AGE AND GROWTH OF THE GIANT SEA BASS, *STEREOLEPIS GIGAS*

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ABSTRACT

The giant sea bass, *Stereolepis gigas*, is the largest bony fish that inhabits California shallow rocky reef communities and is listed by IUCN as a critically endangered species, yet little is known about its life history. To address questions of growth and longevity, 64 samples were obtained through collaborative efforts with commercial fish markets and scientific gillnetting. Sagittae (otoliths) were cross-sectioned and analyzed with digital microscopy. Age estimates indicate that *S. gigas* is a long-lived species attaining at least 76 years of age. Over 90% of the variation between age (years) and standard length (mm) was accounted for in the von Bertalanffy growth model ($R^2 = 0.911$). The calculated von Bertalanffy growth function parameters ($K = 0.044$, $t_0 = -0.339$, $L_\infty = 2026.2$ mm SL) for *S. gigas* were characteristic of a large, slow-growing, apex predator.

INTRODUCTION

The giant sea bass, *Stereolepis gigas*, is the largest bony fish associated with the California rocky reef communities. The species is a grouper-like member of the wreckfish family, Polyprionidae (Shane et al. 1996). Historically, giant sea bass were distributed from Humboldt Bay to southern Baja California and the Sea of Cortez with populations concentrated south of Point Conception in shallow rocky reefs. Giant sea bass were commercially and recreationally sought after for most of the twentieth century in California waters. Commercial fishing of this species shifted south of the US border as population numbers in the southern California peaked in 1934 and declined after 1935 when this species became relatively rare in catches (Crooke 1992). Commercial fishers originally caught giant sea bass by hand line then switched to gillnetting, significantly decreasing fish numbers off California by 1934. Commercial landings from US waters peaked in 1932 near 90 mt before declining dramatically to under 10 mt by 1935. US landings coming from Mexican waters were generally higher (peaking at over 360 mt in 1932) and did not permanently sink below 90 mt until 1964 and were below 5 mt when US take from Mexican waters was banned in 1982 (Domeier 2001). Commercial and recreational fishing depleted giant sea bass stocks to the point that a moratorium was declared in 1982. Although this species cannot be targeted, commercial vessels are now allowed to retain and sell one individual per trip as incidental catch. Giant sea bass caught in Mexican waters by recreational anglers are allowed to be landed and sold in California markets; however the limit is two fish per trip per angler. There are no commercial or recreational restrictions on giant sea bass in Mexico today (Baldwin and Keiser 2008).

In 1994, gillnetting was banned within state waters (three miles off mainland) and one mile from the Channel Islands in southern California. Most recently, concerns over sustained population viability led to the International Union for Conservation of Nature (IUCN) red listing the giant sea bass as a "Critically Endangered" species (Musick et al. 2000; Cornish 2004). The measures taken to protect this species appear to have been effective because the number of juvenile giant sea bass reported as caught and released is increasing (Baldwin and Keiser 2008), and it is one of the five species of large nearshore predators reported as returning to the Southern California Bight (SCB) (Pondella and Allen 2008).

The lack of life history information for giant sea bass is likely a result of the practice of dressing-out (beheading and eviscerating) fish prior to landing to conserve space on fishing vessels (Crooke 1992). Unfortunately, this results in the loss of data on actual fish size and of the head and entrails that contain the structures most useful in life history studies (Allen and Andrews 2012). Because of this practice, little data exist on age, growth, and estimated age at maturity in giant sea bass. Early accounts reported that giant sea bass reach 178 mm (7 in) by age 1 year and twice this length at age 2 years (Fitch and Lavenberg 1971). Age estimates reported for small to medium-sized fish are 6 years at 14 kg (30 lb), 10 years at 45 kg (100 lb), and 15 years at 68 kg (150 lb), but details of the age estimation method were not provided (Domeier 2001). Fitch and Lavenberg 1971 reported an estimated age of 11 to 13 years at sexual maturity. California Department of Fish and Game (Baldwin and Keiser 2008) has reported that females mature between 7 and 11 years of age, however that estimate is unverifiable as there have been no studies confirming age at maturity.

The reported age at maturity of 11 years for giant sea bass is in conflict with the observation by Domeier 2001 that "most fish" were mature at 7 to 8 years.

Gaffney et al. 2007 suggested sex ratios of giant sea bass are approximately 1:1, indicating that giant sea bass are not sequential hermaphrodites. A previous study on two other widespread wreckfishes, *Polyprion americanus* and *P. oxygeneios*, confirmed that both species were gonochores, although some studies have suggested otherwise (Roberts 1989).

Age and growth information is essential to the management of recreational and commercial fisheries and must be considered when assessing the status of a fishery (Craig et al. 1999). Prior to the present study, most age and growth information on *Stereolepis gigas* have been poorly documented or unverifiable. Allen and Andrews 2012 were first to validate annual growth rings for one individual and provide a verified maximum age for giant sea bass using bomb radiocarbon dating techniques. Radiocarbon dating of giant sea bass confirmed that a 227 kg specimen was 62 years old, suggesting that previous estimates that this species lives 100 years may be unsubstantiated (Allen and Andrews 2012). In the present study, we seek to provide the first large data set on the age and growth of giant sea bass as it is vital to our understanding of its biology and critical to the effective management of its exploited population. By developing a realistic growth model, we also aim to confirm that this long-lived species has a slow growth rate (k), increasing its susceptibility to overfishing.

MATERIALS & METHODS

Otoliths (sagittae) were extracted from *Stereolepis gigas* heads obtained from the Santa Barbara Fish Market, Santa Barbara, CA between January 2010 and May 2013 (n = 43). These fish were all reported as legal and/or incidental catch taken from the waters off southern California and northern Baja California. Head length (mm) was measured from the tip of the premaxillary bone to the tip of the operculum on each specimen. Sagittal otoliths were also obtained from specimens collected between 2006 and 2010 during a juvenile white seabass (*Atractoscion nobilis*) gill net survey conducted by Allen et al. 2007 for the Ocean Resource and Hatchery Enhancement Program (n = 21) where standard lengths were recorded. Once extracted, sagittae were cleaned in 100% ethanol, rinsed with deionized water, and stored in padded envelopes. Length, width, and depth of both the left and right sagittae (if whole and available) were then measured and recorded to the nearest 0.01 mm using digital calipers. Otolith length measurements were taken along the longest axis, parallel to the sulcus. Width was measured across the shortest axis perpendicular to the sulcus while depth was the distance across the shortest axis of the sagitta at the otolith focus. Unbroken otoliths were weighed on an analytical balance to the nearest 0.001 g.

Two methods of otolith sectioning were used in this study. In the first method, otoliths were embedded in an epoxy mold (mixture of 20 grams of 20-3068RCL15 epoxy resin with approximately 4 grams of CAT.190CL13 catalyst). Each otolith was then placed sulcus side up into a preparatory pool and covered in epoxy. The otolith was then removed from the preparatory pool, air pockets were removed, and then placed into the mold sulcus side down and parallel to the length of the mold. The otolith sat in the mold for 24 hours before being removed from the mold tray and 72 hours before sectioning the otolith within the epoxy mold. A small batch (n = 18) was sectioned using a Buehler-Isomet double-bladed low speed saw and was visually inspected for any signs of cracking or breakage. Although many otoliths were sectioned successfully, breakage occurred in a high percentage (50%) of the subsample. Therefore, other protocols were explored for mounting the otoliths safely without threat of cracking during the sectioning process.

The second sectioning method followed that of Craig et al. 1999, where a cyanoacrylate adhesive was used to mount otoliths to wood blocks. This method proved to be successful for giant sea bass otoliths and was employed for the remaining otoliths not sectioned in epoxy (n = 46). These remaining otoliths were mounted on approximately 5 cm × 2.5 cm × 1 cm blocks with a fast-drying gel cyanoacrylate adhesive and allowed to set for 48 hours. A 0.5 mm section through the nucleus of the otolith was cross-sectioned using a Buehler-Isomet double-bladed low speed saw (Allen et al. 1995). Sections were mounted on glass slides with Crystalbond® 509 adhesive (SPI supplies, www.2spi.com) and polished by hand with 3M® Wet/Dry 500 grit sandpaper followed by 3M® Wet/Dry 1000 grit sandpaper.

Slides were placed in a black bottom Petri dish and digitally photographed using Image Pro 6.3 under a Wilde dissecting microscope. Each photograph was calibrated according to the magnification at which it was imaged and annuli were identified and marked with Image Pro 6.3 Editing software. In total, 64 individuals were aged by viewing digital images along an established axis in the dorso-medial sulcus region. All otolith sections and digital images are archived with the Nearshore Marine Fish Research Program, Department of Biology, California State University Northridge. The digital images of otolith sections were selected randomly and annulus counts made visually on the images with annuli being marked individually on two separate occasions. Where individual counts were in disagreement, otolith images were reexamined by both authors

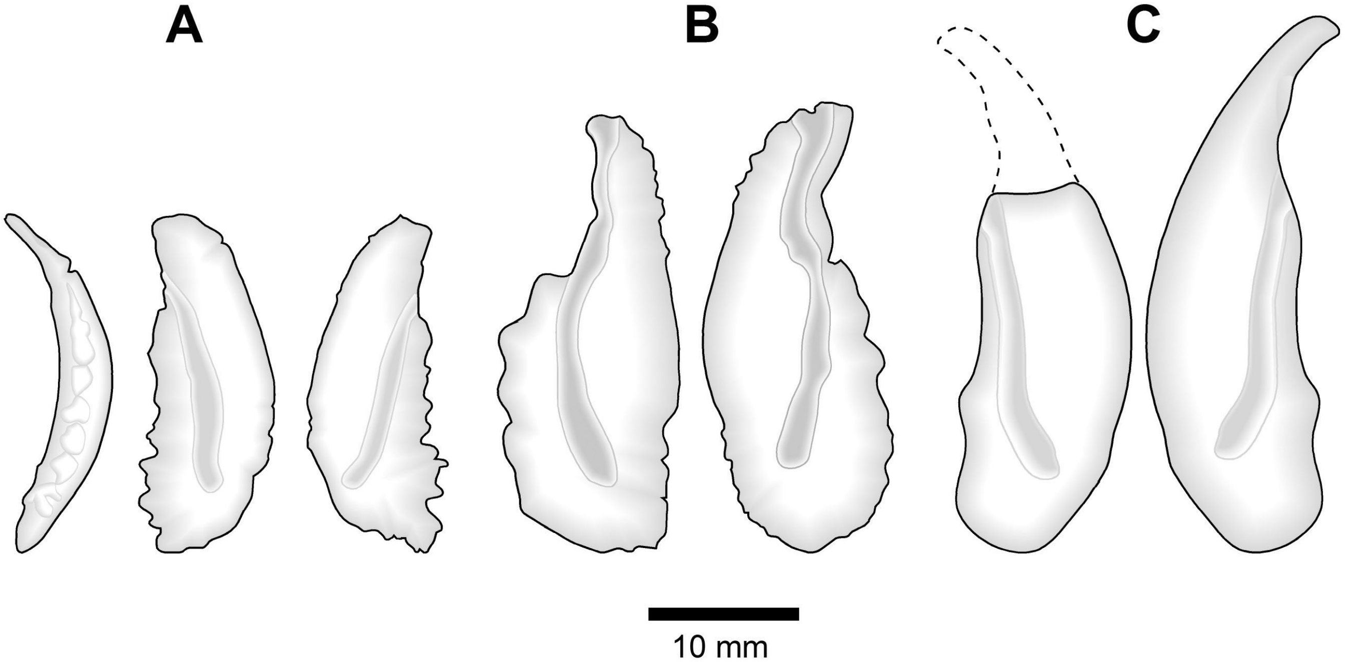

Figure 1. Ontogenetic morphological variation in sagittae of giant sea bass (*Stereolepis gigas*). A) A dorsal view of left and dorso-medial views of left and right sagittae from a 1390 mm SL, specimen and dorso-medial views of left and right sagittae of a B) 1862 mm SL, and a C) 2003 mm SL specimen aged during the present study. © Larry G. Allen.

together, until a consensus age was established by judging the validity of each marked annulus. Head lengths (mm) were converted to standard lengths (mm) for each sample represented only by a head based on the equation: SL = (0.282 * HL) + 11.34 ($R^2 = 0.998$) (L. G. Allen, unpublished data). Lastly, the estimated age of fish obtained from annual increment counts was regressed against whole (unbroken) otolith weight to assess weight as a predictor of age.

As recommended by Cailliet et al. 2006, the relationship between age (yr) and length (mm SL) data was estimated using multiple growth models. In this case, three growth models, the von Bertalanffy, Gompertz, and Logisitic models in Growth II (©2006 Pisces Conservation Ltd.) were used where both the Akaike (AIC) and Bayesian Information Criteria (BIC) were calculated to determine the best fit among the models.

RESULTS

Otolith Structure

In giant sea bass, the sagittae are elongated, laterally compressed, curved, and very fragile in younger specimens (fig. 1a). In younger specimens the lateral surfaces are irregular, with many mounts and depressions while the medial surface is relatively smooth punctuated by the sulcus acusticus opening anteriorly. The dorsal surface of the sagittae in younger individuals is highly crenellated. The external face of the otolith is concave (fig. 1a) with grooves and ridges radiating out from the core. With age, the rostrum becomes highly elongated, conspicuous and curved, the sulcus acusticus gets deeper and elongated, while the dorsal surface becomes smooth (figs. 1b and 1c).

Examined with reflected light over a black background, the central area of the sectioned sagitta is white and may show one to seven false (subannular) rings. The central area is surrounded by the first translucent band followed by a clear and distinct opaque band denoting the first annual band (fig. 2). The first band invariably occurs at a sagitta width of approximately 3.0 mm based on the otolith width of a newly age-1 giant sea bass (Allen and Andrews 2012). The subsequent bands could be easily observed in the dorsal (dorso-medial) region of the sulcus (fig. 2).

Age Determination

The precision of interpreting assumed annual growth bands on digital images was high, with close agreement between the annual counts made by the two readers ($R^2 = 0.990$; $p < 0.0001$; $n = 64$). The number of annuli (age) and otolith weight ($R^2 = 0.913$; $p < 0.001$; $n = 58$; fig. 3), were significantly and positively correlated. This relationship was best explained by the equation: Age = 0.029 × otolith weight (g) –0.089 confirming that the number of annual increments increased linearily as otolith weight increased across the in the range of fish sizes sampled.

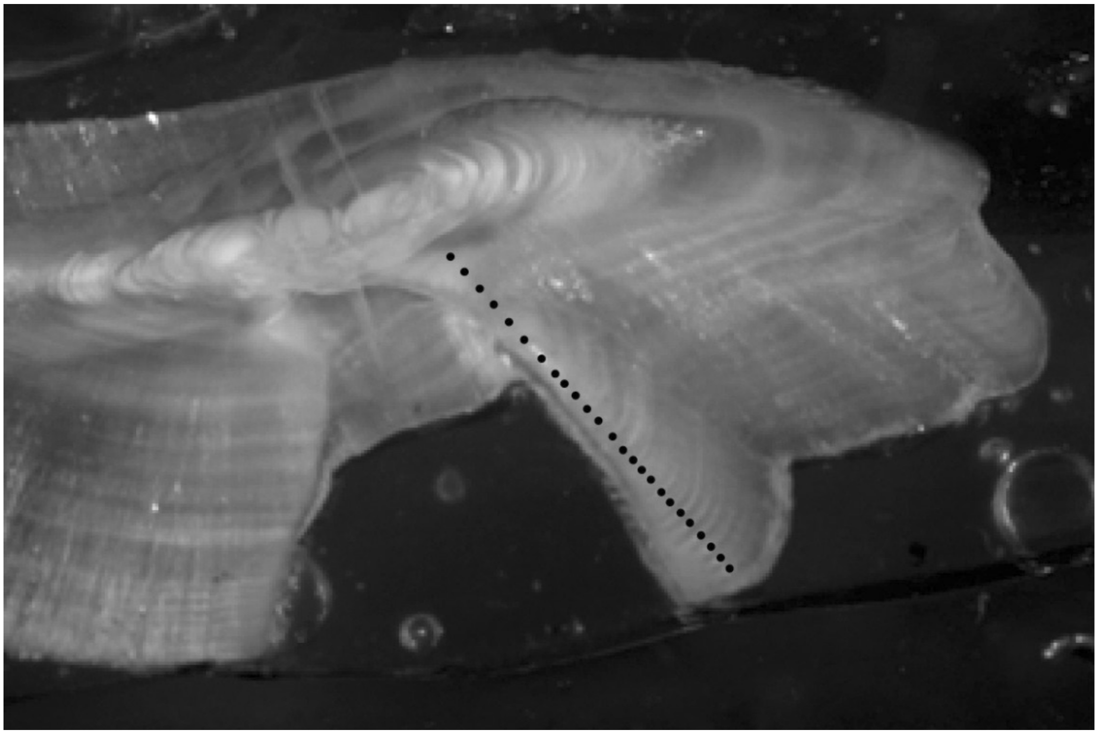

Figure 2. Transverse cross section (25x) of a representative sagitta of 25-year-old, 1572 mm SL *Stereolepis gigas*. Black dots are placed on the image to identify the annuli present.

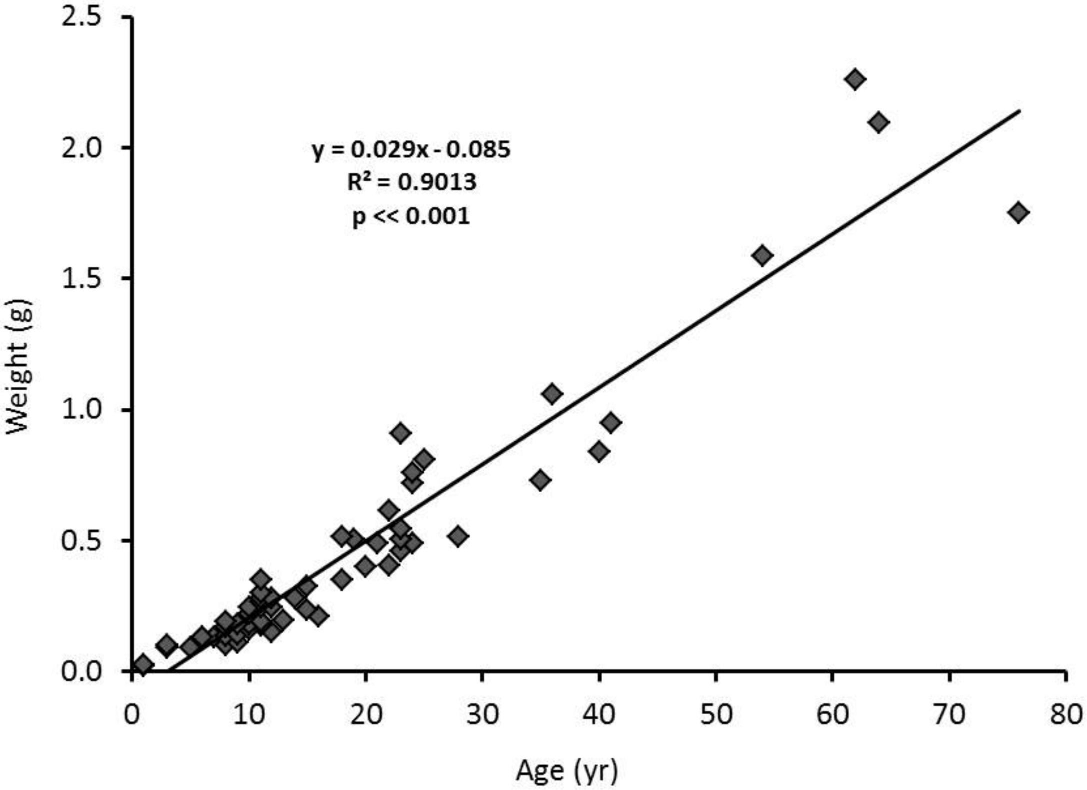

Figure 3. The relationship between otolith weight (g) and estimated age of giant sea bass ($N = 58$).

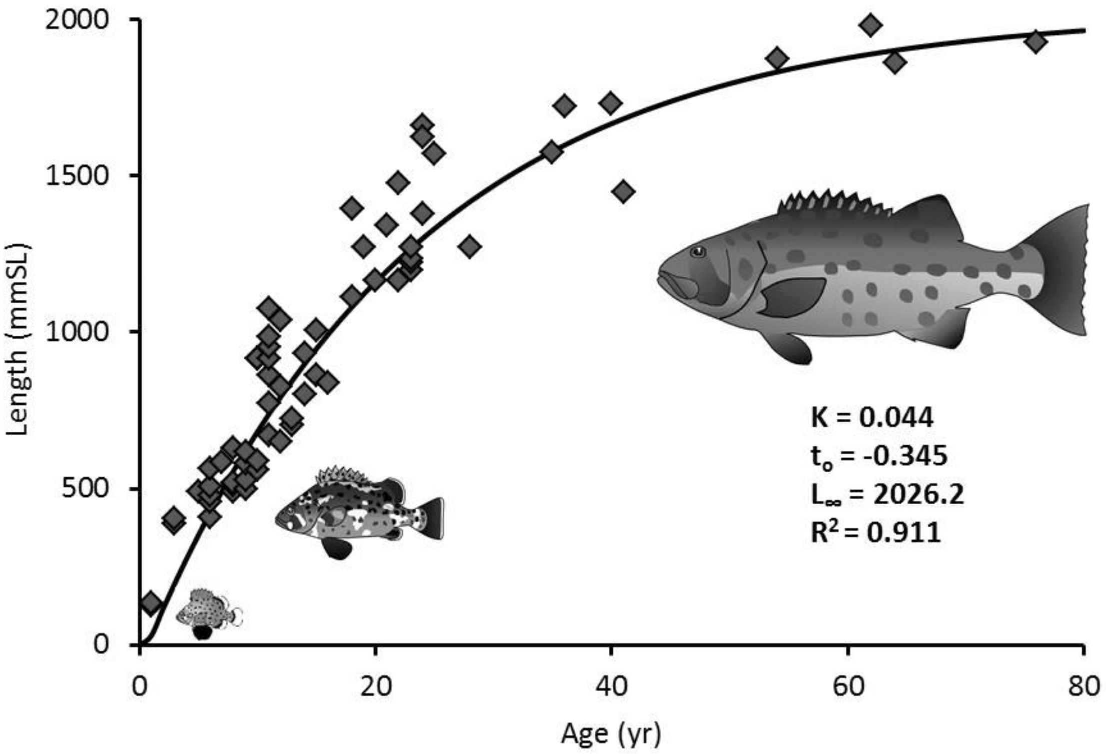

Figure 4. Observed standard length (SL) at age for *Stereolepis gigas* (N = 64) taken off California and Mexico. Line is fit to the von Bertalanffy growth curve with parameters given on figure.

TABLE 1
Parameters and model diagnostics (Akaike Information Criteria, AIC; Bayesian Information Criterion, BIC; and Inflection point, *I*) for three growth models calculated from size at age data for *Stereolepis gigas* (*n* = 64).

	Parameters			Model Diagnostics		
Growth Model	L_∞	K	t_0	I	AIC	BIC
von Bertalanffy	2026.2	0.044	–0.345	—	908*	914*
Gompertz	1708.2	0.104	—	8.774	914	921
Logistic	1794.9	0.120	—	13.765	914	920

* — Denotes minimum values indicating best fit.

Age and Growth

Giant sea bass in this study ranged from 130 mm to 2003 mm SL and from 1 to 76 years old, although only 9.4% of our samples were over age 40 (fig. 4). Of the three growth models tested (table 1), the von Bertalanffy growth function resulted in the best fit with the lowest values calculated for both AIC and BIC diagnostics. Over 90% of the variation between age (years) and standard length (mm) was accounted for in the von Bertalanffy growth model ($R^2 = 0.911$). The growth coefficient (K = 0.044) indicate this species has a slow growth rate, however, the negative value for t_0 ($t_0 = –0.345$) is indicative of a species that grows rapidly in the first year and at a decreased growth rate in the years following. A predicted maximum length with indefinite growth (L_∞ = 2026.2 mm SL) agreed well with the recorded maximum size of giant sea bass. The theoretical age at length calculations agreed well with observed ages with few exceptions. The growth equation fit to calculated standard lengths at age was $l_t = 2026.2\ (1 - e^{-0.044(t + 0.345)})$ (von Bertalanffy 1938).

DISCUSSION

Managing a once heavily fished species such as *Stereolepis gigas* requires robust knowledge of all aspects of the life history of the species. Age validation through otolith analysis allows for a more complete understanding of age, growth, and mortality of *Stereolepis gigas*. Fitch and Lavenberg 1971 published detailed accounts of the natural history of giant sea bass, including reports that a 435 pound specimen was estimated between 72 and 75 years of age. Unfortunately, the methods used to determine its age were not addressed. Otoliths were often read whole at the time (Allen and Andrews 2012), which can lead to a skewed estimation of age. A more recent study using radiocarbon analysis methods validated annular growth rings in giant sea bass, as well as confirmed the oldest (at the time) known individual to be 62 years of age (Allen and Andrews 2012). There has been much speculation and little information on the longevity of giant sea bass, but here we estimate the age of the oldest known individual at 76 years. There are reports that *S. gigas* reaches 90 to 100 years of age and 600 pounds (Fitch and Lavenberg 1971), yet these reports are unverifiable. In the current study, individuals were collected at the upper size limit of expected growth of giant sea bass and none exceeded 76 years.

Morphology of the sagittae varied as fish increased in size, generally becoming proportionally deeper and heavier with greater anterior extension. However, the greatest morphological variation particularly in otolith weight occurred among the largest and oldest specimens (figs. 1b and 1c). Whether this difference represents sexual dimorphism is impossible to tell, unfortunately, because all of the adult specimens were represented only by heads obtained from market.

Stereolepis gigas has only one congener, *Stereolepis doederleini* that occurs in the northwestern Pacific. As with its congener, little life history information is known for *S. doederleini*, but other polyprionids have been the subject of age and growth studies. In a study conducted by Peres and Haimovici 2004 on the Atlantic wreckfish, *Polyprion americanus*, maximum age was estimated at 76 years. Similar to our findings, the von Bertalanffy growth curves for both males and females of *P. americanus* indicated slow growth rates overall, with negative values for t_0. Unfortunately for the purposes of this study, we were unable to differentiate between males and females as *S. gigas* is not an obviously sexually dimorphic species and gonads were always removed before they were brought to market. Sexual size dimorphism has been suggested for another wreckfish species, the New Zealand hapuku, *Polyprion oxygeneios*, whose females grow larger and faster than males (Francis et al. 1999). It would be beneficial in the future to address possible variances in growth rates among males and females giant sea bass because differences can have implications in sexual selection (Walker and McCormick 2009).

Management and conservation of marine fishes requires the consideration of many factors and consequent comprehensive data collection. Such factors may include, but are not limited to, age and growth data (Cailliet et al. 1996), interspecific interactions (Jackson et al. 2001), and species-specific life history traits (Pinsky et al. 2011). Large, long-lived marine fishes that are particularly susceptible to over-exploitation (Reynolds et al. 2005) and recovery of a population after a decline can take well over a decade to several decades, if at all (Hutchings 2000; Russ and Alcala 2004). The resilience of any fish population and its subsequent recovery depends on a suite of variables, many of which will be species specific such as the longevity and growth rate of individuals, fecundity, larval duration, and age at maturation. Russ and Alcala 2004 suggest that it may take 15 to 40 years for a predatory fish population protected by marine reserves to recover fully.

In support of the recovery of giant sea bass, it may be advantageous if marine protected areas (MPAs) were established where spawning aggregations occur. It is illegal to target giant sea bass, but incidental catch-and-release occurs regularly. One model of five mortality regimes predicting the expected mortality of giant sea bass under varying degrees of catch and release mortality indicated that in an aggregation of 100 giant sea bass with 20% mortality due to catch and release would be driven to local extinction after 16 years (Schroeder and Love 2002). Alternatively, with an estimated natural mortality rate of only 6%, an aggregation of 100 giant sea bass would be reduced to 29 individuals after 25 years (Schroeder and Love 2002). An unrealistic, yet important assumption in the model is that no additional recruits are added to the aggregation over time. However, the model does illustrate the impact that catch-and-release mortality may have on this protected species and supports the proposal that MPAs could be useful in the management and recovery of this species.

Giant sea bass in California are currently protected to some degree, yet those in Mexico continue to be targeted both commercially and recreationally. Unpublished data cited in the 2008 Status of the Fisheries Report for giant sea bass (Baldwin and Keiser 2008) suggested that giant sea bass may in fact migrate long distances, placing even more importance on protecting giant sea bass in California as they remain unprotected and subject to different fishing pressure in Mexico (Gaffney et al. 2007). While fishing mortality can cause an adaptive response in growth rates of a population (Bevacqua et al. 2012), an analysis of covariance indicated there is no difference in growth among Californian and Mexican giant sea bass and that the variation found in length and age of giant sea bass is not due to any variation between individuals sampled in California and Mexico. However, the effects of any possible fishing pressure experienced by Mexican giant sea bass may be offset by genetic exchange (Gaffney et al. 2007) with those protected in California.

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