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Life history of the endemic Hawaiian hogfish *Bodianus albotaeniatus*: age, growth, and reproduction

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Abstract

Growth rate, longevity, maturity, and spawning seasonality were estimated for the endemic Hawaiian hogfish *Bodianus albotaeniatus*. The sex-specific von Bertalanffy growth parameters are $L_\infty = 339$ mm fork length (L_F) and $K = 0.66$ year^{-1} for females; $L_\infty = 417$ mm L_F and $K = 0.33$ year^{-1} for males. The maximum age is 22 years. Histological gonad analysis and the absence of small and young males indicate a monandric protogynous hermaphrodite. Size and age at maturity for combined sexes are $L_{50} = 238$ mm L_F and $A_{50} = 1.6$ years.

Key Words

Hermaphrodite, Histology, Labridae, Maturity, Otoliths, Protogyny

The Hawaiian hogfish/ a'awa / table boss / *Bodianus albotaeniatus* (Valenciennes, 1839) is part of the Labridae family, which is one of the most diverse families of fishes found in Hawaii with a total of 46 species (Mundy, 2005). *Bodianus albotaeniatus* was originally recognized as a subspecies of *B. bilunulatus* (Gomon & Randall, 1978) but was later reclassified as a distinct species endemic to the Hawaiian Islands and Johnston Atoll (Gomon, 2006). These fish are common on rock and coral areas to a depth of at least 90 m and feed mainly on small fish, sea urchins, mollusks, and crustaceans (Kosaki et al., 2017). Like other wrasses, *B. albotaeniatus* is sexually dimorphic with males appearing dark reddish to purplish brown in color and females white with brown lines becoming yellow posteriorly, a yellow caudal fin, black spot below the rear of dorsal fin, and white line under the eye; juveniles are yellow dorsally, black posteriorly, and have a white caudal fin (M. Gomon, 2006; M. F. Gomon & Randall, 1978).

Of the wide variety of labrids present in Hawaii, *B. albotaeniatus* is one of the few routinely harvested by both spear and hook and line fishermen for commercial, subsistence, and recreational harvest. The annual mean commercial catch in the main Hawaiian Islands (MHI) from 2011-2020 was 1,376 kg (SD = 507 kg) with a peak in 2012 of 2,162 kg (WPacFIN, 2022). Total catch is likely significantly higher as recreational and subsistence catch data are largely unknown due to no reporting requirements (McCoy et al., 2018). Before the closure of the aquarium fishery in 2017, juvenile specimens of *B. albotaeniatus* were also targeted with nearly 13,000 individuals collected statewide from 1976-2003 (Walsh et al. 2004).

Endemic species such as *B. albotaeniatus* are important contributors to global biodiversity. However, their restricted geographic range makes them more vulnerable to extinction (Roberts et al., 2002). Hermaphroditic fishes may also respond differently to fishing mortality based on size differences between the sexes (Heppell et al., 2006). This study aims to describe the reproductive biology, growth, and longevity of *B. albotaeniatus*, which can be used to help managers and fishery scientists to better manage and protect this endemic stock within Hawaii.

Three fish markets on Oahu were initially sampled from July 2018 – July 2019 to collect length/weight data for local reef species (including each *B. albotaeniatus* specimen present) as part of the Hawaii Biosampling Program (Pardee & Wiley, 2020). All *B. albotaeniatus* specimens observed from these same markets and opportunistically from fishers were then collected for further life history analyses from February 2019 - December 2020. Each specimen was measured to the nearest millimeter fork length (L_F), weighed to the nearest gram, and sexed (male, female, or transition) based on external appearance (color phase). Gonads were extracted, sexed macroscopically, weighed to the nearest 0.001 g, sectioned from the center of one gonad lobe, and preserved in 10% buffered formalin. Sagittal otolith pairs were removed, cleaned with ethanol, and stored dry.

The preserved gonadal cross sections were imbedded in paraffin wax, cut transversally into 6 μm sections, stained with hematoxylin and eosin, and mounted onto microscope slides by the John Burns School of Medicine Histopathology Core Facility at University of Hawaii Manoa. Each prepared slide was then assessed using a compound microscope with transmitted light. Sex and maturity were determined for each sample. Mature female samples were further classified as Developing, Spawning Capable, Actively Spawning, Regressing, or Regenerating based on the standardized terminology of Brown-Peterson et al. (2011).

Reproductive investment with size was also assessed for mature females using the gonadosomatic index ($I_G = \frac{gonad\ weight}{body\ weight}\ x\ 100$). Spawning season was assessed by plotting I_G and the frequency of female reproductive stages by month over the study period.

Size at maturity (L_{50}) and age at maturity (A_{50}) were calculated for combined sexes. Additionally, the size at transition ($L_{\Delta 50}$) and age at transition ($A_{\Delta 50}$) were calculated. A logistic regression analysis was used by fitting the length/age as an explanatory variable and the stage of maturity (0 = immature, 1 = mature) as the binomial response variable. Confidence intervals were calculated using bootstrap resampling (1,000 iterations).

One otolith from each otolith pair was randomly selected for aging from each specimen, weighed to the nearest 0.0001 g, and ground down to a thin (~200 μm) transverse section through the core using a 600-grit diamond lapping wheel based on the methods detailed by Taylor et al. (2017). A stereo microscope was then used to examine the section with adjustable transmitted light. Alternating opaque and translucent bands (presumptive annuli) along a consistent axis out from the core of the otolith section were observed for all size classes and counted to estimate the age of each fish. The annual periodicity of otolith bands has been previously demonstrated in hogfish and other wrasses (Choat et al., 2006; Gillanders, 1995; McBride & Richardson, 2007; Morton et al., 2008). Counts of annuli were conducted on at least two separate instances by at least two readers. If age estimates differed between counts, a third count was conducted to determine the final age. If readers still did not agree, the second otolith was ground down and the aging process repeated. The precision of age estimates between reads was calculated using the index of average percentage error (IAPE) (Campana, 2001). Otolith weight was compared to the corresponding age to determine the allometric relationship.

Growth patterns for both sex-specific and combined sexes were modelled using the von Bertalanffy growth function (VBGF) $L_t = L_\infty[1 - e^{-K(t-t_0)}]$ where L_t is the L_F (mm) at age t (years), L_∞ is the mean asymptotic L_F, K is the growth coefficient depicting the curvature to L_∞, and t_0 is the theoretical age at which the L_F is equal to zero. The model was constrained to 10 mm at age 0 based on the settlement size of the Mexican hogfish of the same genus *Bodianus diplotaenia* (Wellington & Robertson, 2001).

A total of 242 *B. albotaeniatus* specimens were measured from Oahu markets (includes data from Pardee & Wiley, 2020). Based on the external coloration and appearance of specimens, 69% were female, 24% were male, and 7% were transitioning (M:F = 0.35). The mean market L_F was 317 mm (SD = 61 mm) for all combined specimens, 288 mm (SD = 46 mm) for females, 389 mm (SD = 34 mm) for males, and 353 mm (SD = 29 mm) for transitional. The length-weight relationship for combined sexes is as follows: $W = 8.90\ x\ 10^{-6}\ (L_F)^{3.154}\ (r^2 = 0.98)$. Each specimen used in the life history analyses was either purchased from the fish vendors (n = 138) or donated directly by fishers (n = 17) on Oahu.

A total of 142 *B. albotaeniatus* samples ranging in size from 180 mm to 461 mm L_F were successfully aged with well-defined alternating opaque and translucent zones under reflected light (Figure 1a). Age estimates between reads were precise with an IAPE value of 1.45%. Weight of the sagittal otolith is a strong indicator of age and was best explained by a standard linear formula: $Age = 354.0(otolith\ weight) - 1.637\ (r^2 = .912;\ p < \ 0.0001)$.

Sex-specific von Bertalanffy growth parameters were L_∞ = 339 mm and K = 0.66 year^{-1} for females and L_∞ = 417 mm and K = 0.33 year^{-1} for males (Figure 1b, Table 1). The oldest fish examined was a male estimated to be 22 years old.

A total of 148 *B. albotaeniatus* gonad samples were examined histologically resulting in 96 females, 38 males, and 14 transitional (M:F = 0.40). Four female gonads were too far degraded to stage clearly after being stained and mounted to the microscope slide and were not utilized in the study. There was no evidence of primary males within the population as no individuals in initial phase coloring had male gonadal structures when analyzed histologically. No traces of testicular tissue were present within female gonads. Transitional gonads all displayed remnant previtellogenic oocytes along with well-defined crypts of developing germ cells at various stages of spermatogenesis. Samples with terminal phase coloring were mainly found to have testes without previtellogenic oocytes, though five fish externally identified as male had transitioning gonads. Transitional fish were found throughout the year occurring in nine different months.

All 16 samples found to be immature were female. The smallest mature female was 211 mm L_F and contained hydrated oocytes. The $L_{50} = 238$ mm and $A_{50} = 1.6$ years (Figure 1c, Table 1). All fish sampled with a L_F greater than 293 mm were sexually mature. Transitioning samples ranged in L_F from 296 mm to 384 mm. The largest female was 396 mm while the smallest male was 322 mm L_F. The $L_{\Delta 50} = 368$ mm and $A_{\Delta 50} = 7.3$ years.

Spawning occurred from December through June (though no mature female samples were collected in May) with corresponding high I_G (Figure 1d). Seven of the active spawning females had irregular hydrated oocytes, which appear blotchy when compared to the uniform stain in the others. It is likely these samples were more degraded than the others because of how the fish were handled before sale in the markets. These gonad samples were still counted as hydrated oocyte stages in the analyses despite the possible degradation to the cells. No spawning was observed in females landed on Oahu from July through November, and the drop in I_G suggests spawning occurred previously.

This study provides the first growth, length and age at maturity, and longevity parameters for the endemic *B. albotaeniatus*. This fish has a moderately long life span of 22 years and a L_∞ and K comparable to the highly targeted hogfish *Lachnolaimus maximus* in the south Florida fishery (McBride & Richardson, 2007). Fishing mortality of *L. maximus* has had a major impact on this species' life history in this region reducing longevity by nearly half and L_∞ by more than half when compared to the eastern Gulf of Mexico (McBride & Richardson, 2007). Likewise, Oahu represents the highest fishing pressure and most densely populated Hawaiian Island (Williams et al., 2008). The L_{50} for another commonly targeted reef fish *Acanthurus triostegus sandvicensis* is lowest for Oahu followed by Kauai, Hawaii Island, and greatest for Maui (Schemmel & Friedlander, 2017).

Biomass density of *B. albotaeniatus* in the MHI is less than one fourth of that in the relatively unfished Northwestern Hawaiian Islands (NWHI); a significant difference in total length for this species was also observed between the MHI and the NWHI (Friedlander & DeMartini, 2002). $L_{\Delta 50}$ for *B. albotaeniatus* is higher at three NWHI, Pearl and Hermes = 386 mm total length (L_T), Kure = 405 mm L_T, and Midway = 396 mm L_T (DeMartini et al., 2005), than Oahu (368 mm L_F, present study). However, direct comparison of these two studies is difficult with different reported length metrics and the former study based on *in situ* diver observations; we found several specimens with terminal male coloration to have transitional gonads. Future life history studies comparing the same reef fish species between specific MHI and NWHI would help reveal how growth and maturity parameters are affected by varying degrees of fishing pressure and land development in Hawaii.

The adult sex ratio of *B. albotaeniatus* in Hawaii was found to be heavily skewed in favor of females supporting the first evidence of sex change (Sadovy & Shapiro, 1987; Shapiro, 1987; Warner, 1975). No females were found to be larger than 400 mm L_F while no males were found to be smaller than 320 mm L_F. This sex-separated size distribution where the modal size of females is less than the modal size of males is also characteristic of most populations of protogynous species (Gillanders, 1995; Jones, 1980; Nakazono & Kusen, 1991; Shapiro, 1987; Shapiro & Rasotto, 1993). Additionally, female ages ranged from 1-10 years old while male ages ranged from 5-22 years old. Such age distributions provide stronger evidence for protogyny as the possibility of differential growth is removed (Warner, 1975). The absence of small males and no males less than five years old further suggests *B. albotaeniatus* to be monandric. Finally, gonadal histology and the presence of remnant previtellogenic oocytes within transitioning and functioning testes provides the best evidence *B. albotaeniatus* is a protogynous hermaphrodite like other labrids (Cossington et al., 2010; Gillanders, 1995; Jones, 1980; Sadovy & Liu, 2008; Warner, 1975) and hogfish in particular (McBride & Johnson, 2007). The transition from female to male in hogfish is dictated by size of the individual and social dynamics (Collins & Mcbride, 2011; McBride & Johnson, 2007). Single males within different species of hogfish may defend permanent territories and mate with harems of females, defend temporary reproductive territories, or spawn together in groups (Hoffman, 1983, 1985).

Based on the monthly mean I_G and spawning females observed histologically, *B. albotaeniatus* has a distinct spawning season from December-June for Oahu. However, sample size was relatively low and only immature females were collected in May so spawning must be inferred based on the prevalence of spawning during the surrounding months of April and June. Additionally, only one mature female was sampled in December which was actively spawning.

Spawning generally occurs in Hawaiian fish during the relatively low temperatures of winter months, increases through early summer with warming water temperatures, and declines rapidly as maximum water temperature is reached in September-October (Walsh, 1987).

Resource monitors within a community-based fishery management area on the island of Molokai previously recorded the peak spawning season for *B. albotaeniatus* as May-August in 2000, though gonads were not analyzed histologically (Friedlander et al., 2002). On Maui, two females were sampled opportunistically in August during our study, and one was found to be actively spawning. These spawning observations do not align with our findings for Oahu. As spawning can occur throughout the year in other tropical labrid species (Warner & Robertson, 1978), it is possible we missed capturing these individuals. Spawning seasonality for *B. albotaeniatus* may also differ by island as geographic location often affects life history parameters within the same species (McBride & Richardson, 2007; Schemmel & Friedlander, 2017; Towne, 2018). Peak spawning times for *Acanthurus triostegus sandvicensis* varied temporally by month and year within Maunalua Bay, Oahu (Schemmel & Friedlander, 2017).

Spawning of *L. maximus* in the Caribbean has a more protracted spawning period in the Florida Keys (September-April; Davis, 1976) than in Puerto Rico (December-April; Colin, 1982) and southwestern Cuba (November-January; Claro et al., 1989). Patterns in recruitment and spawning in Hawaii are most closely tied to water temperature or photoperiod rather than food availability, ocean currents, or salinity (Walsh 1987). Research buoys on the windward side of Oahu (Kaneohe) show mean monthly sea surface temperatures are slightly lower from February-March and September-December than observed on the windward side of Maui (Pauwela), which may help explain differences in spawning times (PacIOOS, 2022). However, more samples from each MHI are still needed to compare spawning seasonality across islands with any confidence.

This study provides a comprehensive analysis of age, growth, and maturity for the commonly targeted *B. albotaeniatus*. Though life history parameters may differ slightly by region, the information provided in this study is a meaningful step for stock-assessment scientists and managers. The local demographic data can be used in an initial stock assessment for *B. albotaeniatus*, adding to the previous reef fish assessment in Hawaii (Nadon, 2017). These assessments will be crucial for the sustainable management of our coral reef ecosystems where such a diverse array of species are harvested and relied upon to feed local people.

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Figure Caption

Figure 1. (a) Photomicrograph of transverse otolith section of *Bodianus albotaeniatus* with 12 alternating translucent and opaque bands (annuli). Black circles indicate annuli. Scale bar equals 0.5 mm. (b) Sex-specific and combined von Bertalanffy growth curves for *Bodianus albotaeniatus.* Open circles with dotted line represent females, gray triangles represent transitioning, black squares with dashed line represent males, red line represents combined. Yellow arrows show L_{50} (238 mm) and A_{50} (4.6 years); blue arrows show $L_{\Delta 50}$ (368 mm) and $A_{\Delta 50}$ (7.3 years). (c) Plots for L_{50} (I), A_{50} (II), $L_{\Delta 50}$ (III), and $\mathrm{A}_{\Delta 50}$ (IV). Dashed lines indicate 95% CIs and red lines indicate respective values on the figure. (d) Mean gonadosomatic index (I_G) of mature females (n = 72) per month for Hawaiian *Bodianus albotaeniatus*. Numbers in parentheses represent sample size for each month. Error bars represent +/- 1 SE. Dashed line is the mean monthly Sea Surface Temperature for Kaneohe, Oahu 2018-2019 (PacIOOS 2022).

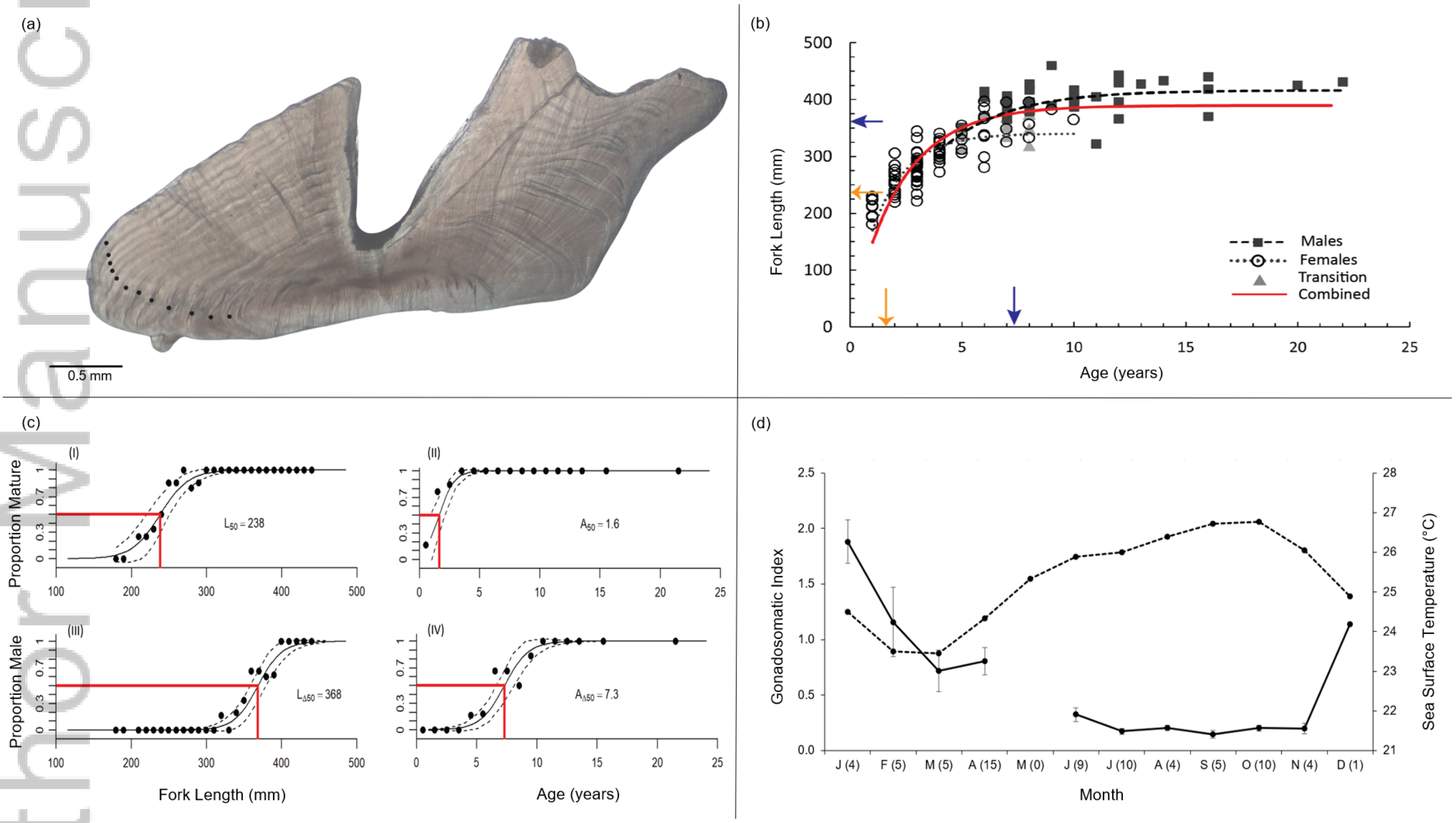

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Table 1. Summary of life history parameters for *Bodianus albotaeniatus* landed on Oahu. Associated 95% CIs are presented in parentheses where appropriate.

	A_{max}	L_{∞} (mm)	K	t_0 (years)	L_{50}	$L_{\Delta 50}$	A_{50}	$A_{\Delta 50}$
Female	10	340 (328-353)	0.46 (0.42-0.50)	-0.045	238 (234-251)	368 (365-380)	1.6 (1.4-2.1)	7.3 (7.0-8.1)
Male	22	417 (399-453)	0.66 (0.59-0.76)	-0.16				
Combined	22	389 (379-399)	0.33 (0.13-0.67)	-0.057				