Environ Biol Fish (2015) 98:2159–2171
DOI 10.1007/s10641-015-0427-z

Ecology and niche specialization of two bonefish species in Hawai‘i

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Received: 8 November 2014 / Accepted: 8 June 2015 / Published online: 30 June 2015

Abstract Bonefishes are a cryptic species complex that are a prized sportfish in many places around the world. In Hawai‘i they have a long history of use and today have important recreational, and cultural value. In the early 1980s, two distinct species of bonefishes were determined to inhabit Hawaiian waters (*Albula glossodonta* “round jaw”, and *A. virgata* “sharp jaw”). Little is known about the life histories of these two species, hindering population assessments and relevant fisheries management guidelines. In addition, no ecological studies have been conducted to examine interactions or separation between these species. This research assesses how differences in size, abundance, diet, growth, reproduction, and habitat preference of the two bonefish species in Hawai‘i can explain the coexistence and persistence of these two closely related species. Differences in size structure, growth rates, and spawning patterns for each species provides species-specific life history information that differentiates them ecologically and is useful for population assessments and in developing species-specific management strategies. We found that the wide-ranging species, *A. glossodonta* had a larger mean size, length at a given weight, and size at maturity than the endemic, *A. virgata*. We found differences in prey preferences between the two species that support our hypothesis that differences in jaw morphologies and habitat preferences translate to dissimilarities in diet. This study contributes to our knowledge about these species and provides an example of niche specialization in two closely related and cohabiting species.

Keywords Bonefishes · Life history · Niche specialization · Hawai‘i

Introduction

Bonefishes are highly prized recreationally in many parts of the world, contributing significantly to local economies (Ault 2007; Fedler 2013). In Hawai‘i, bonefishes, locally known as ‘ō‘io, are an important target of recreational fisheries and have cultural significance (Kahaulelio 2006). Bonefishes were an important food item for early Hawaiian civilization, being both wild-caught and cultured in fish ponds (Titcomb 1972). In modern Hawai‘i, bonefish continue to play an important cultural role through recreation and subsistence as a commonly targeted resource species by non-commercial fishers (Kamikawa et al. 2015). Despite the high recreational importance placed on bonefishes, they have limited economic value as a recreational species and only marginal commercial value in Hawai‘i. The commercial sale

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of bonefishes in Hawaiʻi is permitted, there are no recreational harvest limits, and the minimum legal harvest size is 31.4 cm (14 in), with no distinction between the two bonefish species found in Hawaiʻi, *Albula glossodonta* and *A. virgata* (DAR 2012). By comparison, the state of Florida estimates that>$460 million dollars per year is added to the state's economy through direct and indirect expenditures related to recreational catch-and-release bonefish fishing and commercial harvest is prohibited (Fedler 2013).

Bonefishes are cosmopolitan fishes with few distinguishing morphological differences across species (Colborn et al. 2001). Early researchers believed that the genus *Albula* consisted of only two species, *A. vulpes* and *A. nemoptera* (Whitehead 1986; Colborn et al. 2001; Bowen et al. 2007). Shaklee and Tamaru (1981) questioned the validity of this classification, and distinguished two bonefish species in Hawaiʻi, (*A. glossodonta* and *A. virgata*) which was subsequently confirmed by other researchers (Randall and Bauchot 1999; Colborn et al. 2001; Bowen et al. 2007; Hidaka et al. 2008).

Because research showed no evidence of gene flow between the two species, they were considered sympatric species capable of coexisting in the same habitat due to an inferred difference in their preferred prey items; however this theory was never tested (Colborn et al. 2001). Differences in morphological characteristics (e.g., mouth shapes and size, mean body lengths) and ecological characteristics (e.g., habitat use) have been suggested as indicators of resource partitioning, therefore allowing closely related species to coexist in the same geography while minimizing competition (Hutchinson and MacArthur 1959; Van Valen 1965; Schoener 1974; Ross 1986). However, simply comparing resource use of two species does not provide enough information to demonstrate niche partitioning resulting from selection pressures by evolutionary mechanisms (Walter 1991). Connell (1980) argued that to conclude whether the coexistence of two species is a result of competition alone, field experiments must be performed to test if another mechanism is involved. Therefore, we discuss niche specialization, rather than partitioning, by comparing the two species of bonefishes in Hawaiʻi.

A difference in the feeding apparatus of the Hawaiian bonefish species indicates they could preferentially be feeding on different prey items. Both species possess enlarged molariform teeth positioned as patches in both the upper and lower mouth, but the size of the individual teeth and shape of the patches are significantly different between the two species (Colborn et al. 2001). There is also a significant difference in the number of gill rakers on the lower limb of the first gill arch (Shaklee and Tamaru 1981). Therefore we hypothesize that differences in feeding apparatuses could translate to dissimilarities in prey preferences following evidence from a wide range of coral reef fish taxa (Wainwright 1988; Bond 1996; Wainwright et al. 2004).

Most of the research on bonefishes has been conducted in Florida and the Bahamas, where they are highly prized in the sport fishing industry (Colton and Alevizon 1983; Crabtree et al. 1996, 1997, 1998; Pfeiler et al. 2000; Humston et al. 2005; Adams et al. 2007; Danylchuk et al. 2011). Little is known about the life history of bonefishes in the Pacific despite their long history of use and continued cultural importance in many islands throughout the region today (Friedlander et al. 2007; Allen 2014). This study is the first to examine size, age, growth, diet, spawning, reproduction, recruitment and habitat use of two closely related species of bonefishes in Hawaiʻi and includes a discussion on how differences in the characteristics of their biology influence niche specialization and species persistence. Further, this study serves to provide important life history information for the management of these fisheries by providing species-specific information that can be used to develop more sustainable harvest strategies.

Methods

Species identification

Two species of bonefishes are found in Hawaiian waters, which can easily be distinguished by external morphological characteristics (Shaklee and Tamaru 1981). *A. glossodonta* derives its common name, round jaw, from its rounded lower jaw compared to *A. virgata*, the sharp jaw, that has an angular, sharp pointed lower jaw. The jaw measurement, the distance from the tip of the snout to the posterior end of the maxilla, of *A. glossodonta* is shorter relative to the length of the head compared to *A. virgata* (Fig. 1). The ratio of head length to the jaw measurement for *A. glossodonta* is 3.03–3.31 compared to 2.65–2.87 for *A. virgata* (Randall 2007). Other distinguishing characteristics include a yellow spot on the axil of the pectoral fins in *A. virgata* and 65–66 lateral-line scales in *A. virgata* compared to 72–75 in *A. glosssodonta* (Randall 2007).

Fig. 1 Comparison of two bonefish species that inhabit Hawaiian waters, ratio of head to jaw length is from Randall (2007), fork lengths are means (Table 1)

Species	Jaw Shape	Ratio head to jaw length	Fork Length	Habitat
Albula glossodonta Round jaw		3.03-3.31	49.8 cm	Flats
Albula virgata Sharp jaw		2.65-2.87	45.2 cm	Deeper channels & bays

Collections

Beginning in 2008, samples were collected as part of the ‘Ō‘io Tagging Project (http://www.hawaii.edu/oiotaggingproject/), on the island of Oahu, Hawai‘i (see Kamikawa et al. 2015). Adult fishes were obtained by hook-and-line, fly-fishing, or gill net, and were largely donated by recreational fisherman. Data on juvenile bonefishes were collected by beach seines through a long-term monitoring program of sandy beach fish assemblages (Friedlander et al. 2007).

Demographics

Size frequency histograms were created for adult specimens, defined as individuals>20 cm, all of which were obtained from hook-and-line fishing. Juvenile samples obtained by beach seine were not included in any of the demographic analyses but were used for assessing patterns of recruitment.

The relationship between length and weight was calculated for each species using linear least squares regression of log-log data to obtain best-fit parameters for the allometric equation:

$$W = aL^b \tag{1}$$

where W is total weight in grams, L is fork length (FL) in cm, b is the allometric growth parameter, and a is a scaling constant. Analysis of covariance (ANCOVA) of log-log data was used to compare the relationship between the two species.

Growth

Sagittal otoliths were extracted from a subset of the samples covering a wide range of sizes and were used for aging following methods described by Choat et al. (2003). Otoliths were cleaned in water, rinsed in 95 % EtOH, and once dry, were weighed and measured. The left sagitta was used for aging, and was mounted and sectioned on a microscopy slide in thermoplastic glue (CrystalBond) using a rotary grinder with 800–1200 grit sandpaper followed by polishing with 30–3 μm polishing film. Increments of sequential light and dark bands were counted with a transmitted light microscope at 10–100x magnification. Increments were assumed to be annuli, so age estimates are presumptive.

The von Bertalanffy growth function (VBGF) is traditionally used to describe growth in fishes (Ricker 1987). The generalized equation is as follows:

$$L(t) = L_\infty\left(1 - e^{(-K(t-t_0))}\right) \tag{2}$$

where $L(t)$ is length at age t, L_∞ is mean asymptotic length, K describes how fast the asymptote is reached, t is the age in years, and t_0 is the theoretical age at which length is 0. Growth curves were generated using size at age data obtained from the analysis of 56 saggital otoliths from *A. glossodonta* and 47 from *A. virgata*. A nonlinear least-squares method was used to determine parameters of best fit for the von Bertalanffy curve using the *nls* function in R 3.0.1 (R Core Development Team 2013). For comparison of growth curves between species, a likelihood ratio test was developed for each model and 95 % confidence intervals were constructed around maximum likelihood estimates of L_∞ and K (Kimura 1980).

Diet

Stomachs and intestines from *A. glossodonta* and *A. virgata* were removed and preserved in 10 % buffered formalin for diet analysis. Prey items were extracted, weighed, and identified to the lowest possible taxonomic resolution. When partially digested prey items were encountered, recognizable body parts such as eyestalk pairs or primary chelae pairs were counted as whole individuals. When the number of an item in a sample was undetermined, a single count was recorded for that item. Following identification, prey groups were dried by blotting on a paper towel and weighed to the nearest 0.01 g. Prey volume was measured via displacement in a graduated cylinder containing alcohol to 0.1 ml (Chipps and Garvey 2007).

Numerical abundance, percentage of total volume, and frequency of occurrence were calculated for each taxa or group of taxa in each sample (Chipps and Garvey 2007). To evaluate the relative contribution of each prey taxa to the overall diet of each species we calculated prey-specific abundance, where the proportion of the prey item in a given stomach was considered only when that prey item was present. Prey specific abundance was defined as:

$$P_i = \frac{\sum S_i}{\sum S_{ii}} \cdot 100 \tag{3}$$

where P_i is the prey-specific abundance (volume) of prey i, which is equal to the summed proportion of the total abundance of prey i in each stomach (S_i), and the total abundance of all prey in stomachs that contain prey i (S_{ii}) (Amundsen et al. 1996). Thus, prey-specific abundance is calculated as the proportion of the sum of each prey in any given stomach compared to the sum of that prey in all stomachs sampled.

Dietary overlap between the two species was assessed by an index of overlap defined as:

$$O_{jk} = \frac{\sum \left(p_{ij} \cdot p_{ik}\right)}{\left(\sum p_{ij}{}^2 \cdot \sum p_{ik}{}^2\right)^{\frac{1}{2}}} \tag{4}$$

where p_{ij} and p_{ik} are the proportions by volume of the stomach contents for p prey item, in i stomach for j and k species (Horn 1966). Index values range from 0 to 1, where values closer to zero indicate less overlap in prey items between the two species.

Spawning and recruitment

Gonad tissues were preserved in 10 % buffered formalin for a minimum of 3 days, dehydrated in graded ethanol series, and embedded in paraffin or glycol methacrylate (JB-4 Embedding Kit, Electron Microscopy Science). Embedded gonads were sectioned at 3–7 μm using a rotary microtome. Sections were fixed and stained with hematoxylin and eosin or toluidine blue.

Histological methods were used to determine gender, length at maturity (L_{50}), and reproductive state. Each gonad was classified based on standardized reproductive assessment (Wallace and Selman 1981; Brown-Peterson et al. 2011). Females that had vitellogenic, hydrated oocytes, atresic oocytes, or post-ovulatory follicles were considered mature. Females with vitellogenic, hydrated oocytes, or post-ovulatory follicles were considered to be within the spawning season. Males with spermatozoa, as assessed histologically, were considered mature.

Length at maturity was calculated from the proportion of reproductively mature individuals from both histological and macroscopic assessment. Length at sexual maturity was defined as the size at which 50 % of individuals were mature for a given length (Lowerre-Barbieri et al. 2009). We calculated maturity schedules by regressing length against the probability of mature individuals using the *glm* function in R with the binomial family and a logit link. Confidence intervals for L_{50} estimates were obtained with bootstrapped estimates of coefficients from the logistic models.

Monthly beach seining using a 24 × 1.8 m long seine net with a 1.3 cm mesh was used to assess juvenile recruitment at four sites along windward Oahu from 2008 to 2013. Each site consisted of replicate sampling

Table 1 Summary of collections of Hawaiian bonefishes used in this study

Species	No. samples	No. aged	No. stomachs analyzed	Minimum size	Maximum size	Mean adult size
Albula glossodonta	84	56	26	10.4	67.0	49.8 (8.2)
Albula virgata	96	47	63	10.0	66.5	45.2 (8.5)

Sizes are in cm with standard deviation of mean size in parentheses

stations where three hauls were performed at each station. All fishes were counted, measured, and identified to species and held in an aerated bucket. After each station was completed, all fishes were released alive back into the water. Data were summarized by month across years to determine seasonal recruitment patterns. To further investigate seasonal patterns of spawning we used lengths to back-calculate age from the von Bertalanffy growth function:

$$t = \left[\left(t_0 + \ln\left(1 - L_t \middle/ L_\infty\right) \middle/ -k\right) * 360\right] + PLD \tag{5}$$

$$D_s = D_c - t \tag{6}$$

where t is the age in days when the individual was sampled, and PLD is the pelagic larval duration, which was assumed to be 57 days (Friedlander et al. 2007). The date at spawning (D_S) was then estimated by subtracting the age in days from the Julian day the individual was sampled. Frequency of date at spawning was then plotted against the calendar year and a lowess smoother (locally-weighted polynomial regression) was used to visualize seasonal patterns.

Results

Demographics

A total of 180 specimens were collected, consisting of 84 *A. glossodonta* and 96 *A. virgata* with sizes ranging from 10.4 to 67.0 and 10.0–66.5 cm, respectively (Table 1).

Length measurements of both species indicate that, on average, *A. glossodonta* (μ=49.8 cm, S.E.=0.98) is larger than *A. virgata* (μ=45.2 cm, S.E.=1.19) (t=2.95, df=106.25, p<0.01, Fig. 2). The size distributions of both species overlap, with different maximum frequencies, and more *A. glossodonta* in larger size classes (Fig. 2).

Significant relationships exist between weight and length for both species (both species: R^2= 0.99, p<0.01; Table 2, Fig. 3), with no significant

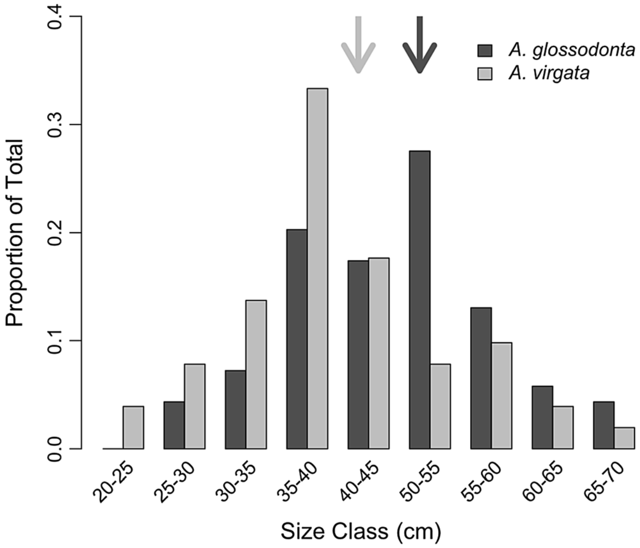


Fig. 2 Length-frequency distribution for *Albula glossodonta* (*dark grey*) and *Albula virgata* (*light grey*). *Arrows* correspond to mean lengths for each species

Table 2 Summary of life history parameters of Hawaiian bonefishes with standard errors in parentheses, with the exception of confidence intervals for L_{50} estimates that were obtained with bootstrapped estimates of coefficients from the logistic models

	Albula glossodonta	*Albula virgata*
a	0.01 (0.09)	0.01 (0.07)
b	3.04 (0.02)	3.02 (0.02)
Min-max *W* (g)	12.2–3016.4	13.7–4127.7
L_∞	67.26 (6.32)	56.39 (4.93)
K	0.18 (0.06)	0.26 (0.08)
t_0	−0.68 (0.73)	−0.49 (0.61)
Min-max Age (years)	1–14	1–11
L_{50} males	41.0 (31.1–47.1)	45.9 (42.8–48.0)
L_{50} females	43.7 (38.2–48.6)	40.4 (37.4–43.3)

difference between the slopes of the two relationships (ANCOVA, $F_{1,2}=0.34$, $p=0.56$). However, the intercepts were significantly different ($F_{2,167}=20{,}900$, $p<0.01$), with *A. virgata* having a smaller intercept ($\beta=-0.10$, $p<0.01$), indicating that the shape of the relationship is the same, but the weight at a given length is smaller for *A. virgata* compared to *A. glossodonta*.

Growth

Parameters of the von Bertalanffy growth function were estimated for each species based on 56 and 46 samples for *A. glossodonta* and *A. virgata*, respectively (Table 2, Fig. 4). Daily growth was not estimated for either species, so the youngest individuals for both species were estimated at 1 year. Maximum ages were 14 years for *A. glossodonta* and 11 for *A. virgata*. Visual inspection of 95 % confidence intervals for best-fit parameters for each species reveal qualitative differences in the direction of each parameter with a larger L_∞ for

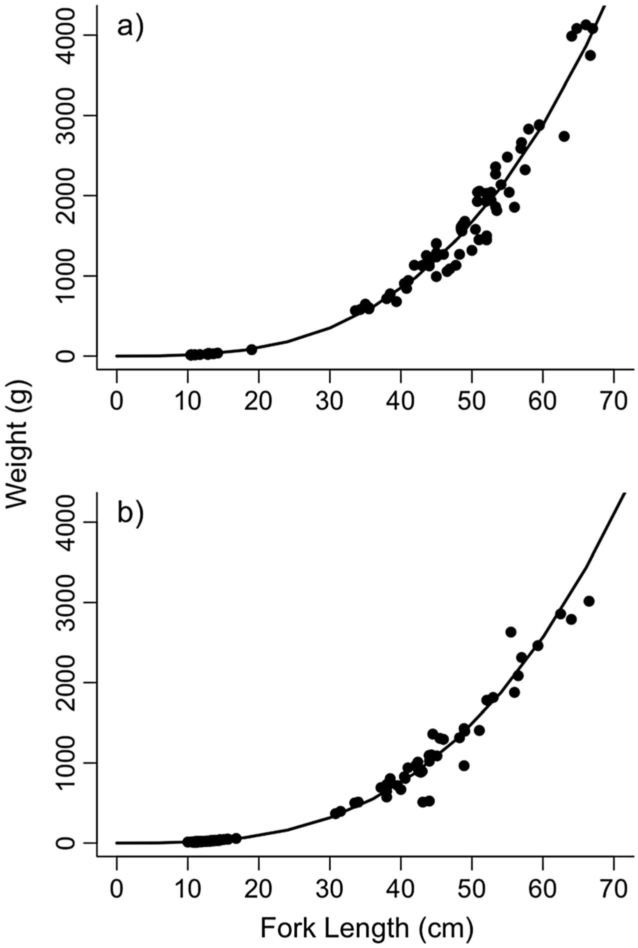


Fig. 3 Allometric length-weight relationships for **a** *Albula glossodonta* and **b** *Albula virgata*

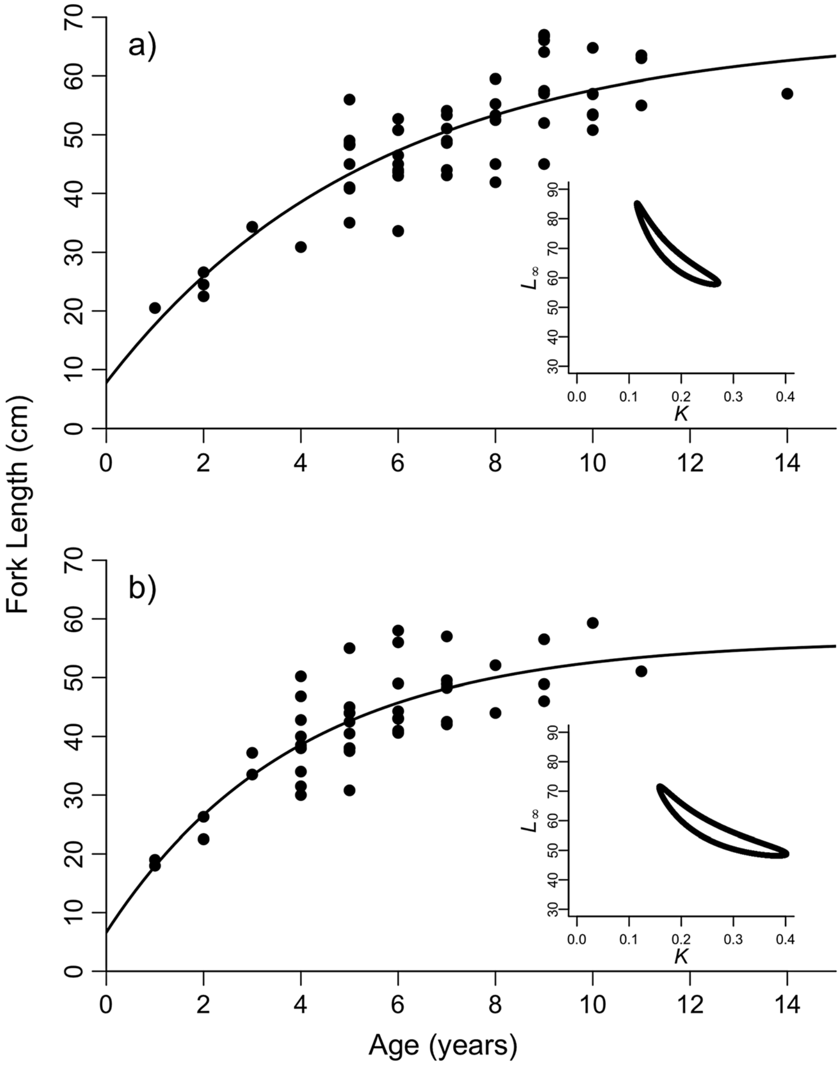


Fig. 4 Size-at-age for **a** *Albula glossodonta* and **b** *Albula virgata* with best-fit curves for von Bertalanffy model and 95 % confidence intervals for L_∞ and K as inset

A. glossodonta compared to *A. virgata* and a larger range of K values for *A. virgata* (Fig. 4 inset). However, a likelihood-ratio test indicates that the two models are not significantly different ($F_{1,9}=1.71$, $p=0.11$).

Diet

Of the 73 stomachs extracted from *A. glossodonta*, 26 contained identifiable prey items and were considered in the analysis (Table 3). Of these, portunid crabs were present in 33.5 % of the samples, followed by brachyuran crabs (31.2 %), and molluscs (mainly mussels, 23.3 %, Table 3). These three prey items also had the highest prey specific abundance, with molluscs having the highest within-sample abundance resulting in a prey-specific abundance of 68.5 (Fig. 5).

Of the 84 stomachs extracted from *A. virgata*, 63 contained identifiable prey items and were considered in the analysis (Table 3). Similar to *A. glossodonta*, brachyuran crabs were present in 31.7 % of the samples, with a prey-specific abundance of 41, reflecting high within-sample abundance (Table 3, Fig. 5). Otherwise, the diet of *A. virgata* was more varied, with high prey-specific abundance of sand crabs (Albuneidae), sea cucumbers (Holothruidae), mantis shrimps (Stomatopoda, Gonodactylidae), snapping shrimp (Alpheidae), fishes, mud crabs (Xanthidae), and portunid crabs (Table 3, Fig. 5).

Table 3 Summary of stomach content analysis for two species of Hawaiian bonefishes, including prey-specific abundance, frequency of occurrence across samples and the total abundance of each prey in stomachs that contain that prey (S_{ii})

							Albula glossodonta			*Albula virgata*		
Taxa						Common name	Prey-specific Abund.	Freq. Ocurr.	S_{ii}	Prey-specific Abund.	Freq. Ocurr.	S_{ii}
Annelida						Worm	23.9	0.4 %	1.3	3.9	2.4 %	14.2
Anthropoda												
	Malacostraca											
		Stomatopoda				Other mantis shrimps	4.6	1.5 %	28.1	16.3	7.7 %	11.1
			Unipeltata		Gonodactylidae	Mantis shrimp	6.6	1.9 %	26.1	16.0	4.2 %	6.2
		Decapoda										
			Pleocyemata	Caridae	Alpheidae	Snapping shrimp	1.2	0.5 %	36.1	16.0	10.0 %	14.7
				Brachyura		Other crabs	44.7	31.2 %	61.4	41.0	31.7 %	18.2
					Majidae	Spider crab	0.0	0.0 %	0.0	1.0	0.0 %	1.0
					Portunidae	Swimming crab	41.0	33.5 %	72.0	10.5	9.4 %	21.1
					Xanthidae	Mud crab	11.9	7.6 %	56.2	15.3	7.0 %	10.8
				Anomura	Albuneidae	Burrowing sand crab	0.0	0.0 %	0.0	67.0	5.2 %	1.8
				Axiidae	Axiidae	Lobster shrimp	0.3	0.1 %	31.8	0.0	0.0 %	0.0
			Natantia			Swimming shrimp	0.1	0.0 %	9.9	3.9	2.5 %	15.3
		Amphipoda				Sideswimmers	1.2	0.0 %	3.4	9.1	3.1 %	7.9
Mollusca						Molluscs	68.5	23.3 %	29.9	5.6	0.9 %	3.8
Echinodermata					Holothuriidae	Sea cucumber	0.6	0.0 %	1.7	34.5	7.0 %	4.8
Chordata												
	Osteichthyes					Fish	0.0	0.0 %	0.00	15.4	3.2 %	4.9

An index of diet overlap was calculated for the two species resulting in a value of $O_{jk}=0.14$, which translates to a low probability of randomly drawing two individuals from the same taxon (Horn 1966).

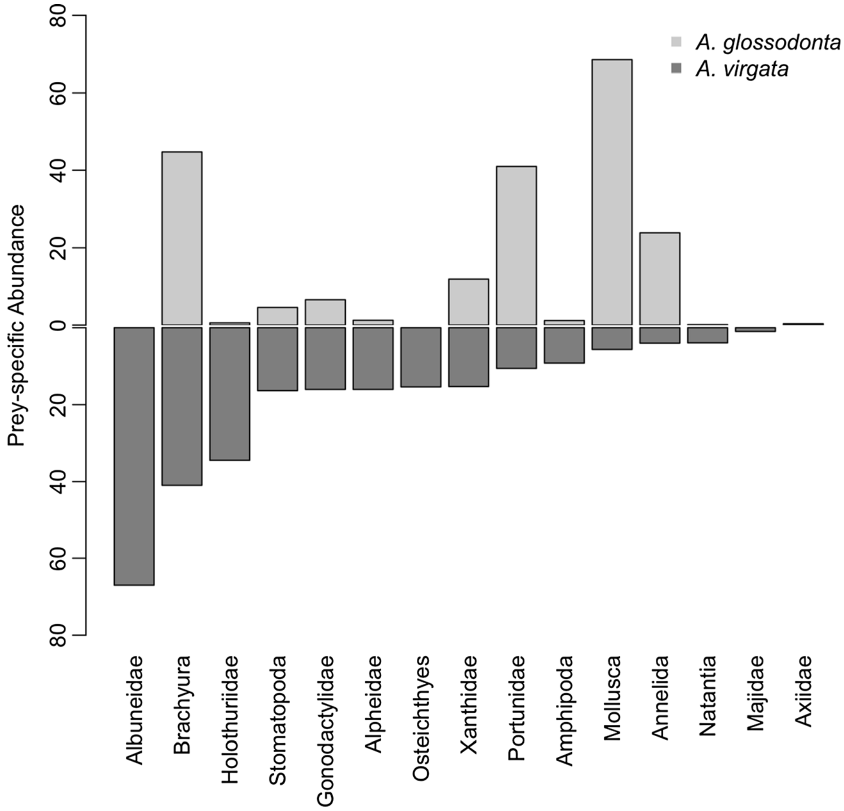
Spawning and recruitment

Mean size of females was significantly larger than males for both species (*A. glossodonta*: $F_{1,40}=4.04$, $p=0.05$; *A. virgata*: $F_{1,22}=4.93$, $p=0.04$). The size at maturity among species was different for the two sexes, with females maturing at a smaller size for *A. virgata* and males for *A. glossodonta*. Female size at maturity was 43.7 cm (38.2–48.6 cm; $n=56$) for *A. glossodonta* and 40.4 cm (37.4–43.3 cm; $n=49$) for *A. virgata*. Male size at maturity was similar to females, with male size at maturity at 41.0 cm (31.1±47.1 cm; $n=16$) for *A. glossodonta* and 45.9 cm (42.8±48.0 cm; $n=25$) for *A. virgata* (Fig. 6).

The reproductive status (i.e., spawning, regressing, regenerating) was determined for 19 *A. virgata* and 57 *A. glossodonta* across all years pooled. Based on histological analysis we found evidence of spawning from November through April for both species.

Patterns of recruitment were variable between the species (Fig. 7). In general, the abundance of juvenile bonefishes along sandy beaches where sampling occurred was significantly greater for *A. virgata* compared with *A. glossodonta* ($t=-3.83$, df=11, $p<0.01$). The abundance of juvenile *A. glossodonta* was variable throughout the year

Fig. 5 Prey-specific abundance by taxa for *Albula glossodonta* (*top*) and *Albula virgata* (*bottom*)



with a peak in December (Fig. 7a). The abundance of juvenile *A. virgata* was low from January through July and peaked from August to October, with slightly elevated abundance from November through December (Fig. 7b). Smoothed estimates of inferred spawning peaks were different between the two species, with one peak from November to April for *A. virgata*, which matches our observations from histologically assessed gonads. Two peaks were estimated for *A. glossodonta*, one from November to December and another from March through June.

Discussion

This study is the first documentation of the life histories of bonefishes in Hawai‘i, and provides a unique opportunity to compare two closely related sympatric species. We found that the demographics, growth, diet, reproduction, and recruitment of the two species differ, which may explain species persistence. This study also provides useful information for conducting population assessments and employing species-specific management in Hawai‘i that takes into consideration growth rates, and size and age at maturity by species.

Spatial partitioning of the two Hawaiian bonefish species has been found in previous studies (Shaklee and Tamaru 1981; Friedlander et al. 2007). Additional, anecdotal information from fishing supports these findings as the authors' personal communications with fly-fishing guides and recreational anglers from our angler-based tagging project (Kamikawa et al. 2015) indicate that *A. virgata* is rarely, if ever, captured on shallow reef flats. In general, fishermen report catching *A. virgata* in deeper habitats around Oahu, while *A. glososdonta* is captured on sandy-shallow flats, providing evidence of spatial separation of the two species. Our findings parallel conclusions of Adams et al. (2007) who documented the existence of the sympatric species *A. vulpes* and *A. sp. B* (also known as *A. garcia*) in the Atlantic, where

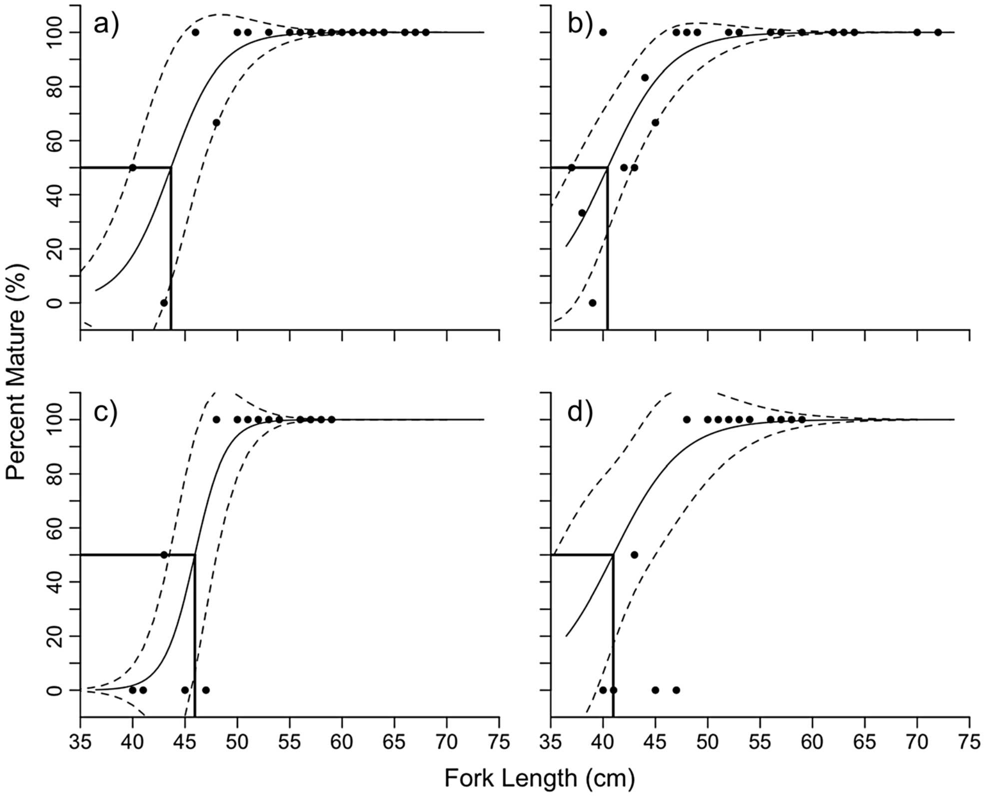


Fig. 6 Proportion of mature individuals as a function of length for **a** *Albula glossodonta* females, **b** *A. virgata* females, **c** *A. glossodonta* males, and **d** *A. virgata* males. *Vertical lines* correspond to length at 50 % maturity (L_{50}) and *dashed lines* are 95 % confidence intervals

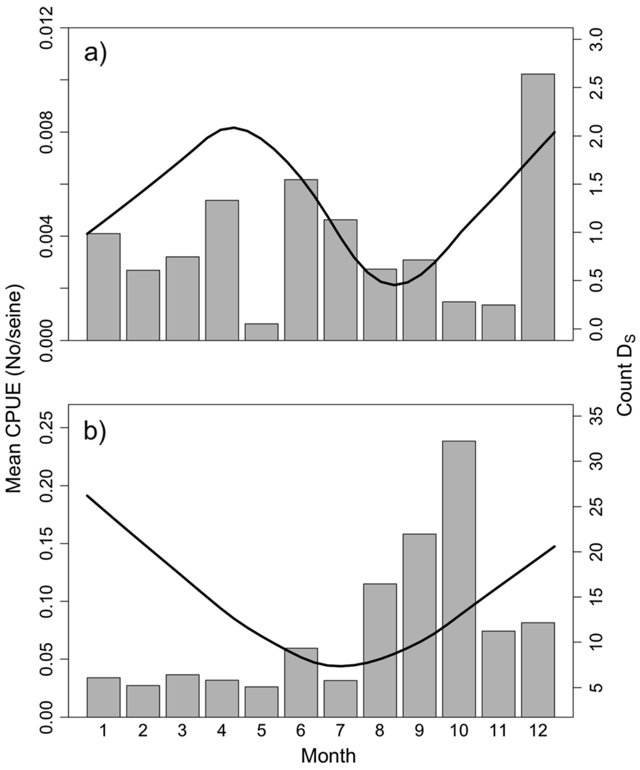
A. vulpes is the dominant species captured in the recreational fishery on the shallow flats, while *A. sp. B* appeared to be restricted to deeper water habitats and was less frequently encountered in the fishery.

The mean sizes of the two species were significantly different, and although there is overlap in the size distributions, *A. glossodonta* covers a greater range of sizes and had a greater abundance of larger individuals than *A. virgata*. Likewise, length at a given weight was greater and the theoretical maximum length (L_∞) was larger for *A. glossodonta*. These observations conform to expectations that body size and range sizes are positively correlated (Gaston and Blackburn 1996), where endemics have a smaller range-size than their wide-ranging congeners.

Within each species, we found females to be larger than males, which was similar to findings from Tarawa and Kirtimati in the western and central Pacific (Kamatie et al. 1995; Beets 2000). However, studies of bonefish in Palmyra and Florida did not find differences between sexes (Ault 2007; Friedlander et al. 2007), which could be due to competition for resources resulting from high densities in those locations. In the case of Palmyra, the large abundance of predators (e.g., sharks and jacks) likely exerts high natural mortality, which in turn limits growth (Friedlander et al. 2007). Although mean sizes were different, we did not find differences in the size at sexual maturity between sexes for either species (Fig. 6). This may be a result of low sample sizes resulting in wide confidence intervals for our modeled estimates (Fig. 6).

From our gonad samples we were also able to provide evidence of spawning during certain times of the year. The patterns corresponded well with our back-calculations from recruit surveys (Fig. 7) with spawning peaks for both species in the winter months (November-April). This is similar to observations of *A. vulpes* from the Florida Keys and

Fig. 7 Seasonal patterns of juvenile catch per unit effort from beach seine surveys (*grey bars*, *left axis*), and patterns of inferred spawning from back calculating date of birth from length from juvenile surveys (*red line*, right axis) for *Albula glossodonta* (**a**) and *A. virgata* (**b**)



The Bahamas where spawning was found to occur between November and May (Crabtree et al. 1997; Danylchuk et al. 2011), while bonefishes from the western Caribbean were found to spawn year round (Vásquez-Yeomans et al. 2009). It remains uncertain if there are additional spawning peaks throughout the year in Hawai i, however our back-calculated spawning time from recruit surveys indicates a second-smaller spawning peak for *A. glossodonta* around April.

There is still much to be learned about the biology of and fisheries for bonefishes in Hawai‘i. We need to understand the dynamics between these two species and how they interact with one another and their environment. More detailed information on catch location from anglers could provide a better understanding of the habitat use of the two species. To achieve higher resolution of habitat use than is achievable from conventional mark recapture, a study using acoustic telemetry would provide useful information for not only defining habitat use, but also for capturing whether bonefish in Hawai‘i are making large movements to spawning locations.

Conclusions

Life history and ecological information is woefully lacking for most nearshore fisheries species in Hawai‘i and this study therefore represents an important contribution to our knowledge of these resources. Partnering with fishermen has greatly increased the efficiency of this work and has helped to build trust between scientists, resource managers, and the fishing community. The collaborative and comprehensive inter-disciplinary approach taken in this study proved to be highly effective for collection of biological data for important resource species and can be a model for future efforts to more effectively manage coastal marine resources in Hawai i and elsewhere.

Effective management requires a sound understanding of biology and fisheries dynamics of the species, and information provided by this work will greatly aid in the development of better management related to these and other species in Hawai‘i. The ecological separation of the two bonefish species was supported by habitat and location observations, diet, and length-weight relationships, supporting species-specific management. We found that the size at sexual maturity for both species and both sexes was greater than the current legal size for the State of Hawai'i; therefore these results indicate that, to better manage the fishery, it may be necessary to increase the minimum size. We also provide evidence that both species spawn during the winter months, so a seasonal closure may be another appropriate management tool. Further, the current regulations for these species that do exist do not differentiate between the two species, which is cause for concern given the differences in life histories described in this study.

Acknowledgments The authors would like to thank the Harold L. Castle Foundation, The University of Hawai'i Sea Grant Program, Richard Gushman, and The Nature Conservancy Hawai'i for their generous support of this research. The fisherman who participated in the 'Ō'io Tagging Project, and those who donated samples at local fishing events made this project possible. We would like to specially thank Matt Ramsey from the NOAA Pacific Islands Regional Office for his help in forming collaborations with local fishermen and obtaining samples. We thank two anonymous reviewers for their constructive feedback that improved the manuscript.

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