most surgeonfishes is poorly understood. Surgeonfishes have a number of characteristics in common: most species are capable of extended pelagic larval durations and settle onto the reef at relatively large sizes (20 – 80 mm total length, TL), biphasic growth patterns characterized by rapid growth in their first few years after settlement followed by extremely slow growth, achievement of sexual maturity at relatively young ages, and potentially long lifespans (30 + yrs; Choat and Axe 1996; Randall 2001; Tebbett et al. 2022). There can be considerable variability in life-history traits both between species and within a species across its range (Choat and Robertson 2002; Robertson et al. 2005a, 2005b). For example, larger-bodied acanthurids, i.e., species reaching maximum lengths > 300 mm, such as bluespine unicornfish, can reach sexual maturity in 2–3 yrs and its asymptotic length of 400 – 500 mm fork length (FL) within 4 yrs while exhibiting a lifespan of > 50 yrs in the Hawaiian Islands (Andrews et al. 2016). However, bluespine unicornfish from populations at lower latitudes, such as Guam or Pohnpei, grow more slowly and exhibit smaller maximum lengths (< 500 mm FL) as well as shorter lifespans (16 – 23 yrs; Taylor et al. 2014) than those in Hawai'i. Larger-bodied surgeonfishes in the genus *Acanthurus* follow a similar life-history strategy to that described for bluespine unicornfish, though their lifespans seem considerably shorter (≤ 30 yrs; Pardee et al. 2022). Smaller-bodied surgeonfishes, i.e., species reaching maximum length ≤ 300 mm, are not as well studied in Hawai'i. Of those that are, such as yellow tang (*Zebrasoma flavescens* Bennett), have a maximum lifespan of at least 41 years but approach their asymptotic length within their first 3 – 6 years (Claisse et al. 2009). Despite this comparatively slower growth than what has been described for larger-bodied acanthurids, yellow tang can reach sexual maturity at very small sizes, i.e., 65 mm total length (TL; Schemmel 2021).

Achilles tang (*Acanthurus achilles* Shaw) is a broadly distributed, small-bodied acanthurid found throughout the islands and atolls of Polynesia, Micronesia, and the tropical Eastern Pacific (Randall 2001, 2007). It is an herbivorous species that reaches a maximum reported size of 250 mm and is associated with high energy, shallow coastal environments including reefs and rocky shorelines (Randall 2001, 2007). Like many other acanthurids, the basic biology and life history of Achilles tang has not been extensively examined. In French Polynesia, the species seems to be one of the fastest growing *Acanthurus* spp. and capable of living at least 20–25 years (Morat et al. 2020). However, there is a great deal of uncertainty about the applicability of these findings to the species in other locations. In Hawai'i Achilles tang, known by its traditional name, pāku'iku'i, has become a priority for nearshore fisheries management since its numbers have recently declined around west Hawai'i Island (Hawaii Administrative Rules [HAR] 2022, §13–60.41), hereafter referred to as West Hawai'i. While the species can be found throughout the Hawaiian Archipelago, it only seems to be heavily targeted by commercial and nearshore non-commercial fisheries around West Hawai'i. Landings of Achilles tang in the commercial food fishery have historically been relatively minimal, with a mean annual catch (±SD) of 176±125 kg/yr (range: 0 – 460 kg/yr; DAR 2023). In contrast, it was a top-5 targeted species by the marine ornamental fishery until the fishery was closed on Hawai'i Island in 2018 and statewide in 2020. In 2017, its last full year of operation, commercial marine ornamental fishers reported landing 5,473 individuals, mostly juveniles, valued at $130,853 (Walsh et al. 2019a). At sites where aquarium collection was allowed, Achilles tang abundance was 57±10% less than that at sites where collection was prohibited (Tissot and Hallacher 2003). Achilles tang was traditionally targeted and consumed by native Hawaiians both prior to and after European contact (Titcomb 1972) and it remains a very popular species for recreational and subsistence fishers in some areas of the state, particularly West Hawai'i. While there are no data available on the non-commercial landings of Achilles tang across the state, non-commercial landings have been estimated at three times that of the aquarium trade in West Hawai'i and target adults (Walsh 2014).

The high level of fishing pressure on both the juveniles and adults of Achilles tang is thought to be one of the primary drivers of the observed decline in population densities. Monitoring of reef fish by the Hawai'i Division of Aquatic Resources (DAR) between 2008 and 2020 indicates sharp declines in Achilles tang biomass (eightfold), density (fourfold), and mean length (by approx. 3 cm) in shallow habitats (2 – 6 m) of West Hawai'i, where adults should be found (DAR, *unpub. data*). On deeper reefs (10 – 20 m) that are considered prime habitat for juveniles, DAR monitoring in West Hawai'i has observed only 62 individuals between 1999 – 2021 (DAR, *unpub. data*). In response to these population declines in West Hawai'i, DAR implemented a two-year closure of the fishery in December 2022 and began developing an adaptive management plan to implement regulations ensuring sustainable harvest upon the re-opening of the fishery (HAR §13–60.41). During the adaptive management planning process, the lack of life-history information on Achilles tang from Hawai'i, or anywhere else in their range, was repeatedly noted as an impediment to the decision-making process. Therefore, the objective of the present study was to characterize the age, growth, and reproductive biology of Achilles tang from around Hawai'i Island.

Methods

Sample collection

We acquired Achilles tang through three different collection efforts. A total of 66 individuals were captured and donated by commercial marine ornamental collectors using hand nets during 2018–2019, primarily from around the southeastern portion of Hawai'i Island (Fig. 1). Individuals provided by commercial marine ornamental collectors were fish that died in the collectors' holding facilities prior to shipment. Upon death, these fish were removed from the tanks, frozen, and stored at -20 °C until they could be processed. Individuals captured as part of the marine ornamental fishery were provided at irregular intervals and were unavailable after 2019 due to the closure of the fishery in Hawai'i. Recreational spearfishers allowed us to collect data and samples from their

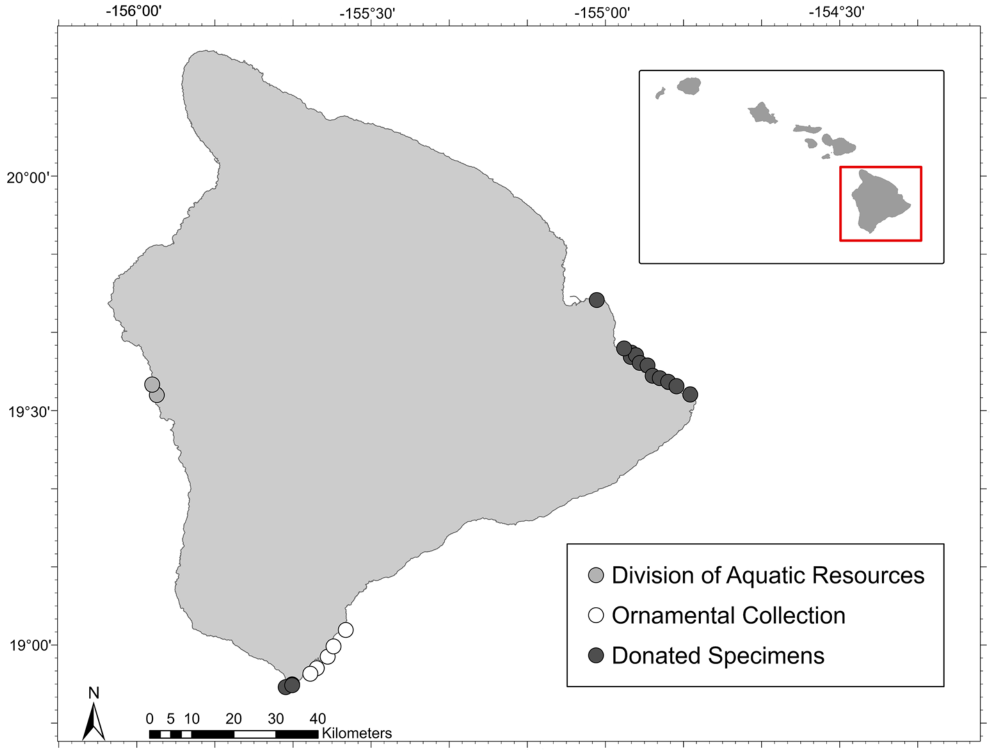

Fig. 1 Collection locations of Achilles tang (*Acanthurus achilles*) around Hawai'i Island during 2018 –2023

catch on a monthly basis during 2021–2022. From spearfishers, 240 Achilles tang were collected from various locations around Hawai'i Island (Fig. 1), primarily the windward (eastern) side. The recreational spearfishers placed the specimens on ice upon exiting the water and we processed the fish within 24 h of capture. We were also provided length and weight data, otoliths, and preserved gonadal tissue samples from Achilles tang ($n=58$) captured by DAR biologists using three-prong spears primarily from West Hawai'i Island (Fig. 1) during quarterly sampling conducted in 2022–2023. Captured Achilles tang were put on ice upon exiting the water and processed within 24 h of capture.

Achilles tang were measured to the nearest mm FL and standard length (SL) then patted dry and weighed to the nearest 5 g. Gonads were removed intact from the body cavity and weighed to the nearest 0.0001 g. A tissue sample of 7.29 ± 4.10 g (mean ± SD) was excised from the middle portion of one of the gonads, placed in a labeled histology cassette, and fixed in a 10% buffered formalin-filtered seawater solution. Tissue samples were held in a 10% buffered formalin and filtered seawater solution until processed. We collected samples from the anterior, medial, and posterior sections of a sub-sample of males ($n=5$) and females ($n=5$) to verify that morphology remained consistent along the length of the gonad. Sagittae otoliths were removed from each fish, cleaned of tissue and rinsed with freshwater before being stored dry.

Otolith preparation and analysis

We prepared the sagittae for age estimation following the procedures described by Long and Grabowski (2017). Briefly, we haphazardly selected the right or left sagitta from each individual and embedded it in epoxy. We cut a 0.5-mm transverse section, inclusive of the nucleus, from each sagitta using a IsoMet low speed precision cutter (Buehler, Lake Bluff, Illinois) fitted with diamond-wafering blades. We mounted the sections to glass slides using Crystal Bond thermoplastic mounting adhesive (Aremco, Valley Cottage, New York) and wet-polished them with increasingly fine grit sandpaper to expose the nucleus (Fig. 2). We then flipped the section over and similarly polished the remaining side as needed. Age was estimated by two independent readers with a third reader resolving any discrepancies and identified annuli using the criteria described by Choat and Axe (1996) and Morat et al. (2020). Individuals for which we were unable to reach a consensus age estimate by two readers were discarded from analysis ($n = 14$). Average percent error (APE) among readers was calculated following Beamish and Fournier (1981) as:

$$APE = \frac{\sum_{j=1}^{n} APE_j}{n} \text{ where } APE_j = 100 * \frac{\sum_{i=1}^{R} \frac{\left|x_{ij} - x_j\right|}{xj}}{R_j}$$

where APE_j is the average percent error for the jth fish, x_{ij} is the ith age estimate of the jth fish, x_j is the mean age estimate of the jth fish, and R_j is the number of age estimates made for the jth fish.

We used the length-at-age data to fit a Von Bertalanffy growth function (VBGF) for individuals whose age was ≥ 1 yr. The VBGF is parameterized as:

$$L_t = L_\infty \left[1 - e^{-k(t - t_0)}\right]$$

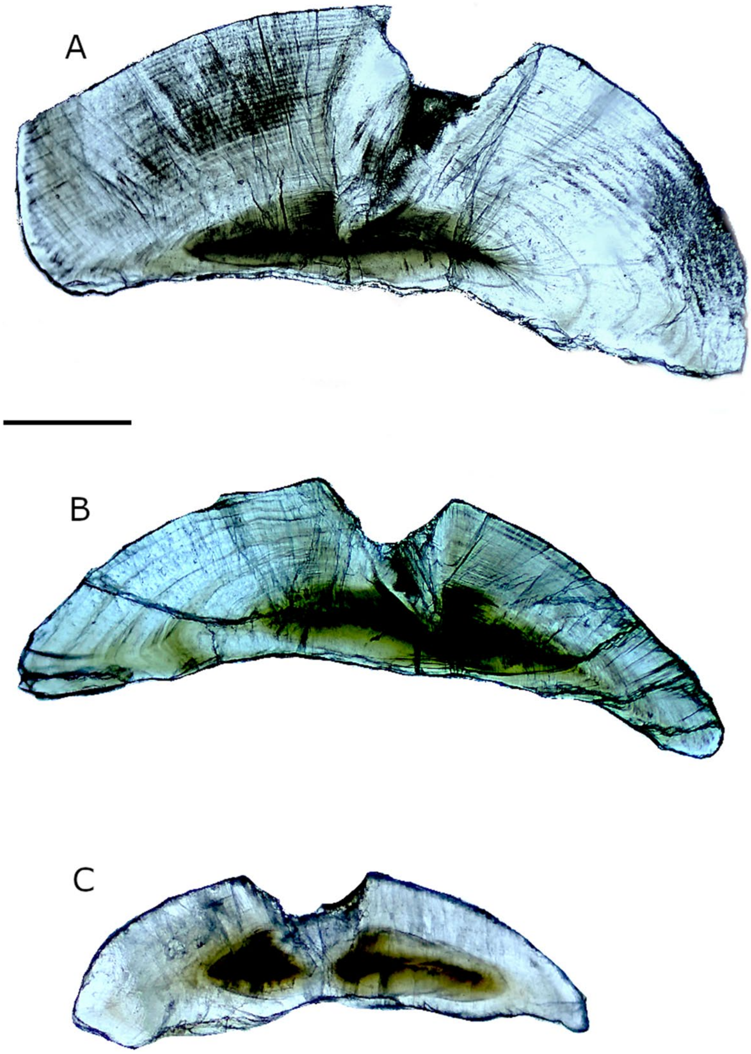

Fig. 2 Photograph of cross sections of sagittal otoliths from three Achilles tang (*Acanthurus achilles*) estimated to be age-26 (A; female, 213 mm FL), age-11 (B; female 212 mm FL), and age-0 (C; male, 123 mm FL) collected from around Hawai'i Island during 2021–2022. Scale bar represents 500 µm and all images are to the same scale

where L_t is the predicted length at time t, L_∞ is the asymptotic average length of the population, k is the growth coefficient, and t_0 is the theoretical time when length is zero (Von Bertalanffy 1938; Beverton and Holt 1957). We attempted to count daily increments on the otoliths of age-0 individuals to assign a more accurate age to these fish for the VBGF. While the daily increment counts from age-0 fish were between 120 –180 days, they were not repeatable between readers and readers reported difficulty discriminating daily increments towards the edge of the otoliths. Therefore, we assigned an age of 0.5 years and randomly assigned a sex to each age-0 individuals of unknown sex ($n = 21$) to fit the VBGF. We evaluated whether the VBGF fitted to both sexes pooled fit the data better than a VBGF where L_∞ and k were allowed to vary by sex using a sum of squares reduction test (Pinheiro and Bates 1995; Ogle et al. 2017). We used the same procedure to evaluate whether a VBGF fitted to all samples pooled fit the data better than a VBGF where L_∞ and k were allowed to vary by side of the Hawai'i Island, i.e., windward vs. leeward, where fish had been captured.

Gonad preparation and analysis

For histological assessment, the gonad tissue samples were embedded in paraffin, sliced into 5.0-µm sections, and counterstained with haematoxylin and eosin by the Histology Core at the John A. Burns School of Medicine, University of Hawai'i-Mānoa. We viewed gonad samples under a compound light microscope (OMAX, Kent, Washington) at 4x, 10x, and 40× magnification to determine sex and classify reproductive phase. We modified the classification used by Brown-Peterson et al. (2011) to include seven female phases and two male phases. For histological assessment, the gonad tissue samples were embedded in paraffin, sliced into 5.0-µm sections, and counterstained with haematoxylin and eosin. We viewed gonad samples under a compound light microscope (OMAX, Kent, Washington) at 4x, 10x, and 40× magnification to determine sex and classify reproductive phase. We identified immature females by the presence of primary growth oocytes and a relatively thin ovarian wall. We classified a female as physiologically mature having primary growth oocytes and cortical alveolar oocytes in the cytoplasm. Females were considered functionally mature if early vitellogenic oocytes were present. If both early stage vitellogenic oocytes and late stage vitellogenic oocytes were present, we classified the female as spawning capable. These spawning capable gonads may also contain late-stage post-ovulatory follicle complexes and evidence of atresia. However, we were able to distinguish actively spawning females from spawning capable females due to the presence of late-stage germinal vesicle migration, germinal vesicle breakdown, hydrated oocytes, ovulated eggs, and/or recent post-ovulatory follicles. Actively spawning ovaries may also contain atretic oocytes. We identified females as regressing when primary growth oocytes were present but were dominated by atretic oocytes even though cortical alveolar oocytes or vitellogenic oocytes may also have been observed. Females were classified as being in a regenerating phase when only primary growth oocytes were present and possessed large muscle bundles and blood vessels, thick ovarian walls, and potentially unabsorbed materials from past spawning events. We classified males as being either immature or mature based on the presence of spermatozoa.

We calculated the gonadosomatic index (GSI) for each individual using the following relationship:

$$GSI = \frac{W_{gonad}}{W_{total}} \times 100$$

where W_{gonad} is the weight of the gonad and W_{total} is the total weight of the individual (Crim and Glebe 1990). We evaluated whether GSI and the proportion of actively spawning or spawning capable females in our samples were related to annual or lunar periodicity using linear-circular regression (Batschelet 1981; Fisher 1993). All statistical analyses were performed using SAS 9.4 (SAS Institute, Carey, North Carolina) at $\alpha = 0.05$.

Results

A total of 363 Achilles tang were collected from around Hawai'i Island during 2018 to 2022. Female Achilles tang were heavier than their male counterparts ($F_{1,322} = 13.73$, $P < 0.001$; Table 1), but there was no difference in the mean length between the sexes ($F_{1,322} = 1.67$, $P = 0.20$). On average, fishes collected from the windward side of the island were

Table 1 Mean (± SE) and range of fork lengths (FL) and weights (W) and von Bertalanffy growth function parameter estimates (± SE) of Achilles tang (*Acanthurus achilles*) collected from around Hawai'i Island during 2018–2022

		n	Mean (SE) FL (mm)	Range, FL (mm)	Mean (SE) W(g)	Range, W (g)	L_∞ (mm FL; SE)	k (yr^{-1}; SE)	t_0 (yr; SE)
Sex	Male	152	183 (2)	96 – 225	196 (5)	22 – 315	191.5 (1.7)	1.17 (0.11)	-0.07 (0.07)
	Female	174	191 (2)	87 – 264	241 (7)	20 – 385	203.9 (1.3)	1.10 (0.10)	-0.07 (0.07)
	Undetermined	37	108 (4)	69 – 189	43 (8)	7 – 236	-	-	-
Site	Windward	305	181 (2)	69 – 264	205 (5)	7 – 385	199.3 (1.1)	1.03 (0.09)	-0.04 (0.07)
	Leeward	58	171 (4)	96 – 209	184 (15)	22 – 300	190.8 (2.8)	1.57 (0.18	-0.04 (0.07)

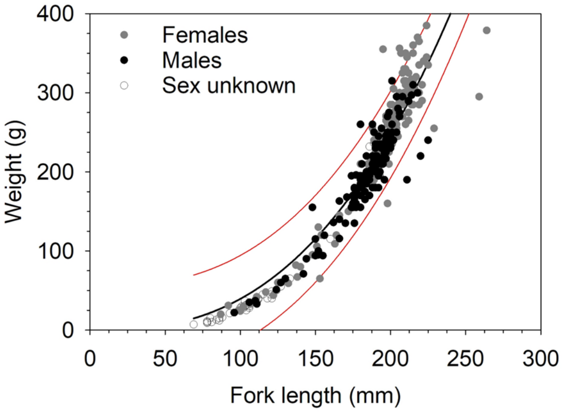

Fig. 3 Length–weight relationship of Achilles tang (*Acanthurus achilles*) captured from around Hawai'i Island during 2018–2022. The solid black line represents the relationship between weight (W) and fork length (FL), $W = 0.00002 \times FL^{2.647}$, and the redlines indicate the 95% confidence interval

both larger and heavier than those collected from the leeward side ($F_{1,322} \geq 5.17$, $P \leq 0.02$; Table 1). While the sex ratio of our sample was 1.00:1.14 male-to-female, this was not a meaningful departure from a 1:1 ratio ($\chi^2 = 1.48$, df = 1, $P = 0.22$). Further, there were an additional 37 individuals, mostly those donated by commercial marine ornamental collectors as frozen specimens, for which sex could not be determined. Due to this disparity in size and their irregular availability, the individuals provided by the ornamental collectors were only used for assessing the growth curve, and not included in any spatial comparisons or used to assess sexual maturation. Achilles tang collected around Hawai'i Island exhibited a length–weight relationship with parameter estimates (± SE) of $a = 0.00002 \pm 0.00001$ and $b = 2.647 \pm 0.068$ ($R^2 = 0.91$; Fig. 3).

The majority of Achilles tang sampled around Hawai'i Island were between 180 – 210 mm FL (Fig. 3). We were able to successfully estimate age 306 of 363 of the sampled fish. Achilles tang ranged in age from 0 – 39 years; however, half of the sampled fish were ≥ age-7 (Fig. 4). Our APE among readers was 1.60%.

Achilles tang grow quickly during their first year, reaching 138 ± 11 mm FL (mean ± SE) or approximately 62 – 78% of the asymptotic average length of the population, and then exhibit relatively slow growth for the remainder of their lives (Fig. 5). Male and female Achilles tang exhibit different growth patterns ($F_{5,294} = 22.21$, $P < 0.001$; Table 1; Fig. 5) resulting in males tending to be smaller than females of the same age starting at age-2. The sample size of individuals captured from West Hawai'i was insufficient to evaluate the interactive effect of sex and capture location on growth; however, the VBGF for both sexes pooled suggests Achilles tang off windward Hawai'i Island may grow faster than their counterparts from West Hawai'i ($F_{5,294} = 14.58$, $P < 0.001$; Table 1).

Gonads were successfully harvested from 132 males and 169 females, which were examined histologically to determine sex and reproductive phase. Reproductive state classifications were in agreement across the anterior, medial, and posterior section for each of the male ($n = 5$) and female ($n = 4$) gonads that were subsampled. There was no evidence of sequential hermaphroditism observed during the histological examinations and this gonochoristic reproductive pattern was further supported by males and females having similar length and age distributions (Fig. 3).

The majority of females (89.9%) were classified as being spawning capable and actively spawning.

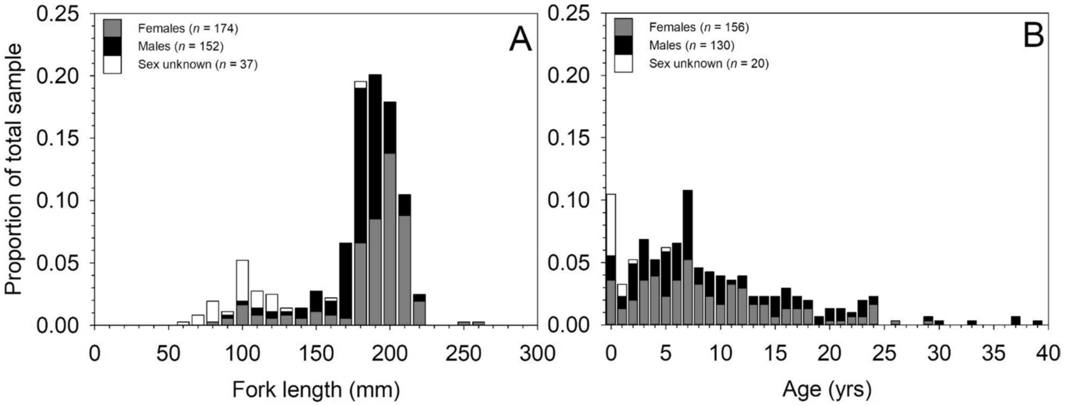

Fig. 4 Length-frequency (**A**) and age-frequency (**B**) distributions by sex of Achilles tang (*Acanthurus achilles*) sampled from around Hawai'i Island during 2018–2022. Age was successfully estimated for a smaller number of individuals ($n = 306$) than for which a fork length (FL) was recorded ($n = 363$). Individuals are grouped into 10-mm FL bins

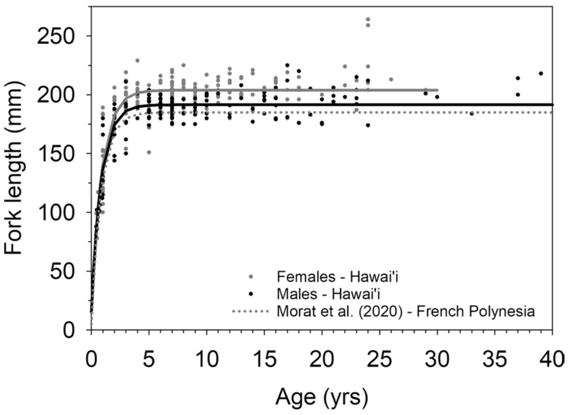

Fig. 5 Length at age for male ($n = 130$) and female ($n = 156$) Achilles tang (*Acanthurus achilles*) sampled from around Hawai'i Island during 2018–2022. Von Bertalanffy growth functions for each sex and from a previous study of Achilles Tang ($n = 12$) growth in French Polynesia (Morat et al. 2020) are shown

Females were classified as spawning capable ($n = 53$; Fig. 6A), actively spawning ($n = 99$; Fig. 6B/C), regressing ($n = 16$; Fig. 5D), or regenerating ($n = 1$; Fig. 6E). No females in the immature or developing phases were observed. All males possessed testes containing spermatozoa and were therefore classified as reproductively mature and considered spawning capable (Fig. 7). Age and length at sexual maturity could not be calculated in terms of an A_{50} or L_{50} value for males or females as gonadal samples from immature individuals were not collected in this study due to samples from ornamental collectors having been previously frozen. However, our data indicate that Achilles tang can reach sexual maturity within their first year and at < 130 mm FL.

While spawning capable and actively spawning individuals were captured in every collection event during 2021 – 2022, there was no evidence that the proportion of spawning capable and actively spawning individuals in a collection event was related to annual or lunar periodicity ($F_{2,32} \leq 1.14$, $P \geq 0.33$; Fig. 8). The mean (± SE) proportion of individuals in a sample classified as actively spawning or spawning capable was 0.76 ± 0.06, and there was no collection event where actively spawning and spawning capable individuals represented < 0.64 of the individuals collected during that event (Fig. 8).

Similarly, the mean GSI of male and female Achilles tang did not exhibit any annual or lunar periodicity ($F_{2,261} \leq 0.58$, $P \geq 0.53$; Fig. 9). The overall mean (± SE) GSI for females was 2.54 ± 0.11 with collection event means (± SE) that ranged from 1.62 ± 0.62 on 14 June 2022 to 3.75 ± 0.10 on 29 April 2022 (Fig. 9). The collection event mean (± SE) GSI for males ranged from 0.09 ± 0.03 on 18 August 2022 to 0.73 ± 0.17 on 19 October 2022 and the overall mean GSI for males was 0.38 ± 0.03.

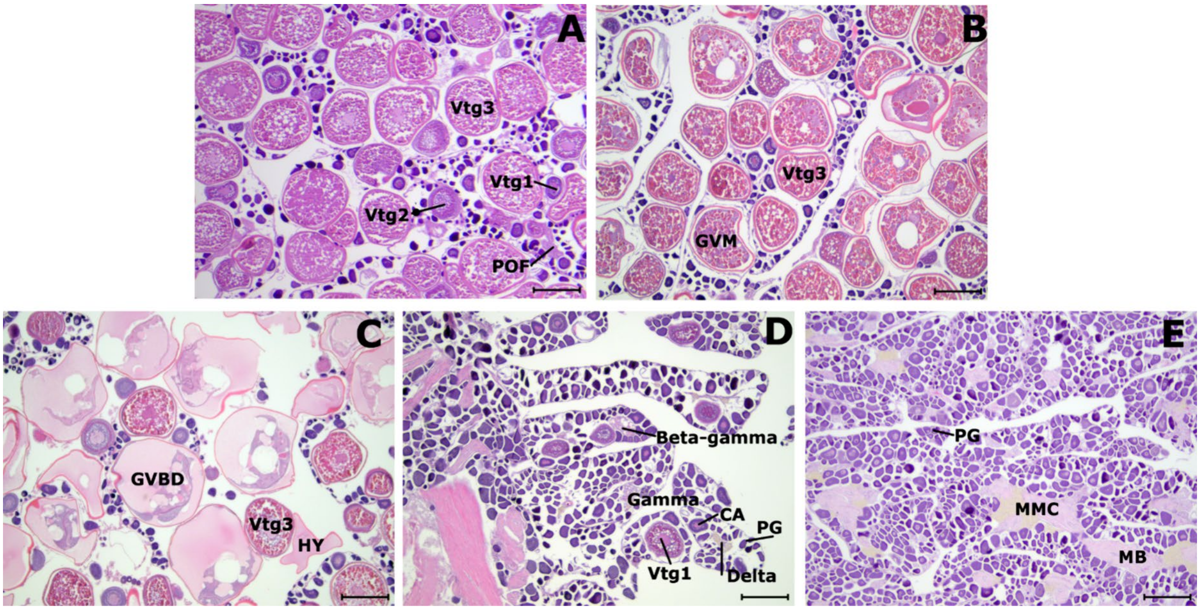

Fig. 6 Reproductive phases of female Achilles tang (*Acanthurus achilles*) individuals sampled from around Hawai'i Island during 2018–2022. (**A**) Mature spawning capable female with early vitellogenic (Vtg1, Vtg2) and late stage vitellogenic oocytes (Vtg3), and late-stage post ovulatory follicles (POF). (**B**) Mature actively spawning female early in phase with late-stage vitellogenic (Vtg3) and germ vesicle migrating (GVM) oocytes. (**C**) Mature late stage actively spawning female with germ vesicle breakdown (GVBD) and hydrated (HY) oocytes. (**D**) Inactive regressing female with primary growth (PG) and early vitellogenic (Vtg1) oocytes, and atretic oocytes. (**E**) Inactive regenerating female with only primary growth oocytes (PG), melanomacrophage centers (MMC) present and prominent muscle bundles (MB). Scale bars = 250 µm for all photographs

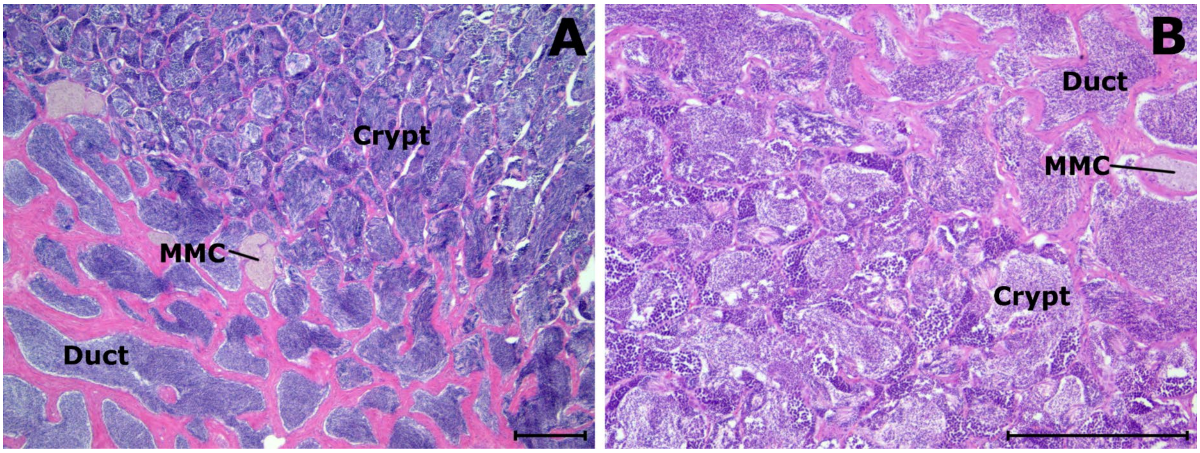

Fig. 7 Representative images of the testes of spawning capable male Achilles tang (*Acanthurus achilles*) sampled from around Hawai'i Island during 2018–2022. (**A**) Mature male with melanomacrophage centers (MMC) present and spermatozoa in ducts and crypts (scale bar = 250 µm). (**B**) Close up of spawning capable male with spermatozoa in the ducts and crypts and MMC (scale bar = 250 µm)

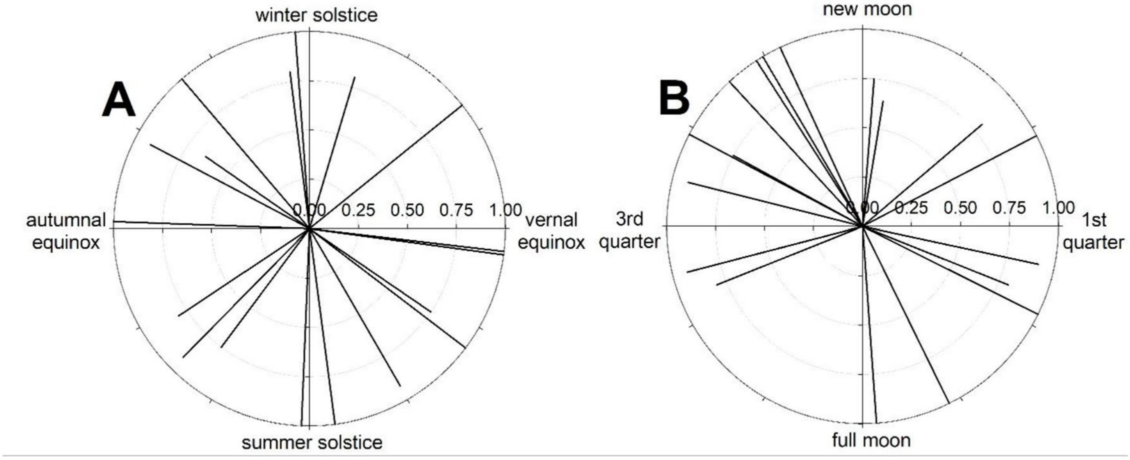

Fig. 8 Annual (**A**) and lunar (**B**) periodicity in the proportion of Achilles tang (*Acanthurus achilles*) classified as "actively spawning" or "spawning capable" from samples collected from around Hawai'i Island during 2021–2022. Classification based on histological examination of gonadal tissue and following Brown-Peterson et al. (2011)

Discussion

Acanthurids have been widely reported to exhibit high growth rates, particularly in their first year (Choat and Axe 1996; Choat and Robertson 2002). Our study shows that young-of-year (YOY) Achilles tang in Hawai'i exhibit one of the highest growth rates reported for acanthurids. Achilles tang growth rates reported in this study, exceed that reported for sympatric congeners that are often found in similar habitats, such as convict surgeonfish (Randall 2001; Morat et al. 2020; Taylor et al. 2024), brown surgeonfish (*Acanthurus nigrofuscus* Forsskål; Hart and Russ 1996; Fidler et al. 2018), and lined surgeonfish (*Acanthurus lineatus* Linneaus; Craig and Axe 1997). Young-of-year Achilles tang exhibit growth rates comparable to that observed in YOY ocean surgeonfish (*Acanthurus bahianus* Castelnau), which has the highest growth rates reported for any *Acanthurus* spp., throughout their range in the Caribbean, Gulf of Mexico, and western Atlantic Ocean (*k:* 1.061 – 1.584; Choat and Robertson 2002; Robertson et al. 2005a). The ecological and biological mechanisms underlying the rapid growth of Achilles tang remain unknown and an avenue for future research.

It is important to note, that while our growth results are consistent with those previously reported for Achilles tang (Morat et al. 2020), annual increment formation in this species has not been validated. Annual increment formation has been validated for other species of *Acanthurus* (Choat and Axe 1996; Robertson et al. 2005a, b), this process has not been performed for any member of the genus around Hawai'i. Age validation of tropical reef fishes presents a daunting challenge relative to temperate species and is therefore sorely lacking in the literature (Choat and Robertson 2002; Choat et al. 2009); however, Choat et al. (2009) also raise a valid point that validating the assumption of yearly formation of annuli should not delay the dissemination of age-based data to the resource managers in need of it.

Achilles tang is a widely distributed species that exhibits different growth rates across its range, also similar to ocean surgeonfish (Choat and Robertson 2002; Robertson et al. 2005a). Individuals from around Hawai'i Island grow faster and reach a larger maximum size, on average, than counterparts from French Polynesia (Morat et al. 2020). This pattern of faster growth and larger sizes at the northern and southern extents of the range has been described for ocean surgeonfish (Robertson et al. 2005a) and other reef fishes (Floeter et al 2005). These studies show trends in population differences throughout acanthurid ranges and demonstrate a negative relationship to latitude and a positive relationship to sea surface temperature. These relationships not only result in

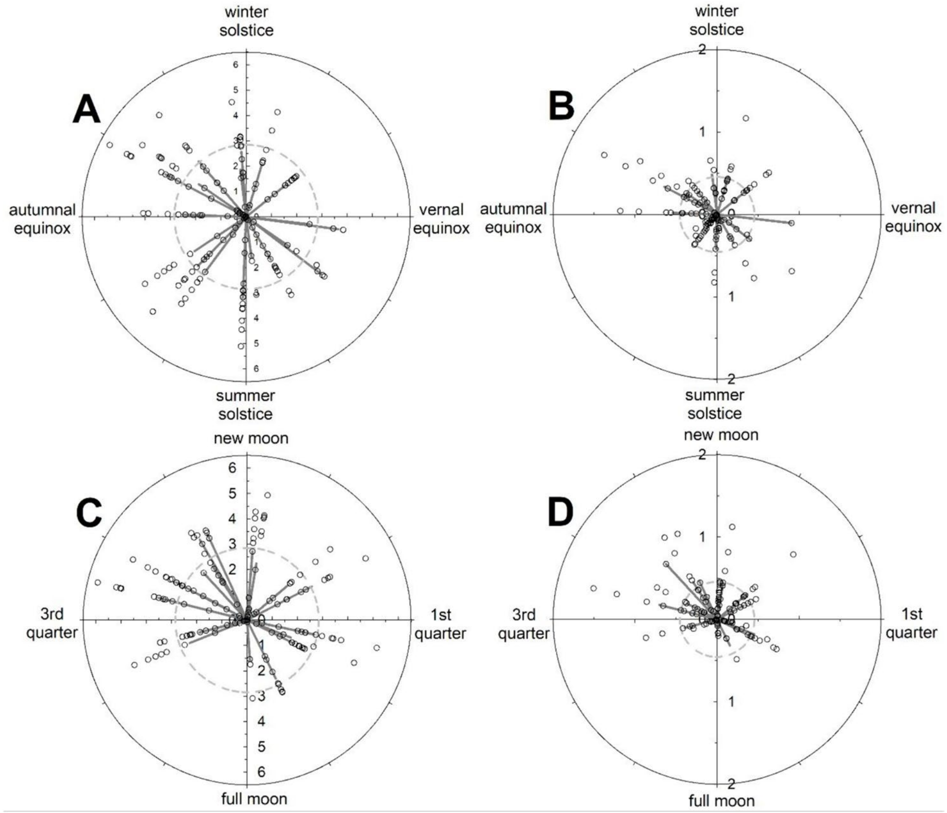

Fig. 9 Evaluation of annual (**A**, **B**) and lunar (**C**, **D**) cycles in gonadosomatic indices (GSI) of female (**A**, **C**) and male (**B**, **D**) Achilles tang (*Acanthurus achilles*) collected from around Hawai'i Island during 2021–2022. The GSI of individual fish are plotted as circles in each panel. Mean GSI of all the males or females during a sampling event are represented by solid radii extending from the origin while the dashed line represents the overall mean GSI of all males or females classified as "actively spawning" based on histological examination of gonadal tissue and following Brown-Peterson et al. (2011)

size differences but also potentially influence herbivore species richness and relative abundance. In addition to differences in growth rates at broad spatial scales, differences have been detected at considerably finer spatial scales in some species. For example, ocean surgeonfish (Risk 1997) and goldring bristletooth (*Ctenochaetus strigosus*; Winston et al 2017) can exhibit different growth rates dependent on local environmental conditions, such as substrate type or depth. Although our study suggests that Achilles tang populations may exhibit different growth rates around Hawai'i Island, applying this finding to Achilles tang management in Hawai'i without further investigation is not recommended. The present study was not designed to directly evaluate spatially-explicit differences in growth rates and the sample sizes from West Hawai'i are not sufficient to characterize potential differences with a high degree of confidence.

The reproductive development and histology of Achilles tang is consistent with what has been described for other acanthurids. The lack of immature individuals encountered in this study combined with the observed rapid growth suggest that Achilles tang are capable of reaching sexual maturity at young ages, e.g., age 1, and small sizes, e.g., ≤ 130 mm FL. This is rapid development comparable to that described in other *Acanthurus* spp., such as ringtail surgeonfish (*A. blochii* Valenciennes), eyestripe surgeonfish (*A. dussumieri* Valenciennes), orangeband surgeonfish (*A. olivaceus* Forster), and yellowfin surgeonfish (*A. xanthopterus* Valenciennes; Pardee et al. 2022), and other large-bodied acanthurids, such as *Naso* spp. (Taylor et al. 2014; Pardee et al 2020). These larger acanthurids generally do not reach sexual maturity before 18 – 24 months or reaching lengths of 166 – 292 mm FL. Instead, Achilles tang development seems more similar to that of smaller *Acanthurus* spp. and other smaller-bodied acanthurids, such as *Ctenochaetus* spp. and *Zebrasoma* spp. which tend to be capable of reaching sexual maturity at young ages and small sizes. For example, sexually mature YOY yellow tang (62.7 – 70.3-mm TL; Schemmel 2021), goldring bristletooth (< 65 mm; E. Schemmel, *unpub. data*) and convict surgeonfish (97 – 101 mm SL; Randall 2001) have been observed in Hawai'i.

The absence of any seasonal or lunar periodicity in the mean GSI or the proportion of individuals classified as spawning capable or actively spawning among the Achilles tang collected around Hawai'i Island is an unusual finding. Acanthurid reproduction has generally been described as occurring within a prolonged, i.e., February through June, but defined, spawning season (Walsh 1987; Lobel 1989). Further, most studies also note some degree of lunar or semi-lunar periodicity associated with spawning activity predominantly around the full moon (Bushnell et al 2010). In contrast, Achilles tang around Hawai'i Island seem to be spawning throughout the year with no distinct period when a significant proportion of the population exhibits resting or regenerating gonads. Furthermore, gonad condition does not seem to be associated with moon phase. There is not enough known regarding the ecology and life history of Achilles tang to understand why this species differs from congeners in spawning periodicity. Achilles tang has been reported to be significantly larger at settlement than other acanthurids (60 – 80 mm vs 20 – 40 mm; Randall 2001), suggesting a longer pelagic larval duration than is typical of most species. We speculate that this longer pelagic larval phase and larger size at settlement may decouple successful recruitment from the cyclical environmental conditions that seem to be important drivers of recruitment in other species, such as moon phase during periods of larval settlement (Fisher 2005; Kendall et al 2013).

Achilles tang seems to exhibit an opportunistic life history compared to other acanthurids with their fast growth, apparent ability to reach sexual maturity at small sizes/young ages, and year-round reproduction making them potentially well-adapted for dispersal and colonization. Therefore, it is a fair question as to why Achilles tang populations in West Hawai'i are in decline while the population densities of other, arguably more heavily targeted, acanthurids, such as convict surgeonfish and goldring bristletooth, have remained relatively stable or even increased (Walsh et al. 2019a). Achilles tang and goldring bristletooth were among the few species of acanthurids that received significant fishing pressure across their life history with small juveniles heavily targeted in the marine ornamental fishery and the adults targeted in the non-commercial fishery (Walsh et al. 2019b). However, the marine ornamental fishery has been closed in West Hawai'i since 2018 and Achilles tang population densities have continued to decline.

The traditional management tools that could be used to regulate the harvest of adults in the non-commercial fishery, such as length limits and seasonal closures, may have limited effectiveness to Achilles tang due to their growth and reproductive patterns. For example, the relatively small difference in size between older and younger fish means that a maximum length limit may not offer much benefit protecting older and presumably more fecund females. Further, the lack of a seasonality in spawning means there is no obvious period for a seasonal closure to be effective in protecting spawning individuals. While our study highlights the basic biology of Achilles tang, it shows that the species may pose unique challenges to fisheries managers looking to ensure sustainable harvest. In addition to validating the life history parameters estimated here, a focus on the recruitment processes and early life history requirements of the species may aid in identifying potential management actions that offer a greater chance of success than size limits and seasonal closures. The recovery of this species in West Hawai 'i will likely require an iterative approach that combines research, monitoring, cooperation with affected fishing communities, and the development of adaptive resource management tools, which can be robust in the face of complex and uncertain fishery outcomes.

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Data Availability At the time of publication, data cited in text were not publicly available from the Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources (DAR), all other data are available in supplementary materials, Table S1.

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