

FULL RESEARCH ARTICLE

Validated age and growth of Barred Sand Bass within the Southern California Bight

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The recreational fishery for Barred Sand Bass (*Paralabrax nebulifer*) has recently shown declines in catch prompting a need for updating life-history attributes. The objective of this study was to provide a more extensive and current examination of Barred Sand Bass age and growth. Fish were collected from the southern California bight from 2011 to 2015. Using Akaike Information Criteria analysis we determined that the three-parameter von Bertalanffy growth model was the best fit out of the four tested models (Gompertz, Logistic, Power, and von Bertalanffy). Males grew slightly quicker than females (k , males = 0.10, females = 0.08). Males and females did not differ in length, weight, or the length-weight relationship. We also validated yearly banding of Barred Sand Bass with oxytetracycline marking of two fish in captivity for one year. Location of the first annulus was also validated with otolith diameter measurements. Finally, we compared the current study to a past 1990's study and observed different growth parameters. The growth difference after thirty years showed that possible fishing pressure and environmental factors might have influenced changes in growth. This study provides current information on age, growth over time and, otolith morphometrics, for Barred Sand Bass.

Key words: age estimation, age validation, Barred Sand Bass; growth; otolith, *Paralabrax nebulifer*

Barred Sand Bass (*Paralabrax nebulifer*) range from Central California to Baja California (Miller and Lea 1972) and can be found at depths up to 183 m (Eschmeyer and Herald

1983). Barred Sand Bass has been a popular sportfish in southern California since the early 1900s (Collyer 1949) and caught commercially until 1953 when commercial fishing of Barred Sand Bass was prohibited in California. They are most often targeted during summer months when they form large spawning aggregations (Love et al. 1996; Allen and Hovey 2001; Jarvis et al. 2010). Barred Sand Bass along with its congener Kelp Bass (*Paralabrax clathratus*) are held in high esteem by recreational anglers in southern California and together the two fisheries earned 2.9 billion dollars in 2015 (NMFS 2017). They consistently have been in the top ten ranked fish caught in California on CPFVs (Commercial Passenger Fishing Vessels) since the late 1970s; however, overall catch of Barred Sand Bass has decreased dramatically since 2004 (Erisman et al. 2011; Jarvis et al. 2014), and in 2013 a regulation change occurred for all three *Paralabrax* species, including kelp bass and spotted sand bass. The daily bag limit decreased from ten to five fish in combination of all three species and the size limit increased from 12 to 14 inches total length. In the years after the regulation change (2014 to 2019), landings data indicate kelp bass are re-bounding while Barred Sand Bass numbers continue to decline (CDFW, unpublished data).

Determination of life history traits of marine fishes provides an increased understanding of population dynamics and sustainable fishery yields which support better management decisions (Treble et al. 2008; Zischke et al. 2013). The age of a fish is one of the most important biological factors measured, and informs researchers about recruitment, growth, and mortality (Leung and Allen 2016; McBride et al. 2008). These biological estimates are essential when managing marine fisheries, especially an overfished species like Barred Sand Bass. For example, life history traits may change over time in response to fishing pressures (Enberg et al. 2010). These changes are likely to require re-evaluation of fishery management tools that are based on specific life-history parameters (e.g., size at age). Thus, it appears prudent that age and growth rates of fishes be evaluated regularly (Ong et al. 2015; Williams et al. 2007). A study published over 30 years ago by Love et al. (1996) explored life history traits of Barred Sand Bass and included an assessment of age and growth and age and size at maturity. However, sample size for Barred Sand Bass were very limited (109 fish) and age validation was conducted using only marginal increment analysis (MIA). Currently, Barred Sand Bass are managed without sex-specific regulations. Sexes were previously determined to not differ for age and growth (Love et al. 1996). However, males and females of many species of fish grow at different rates, possibly because of resource partitioning (Enberg et al. 2010), and growth differences between sexes should be explored.

Aging of fish hard structures can prove to be quite difficult and is often subjective. Although many validating methods are available (radiochemical dating, bomb carbon dating for long-lived fishes, tag-recapture, and MIA to ensure aging accuracy, there are also many roadblocks enlisting these methodologies (time constraints, cost, and utility in the case of MIA). Alternative ways to assess individual ages of fish would be beneficial and should be explored within the aging community. One possible method for estimating fish ages outside of traditional methods (band pair reading of hard parts and scales) is assessing morphometrics of otoliths. Otolith morphometrics (width, thickness, length and mass) may be a good predictor of fish age (Doering-Arjes et al. 2008; Matic-Skoko et al. 2011; Lepak et al. 2012) and the cost and time spent on this method is relatively low.

When evaluating age and growth of fish species, the von Bertalanffy growth model (VBGM) is most often chosen for both sex-specific and for non-sex-specific growth models, with the assumption that this single model will describe growth best. Often, using the von Bertalanffy model *a priori* has been found to poorly describe growth, with negative

results on the fishery (Katsanevakis and Maravelias 2008). Because of this, it is important to evaluate more than one growth model to determine which best fits the available data; other common models used to assess length at age of fish include Gompertz, Power, and Logistic (Williams et al. 2012).

The objective of this study was to provide a more extensive and current examination of Barred Sand Bass age and growth by: 1) aging a large number of otoliths from both males and females; 2) validating annual periodicity of the observed growth pattern; 3) determining the relationship between otolith morphometrics and Barred Sand Bass age; 4) determining the model that best describes Barred Sand Bass growth; and 5) comparing the present models to the past study and its implications for current management of the Barred Sand Bass fishery.

METHODS

Sample collection and length-weight relationship

We collected Barred Sand Bass from 2011 to 2015 in coastal waters from Santa Barbara County to Orange County on predominantly sandy substrate and patch reef habitat using a variety of methods: 1) spearfishing on SCUBA, hook and line, and fish traps, 2) Los Angeles County Sanitation District's Ocean Monitoring hook and line surveys, and 3) donations from anglers on CPFVs. Fish were measured for total length (mm) and whole weight (mg) ($n = 736$) and sexed by macroscopic examination of gonads. We were unable to collect gonads from all fish, so some individuals were left as unsexed. We extracted and cleaned both right and left sagittal otoliths from all usable fish. After otoliths were cleaned with deionized water and air-dried, they were placed in gelatin capsules until further processing could occur. We fit the Barred Sand Bass data to a length-weight model. The logarithmic transformation of the two-parameter power function, was used where W is whole body weight, TL is total length, and the parameters a and b are estimated using least square linear regression. Length and weight data were log-transformed to linearize the length-weight model. Homogeneity of slopes for length versus weight were compared between sexes with analysis of covariance (ANCOVA).

Otolith processing

We selected one otolith from each pair at random and marked at the nucleus, epoxied dorsally/ventrally onto thick paper labeling tags, and cured for 24 hours. Otoliths were cut along the transverse plane through the marked nucleus with a Buehler ISOMET low speed saw using two NORTON Superabrasive Diamond Grinding Wheels set 0.3 to 0.5 mm apart. Otolith wafers were then checked for the least marred side and then affixed that side down with Cytoseal™ 60 adhesive. The slides cured for an additional 24 hours. We wet polished otolith wafers using 600 grit waterproof sandpaper and deionized water with frequent checks under the stereo microscope for the best view of bands to prevent over polishing and diminishing the banding pattern.

Otolith reading/aging

Attempts to read all ($n = 736$) otoliths were made by two readers from a live image that was projected onto a TV screen using a Sony Handycam HDR-SR7 Digital HD Video

Camera Recorder attached to a compound microscope under low magnification (4x). We aged otoliths twice on two separate occasions by each reader (= four assigned ages per otolith) no less than two weeks and no more than four weeks apart. We counted the combination of an opaque and translucent band (annulus) as one whole year of growth. A band is defined as a distinct color change on the otolith; the translucent band is clear and the opaque band is white under the transmitted light of a compound microscope (Beamish and McFarlane 1983; Campana and Neilson 1985). We assigned final ages from the total number of counted annuli. Otoliths that were given the same age three out of four times were considered aged and were not assessed again. If an age was not agreed upon three out of four times, then the readers observed the otolith together and attempted to come to an agreement for an age of the fish. Otoliths that were deemed unreadable, or when the readers could not agree upon an age, were not included in the final analysis. The precision of age estimates between readers was calculated with Chang's coefficient of variation (CV) (Chang 1982). Equation is as follows:

$$CV = \frac{\sqrt{\frac{\sum_{i=1}^N (X_{ij} - X_j)^2}{N - 1}}}{X_j} * 100\%$$

Otolith morphometrics

We obtained measurements for 608 otoliths; the remaining otoliths were missing or damaged in some way and not used in the analyses. Otoliths were measured for mass (gram,g) and length (millimeter, mm) to establish a possible relationship with fish age. Mass was measured with an analytical balance to the 0.0001 g. The length of the whole otolith was measured with calipers to the 0.01 mm, from the longest axis along the anterior and posterior surface of the otolith. Initially, thickness and width were also measured (n = 24) but preliminary regression analysis showed them to be poor potential predictors for age, ($r^2 = 0.41$ and 0.53 , respectively) so these measurements were not obtained for all otoliths. A random otolith of the pair was then chosen and the relationship of mass and length with age was determined through linear regression.

Validation of annual periodicity and edge analysis

The annual periodicity of banding in Barred Sand Bass was evaluated by oxytetracycline (OTC) marking of live fish. To confirm that Barred Sand Bass produce two distinct bands per year, we chemically marked one opaque (white band) and one translucent (clear band) of two adult Barred Sand Bass with OTC by injection. Two adult fish measuring 334- and 349-mm total length caught in Orange County at the same general area as most fish aged in this study were injected in the dorsal muscle with 0.2 to 0.3 mL of OTC. The fish were kept in outside aquaria pens (2013 January to 2014 January) at California State University, Long Beach, then sacrificed for otolith removal after one year. Otoliths were read with an Olympus BX51 microscope under ultraviolet light, and images were taken with an attached digital camera Olympus camera. A green fluorescing band across the face of the otolith indicated the location of the OTC mark. Images were also taken under transmitted light and compared with the fluorescent otolith image so that the matched bands could be visualized. Together, the opaque and translucent banding after the OTC mark and up to the leading edge of the otolith were counted as one full year of growth.

We also performed an edge analysis by recording the growing edge (margin zone) of all otoliths as either opaque or translucent in relation to the fish's month of capture to determine the seasonality of the banding pattern within the year. Although edge analysis is not as reliable a technique for age validation as an OTC marking because light refraction and thinning of the otolith edge may cause misinterpretation (Campana 2001), edge analysis was used to reaffirm annual periodicity of banding.

The first-year annulus was validated by taking measurements of young-of-the-year otolith diameters from fish collected in October to December. We captured images of ten otoliths with a Sony Handycam Digital HD Video Camera Recorder (HDR-SR7) and digitized into ImageJ (version 1x) (Schneider et al. 2012). A digital micrometer within the program was calibrated using an image of a calibration slide. The images were then measured across the otoliths' diameter with the add-in, ObjectJ. We created a regression plot of otolith diameter-total fish length to determine the relationship between the two measurements. The modal total length (mm) of the young-of-the-year measurements was inserted into the young-of-the-year length-otolith diameter regression and the regression line was used to estimate the diameter of the first year annulus.

Growth curve determination and historical comparison

We evaluated four different models that are commonly used to describe fish growth for males, females and the sexes combined. We included smaller unsexed juvenile fish ($n = 21$, TL < 205 mm) in all models to increase an accurate estimate of the parameters (Craig 1999). The sexes combined model also included an additional 100 fish of larger sizes but unknown sex. The model equations are as follows: 3-parameter Gompertz = $L_{\infty} [\exp(-\exp(-k * (t - t_0)))]$, Logistic = $L_{\infty} / [1 + \exp(-k(t - t_0))]$, 2-parameter Power = $a * (t^b)$, and 3-parameter von Bertalanffy = $L_{\infty} [1 - e^{-K(t-t_0)}]$. Parameters are defined as follows for all equations: L_{∞} maximum asymptotic length, k = relative growth rate, t = age of fish, and t_0 = theoretical age at time that length is zero, and a and b = describe the shape of the curve with no biological meaning. The models were compared using Akaike Information Criterion (AIC) to determine which model fitted the data best; the lowest AIC being the better fit model (Katsanevakis and Maravelias 2008).

We determined if growth was equal between males and females with a family of six nested models. We used planned contrasts to compare all combinations of the VBGF parameters to a general model. Separate parameters were estimated between groups (sexes) with analysis of variance.

The observable change in age and growth over time was evaluated by comparing parameters from Love et al. (1996) to the current study. We did not have access to the raw historic data, so no statistical analysis was conducted, and parameters were compared qualitatively.

All data analysis was conducted in R package v3.3.2 (R Core Team, 2017) unless otherwise noted.

RESULTS

Sample collection and length-weight relationship

We prepared 736 Barred Sand Bass otoliths for aging. Of the 736 fish assigned ages, 370 were female, 245 were male, and 121 were of unknown sex. The male: female ratio was

1:1.5 and was significantly different from a 1:1 expected ratio (Chi-Square analysis; $\chi^2 = 25.407$, $d.f. = 1$, $P < 0.001$). The total length (TL) of female Barred Sand Bass ranged from 245 to 600 mm and males from 146 to 593 mm TL. The total length of fish with unknown sex ranged from 117 - 566 mm. The total body weight for females ranged from 180 to 3400 g and 220 to 2310 g for males. There was no significant difference of distribution between male and female total length (mm) or total body weight (g) (two-sample Kolmogorov-Smirnov test, $D(615) = 0.06442$, $P = 0.5734$, and $D(381) = 0.11271$, $P = 0.1993$, respectively). The length-weight parameters were estimated to be $a = -4.5935$ and $b = 2.8868$ for males, $a = -5.1121$ and $b = 3.0951$ for females, and $a = -5.0147$ and $b = 3.0546$ for sexes combined (Table 1). Analysis of covariance for length-weight relationship of males and females were found to not have significantly different slopes (ANCOVA, $P = 0.9904$) and were pooled together for fitting of the power curve. The pooled data showed a strong relationship ($R^2 = 0.9320$) between length and weight (Table 1, Figure 1).

Table 1. Barred Sand Bass length-weight parameters estimated from the two-parameter power function, $W = aTL^b$. Where W is log-weight and TL is log-length.

Sex	n	a (intercept)	b (slope)	SE of b	r^2
Male	149	-4.6742	2.9219	0.3240	0.7833
Female	232	-5.1121	3.0951	0.0558	0.9305
All	381	-5.0192	3.0579	0.0503	0.9062

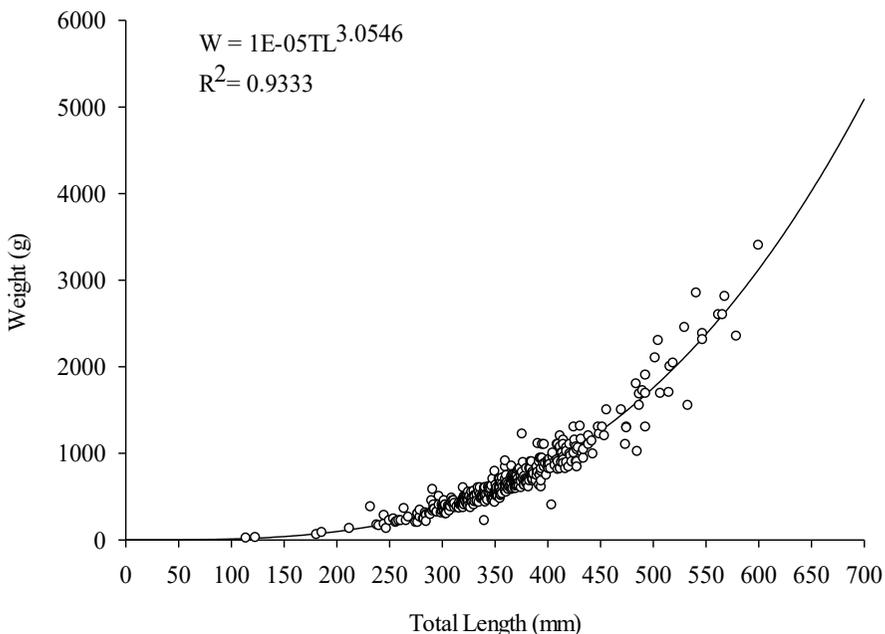


Figure 1. Total length (mm) and whole weight (g) relationship of barred sand bass, all sexes combined. Dashed line represents fitted power curve. Power function and R^2 value is reported. $n = 379$.

Otolith aging

Barred Sand Bass otoliths exhibited the common pattern of alternating translucent and opaque bands radiating out from a central opaque zone (nucleus). The bands started wide then became thinner as they radiated towards the edge until they were no more than a thin line. From the thin otolith wafers, the maximum age given to a female, also the oldest aged fish in the sample, was 25 years old (600 mm TL), and the oldest male was aged at 19 years (453 mm TL). The coefficient of variation (CV) was calculated as 9.9%. Bias plots showed that both agers tended to age younger fish older than the final agreed upon age, and older fish younger than the final agreed upon age. (Figure 2, A and B). Bias plots also showed that agers differed from each other, on average, and generally underaged otoliths (Figure 2, C).

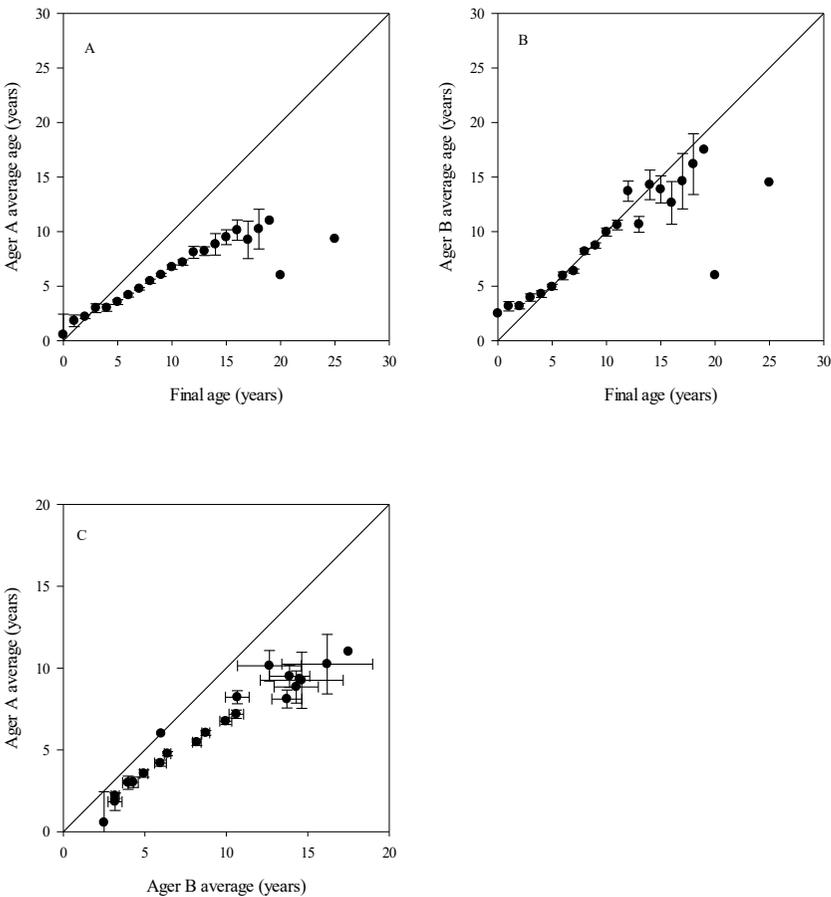


Figure 2. Age bias plots of average (n=4) age assigned by readers A and B for Barred Sand Bass, plots A and B. Comparison is between each reader's age and average age against the final agreed upon age. Letters indicate different agers, A and B. Numbers indicate different readings, 1 and 2. Number of otoliths read (n): A1 = 756, A2 = 751, B1 = 740, and B2 = 741. Error bars are 95% confidence intervals.

Otolith morphometrics

Otolith length and mass increased curvilinearly with age reaching an asymptote. There was a significant difference between sexes for mass and length measurements (ANCOVA; $p < 0.05$ for both measures), so sexes were analyzed separately. Linear regression models showed that otolith mass explained 72% female and 70% male variation; otolith length explained 53% female and 64% male variation of Barred Sand Bass ages (Figure 3).

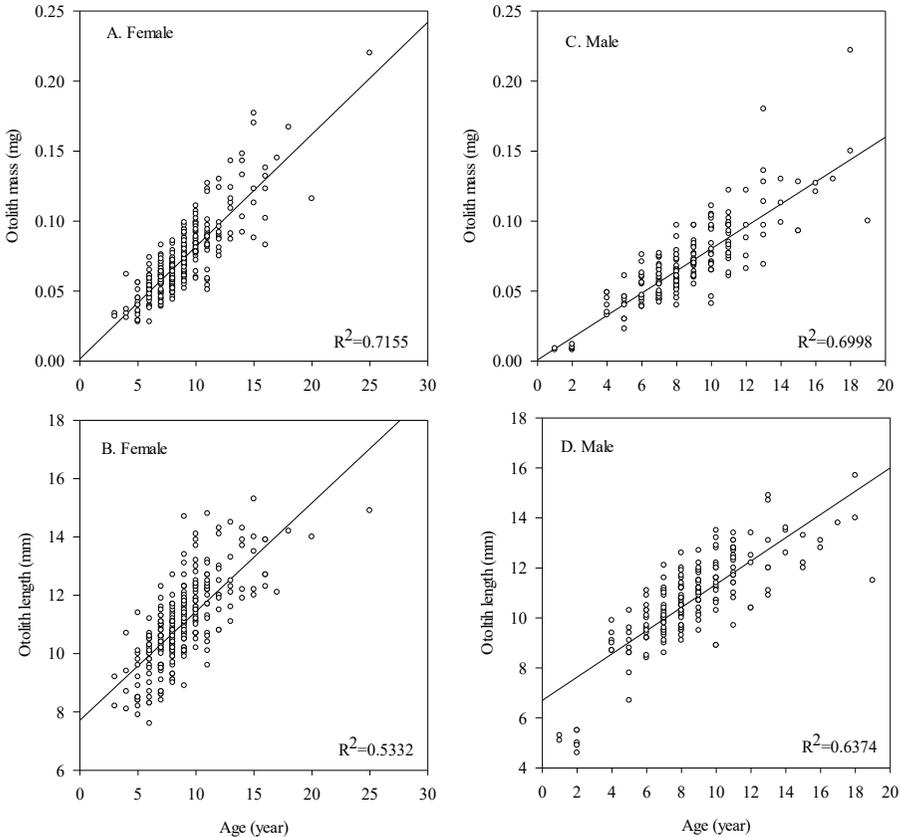


Figure 3. Linear relationships between otolith morphology and age estimates of *Paralabrax nebulifer*, within the Southern California Bight. The coefficient of determination (r^2) values are reported for the relationship between both length and mass with age. $n = 581$, for both length and mass measurements. Panels A and B are Females, panels C and D are Males. Solid lines are regression lines.

Validation of annual periodicity and edge analysis

The OTC mark was observed as a fluorescing line on both sagittal otoliths of injected Barred Sand Bass (TL = 426, aged as a 10-year-old fish). One of each translucent and opaque band followed the fluorescing mark and were of the same width as bands before the OTC mark indicating an annual banding pattern (Figure 4).

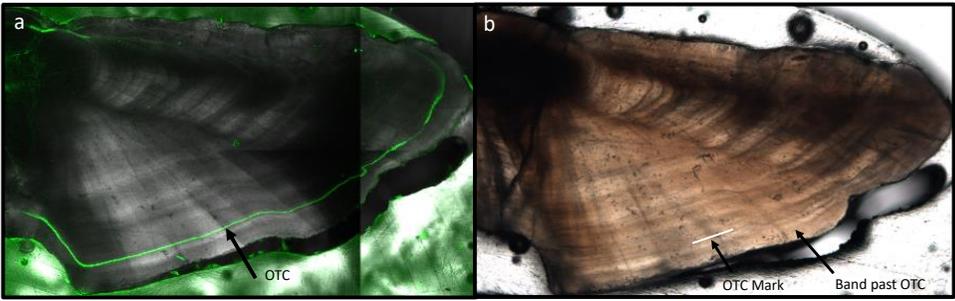


Figure 4. Oxytetracycline treated barred sand bass (TL = 426, aged as a 10-year-old fish) thin-sectioned sagittal otolith. a. under fluorescent lighting and b. without. Oxytetracycline mark is indicated by white line and black arrow; the year of growth is also marked. Scale bar is equal to 1 mm.

Opaque bands were found most frequently in the summer months (June to September) and translucent bands were more prevalent during the other months (January to May and October to December). The proportion of opaque and translucent bands during the summer months was approximately 50% for each and during the other months, edges were > 70% translucent (Figure 5) suggesting a seasonal growth pattern.

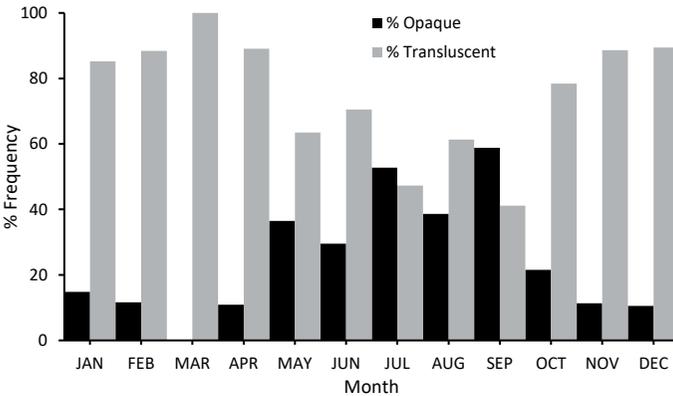


Figure 5. Percent frequency of otolith margin zone (opaque versus translucent) for all aged barred sand bass otoliths captured from 2011 to 2015.

Validation of the first annulus was confirmed by establishing a relationship between otolith diameters of zero and fish total length of zero and one-year aged fish. None of the fish in our sample (n = 10) were the exact total length, so fish were binned in 20 mm increments and the most common mode was the 140 mm bin. Based on a total length of 140 mm for age one fish, the annulus diameter of age one fish was estimated as 2.2 mm. This value corresponded with the predicted annulus diameter of age one fish when otoliths of fish of all ages were included in the regression. Regression analysis showed fish total length explained 73% of otolith diameter (Figure 6).

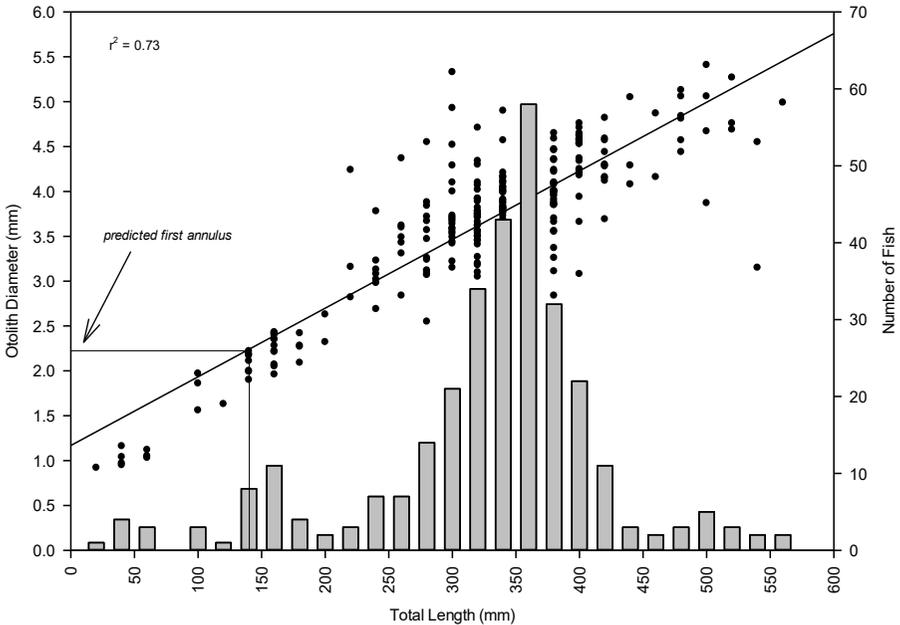


Figure 6. Validation of the annulus on first-year barred sand bass otoliths. Scatter plot of otolith diameter (mm) and fish total length (mm) including distribution of fish at size (total length, mm). Solid line is a regression of otolith diameter and fish total length. Inserted into the graph is the mode of one-year old fish. $n = 309$.

Growth curve determination

We found that the VBGM was the best fit to the size-at-age curve for the male, female and sexes combined (includes unsexed fish) data sets (Table 2). The power function was the next best fit for females and sexes combined; however, it was the poorest fit for males.

Significant differences were found between male and female von Bertalanffy growth model parameters L_{inf} (ANOVA: $F = 5.6326$, $P = 0.01792$). Therefore, von Bertalanffy growth curves were fit separately for male and female Barred Sand Bass. Both sexes grew relatively fast in early years but slowed down around age five (Figure 7).

Growth parameters for the current study of all sampled fish ($n=736$) were estimated to be $L_{inf} = 606$, $k = 0.09$, and $t_0 = -2.32$

DISCUSSION

We found and verified that sectioned sagittal otoliths were useful and reliable for estimating age of Barred Sand Bass in southern California. This finding is in line with the previous study from Love et al. (1996) that also found sagittal otoliths of Barred Sand Bass to be appropriate for estimating age. The CV calculated for this species also indicates the viability of using sagittal otoliths for aging of Barred Sand Bass. Campana (2001) suggests that designated CV target levels may be difficult to attain because of morphological and environmental species differences and the complex nature of otoliths. They found that across 117 studies, the median CV was 7.6% and the mode was 5%. Barred Sand Bass are

Table 2. Results for model selection. Models ranked by lowest difference in AIC scores (ΔAIC) and larger weight (W_i). A lower model AIC and ΔAIC indicates a better fit model to the data.

		AIC	ΔAIC	W_i
Both Sexes	VBGM	7322.97	0	0.98
	Power	7330.37	7.4	0.02
	Gompertz	7338.5	15.53	0
	Logistic	7357.12	34.15	0
Female	VBGM	3911.64	0	0.91
	Power	3916.4	4.76	0.08
	Gompertz	3920.99	9.35	0.01
	Logistic	3932.42	20.78	0
Male	VBGM	2614.23	0	0.85
	Gompertz	2617.68	3.45	0.15
	Logistic	2625.97	11.74	0
	Power	2723.17	108.94	0

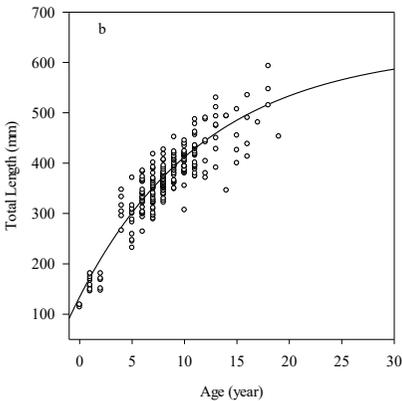
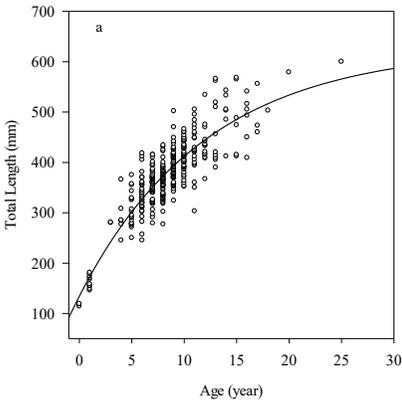


Figure 7. Length at age data (open circles) of fit with the von Bertalanffy growth curve (solid black line) of female (a) and male (b) barred sand bass collected within the Southern California Bight, and $n = 391$, female and $n = 266$, male.

relatively long-lived fish and the otolith-banding pattern was more complex than other species with shorter life spans. Therefore, our reported CV was deemed acceptable and within the range of other long-lived species.

There was a slight sex skew towards more females than males, also a finding from the past study, although the implications of this for Barred Sand Bass populations is not well known. It has been noted that a small number of Barred Sand Bass may be hermaphroditic, which may explain the sex skew (Baca-Hovey et al. 2002). We found the length-weight relationship to be strong, with length a good predictor of weight for males and females combined. Male and female length-weight relationships did not differ significantly from each other,

Otolith banding was also validated with OTC marking of captive adult fish. Often, OTC marking of captive fish is not a reliable method (Campana 2001), because of the inability to control environmental factors. In the case of our captive fish, they were kept in temperature controlled outdoor aquaria that resembled their natural seasonal environment. The creation of both bands during the captive year was of similar width to those prior to OTC marking giving evidence that being in captivity did not inhibit the growth of our OTC marked fish. The location of the first annulus was also confirmed in this study. Establishing the first annulus is an often neglected but important step in aging studies. Studies have found that previous age estimates were inaccurate based on newer studies' location of the first-year annulus (Beamish and McFarlane 1995; Natanson et al. 2006). Edge analysis of Barred Sand Bass otoliths indicated seasonal band formation and reinforces annual periodicity of banding in Barred Sand Bass otoliths. The banding pattern of Barred Sand Bass otoliths showed some seasonality trends. The observed edge pattern consisted of translucent bands appearing more frequently during winter months compared to opaque bands, which were observed in the summer months. The mechanisms of band formation are not well understood but it is widely accepted that they are influenced by temperature and nutrient availability (Weidman and Miller 2000). The winter months produce slow growth with narrow translucent banding (Campana 1999). The summer months of fast growth produce wide opaque bands (Campana 1999).

Very few species of fish are re-evaluated over time for age and growth. Most often, once an analysis occurs and growth parameters have been calculated the data are used for many years to follow, and for some species, this may be appropriate. Commonly, the data are used in stock assessments and other studies that describe a stock to determine the best management strategy. The fit of fish growth to an appropriate growth model is dependent on life history, environment and unseen properties. The shape of the curve may vary, again depending on variations in fish species. The best-fit model for age and growth of Barred Sand Bass was determined to be the von Bertalanffy Growth Model (VBGM). The VBGM is the most used growth model for most marine fish and was used in the past study for Barred Sand Bass (Love et al. 1996). However, unlike the past study, our sample size was large enough to allow accurate fitting of the Von Bertalanffy curve separately for males and females and showed that females grew faster than males, and that females were larger.

The utility of using morphometrics was also explored in this study and we found otolith length and mass may be good indicators of Barred Sand Bass age. Otolith mass was the better predictor of age explaining about 76% of the variation within ages. Considering the difficulty of aging fish species (otoliths of older/larger were difficult to differentiate the annulus versus checks), it seems some otolith morphometrics may be a better alternative to aging of fish otoliths.

Despite a similar maximum age of 25 years in the current study versus 24 years in Love et al (1996), current study had a much smaller L_{inf} (606 mm) compared to the 1990's study L_{inf} (662 mm), indicating that maximum size of Barred Sand Bass has decreased over time. However, the growth coefficient k (0.08 for 1990's and 0.09 for current study) is similar for both studies indicating that growth rate is approximately the same from both studies. Differences in L_{inf} may be attributed to environmental factors and/or increased fishing pressure. Within the Firth of Clyde in Scotland five species of marine fish were shown to have differing growth rates based on location (Hunter et al. 2016). The locations studied were experiencing different temperature regime changes over decades, starting in the 1980's and continuing to today, like what Barred Sand Bass has experienced in southern California. Another explaining factor is size selective fishing. Changes in phenotype have long been associated with fishing pressure. For example, Sharpe and Hendry (2008) reviewed several studies of changes in commercial fisheries associated with increased fishing pressure and found evidence that fishing pressure is a major driver that influences life history traits that are heritable within a species. The large growth parameter differences found between the 1990's study and this study highlight the importance of updating life history traits for managed marine species.

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Author Contributions

Conceived and designed the study: ETJ-M, CFV, KMP, KMW

Collected the data: ETJ-M, KMP, KMW

Performed the analysis of the data: KMW

Authored the manuscript: KMW

Provided critical revision of the manuscript: ETJ-M, KMP, CFV

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