Copeia 106, No. 2, 2018, 312–320

Distribution and Recruitment of Young-of-the-Year Giant Sea Bass, *Stereolepis gigas*, off Southern California

Stephanie A. Benseman[1] and Larry G. Allen[1]

This study identified nursery habitat, recruitment patterns, the planktonic larval duration (PLD), size and age at settlement, and growth rate of the young-of-the-year (YOY) Giant Sea Bass (GSB), *Stereolepis gigas*, off Southern California. A total of 160 YOY GSB were sighted on 150 transects over a three-year period. Young-of-the-year GSB were relatively rare (maximum density of 40/ha) and recruitment was limited to a few areas. In 2014–2015, densities of YOY GSB were significantly higher at six locations off sandy beaches nearest the heads of submarine canyons off Redondo Beach, Newport Beach, and La Jolla, California. The vast majority of occurrences of YOY (73%) were within 500 m of the heads of submarine canyons. Three color phases of YOY were discovered ranging (smallest to largest individuals) from black to brown to orange. Recruitment occurred from July through February with peak abundances occurring in the late summer months from August through October. YOY occurred at depths from 2 m to nearly 10 m. Overall, size of YOY GSB increased with depth in the shallow sand riffle zone. YOY grew rapidly at 1.23 mm/day ($n = 23$) with collected individuals ranging from 31 to 84 d old based on daily ring increments in otoliths. The planktonic larval duration was estimated to be about one lunar month (26.8$\pm$2.4 d) based on the presence of the first settlement check and size of earliest settlers. Size at settlement was estimated to be 14.4$\pm$3.0 mm TL (10.6$\pm$2.5 mm standard length [SL]). This information adds substantially to our knowledge of early developmental processes and recruitment patterns of Giant Sea Bass that are crucial to our understanding of their life history and to making informed decisions regarding fisheries management policies and conservation efforts.

IN marine ecosystems worldwide, overfishing is the main cause of the removal of large predatory fishes from ecological communities (Myers and Worm, 2003; Baum and Worm, 2009). A knowledge of the life-history traits of these species, such as age and growth, is the starting point for any effective management framework (King and McFarlane, 2003) and is crucial to the sustainability of species. Specifically, early developmental processes and recruitment patterns are crucial for completing the life history for any species, allowing us to make increasingly intelligent decisions about current fisheries management policies as well as future conservation efforts (Cailliet et al., 1996; Craig et al., 1999).

Until recently, little was known about the basic biology and life history of Giant Sea Bass (*Stereolepis gigas*) due to fishery overexploitation in the early 1900s. This led to depressed populations that prevented research for most of the last century (Domeier, 2001; Pondella and Allen, 2008; Allen and Andrews, 2012). Therefore, a completed life history on this ecologically, and once economically, important species is critical for the continued successful management of its fishery.

Giant Sea Bass adults (Fig. 1) are the largest nearshore teleost off the Southern California coast (Pondella and Allen, 2008; Hawk and Allen, 2014) and occur at depths ranging from 5–46 m (Love, 2011). The species is found from Humboldt Bay to along the outer coast of Baja California into the Gulf of California and southward as far as Oaxaca, southern Mexico. It is most abundant south of Point Conception (Miller and Lea, 1972; Love, 2011; House et al., 2016). They grow to over 250 kg (Domeier, 2001) and live up to 76 years (Hawk and Allen, 2014), but recent studies have demonstrated that they may reach a length of 275 cm (9 ft) and an estimated weight of 381 kg (839 lbs; House et al., 2016). This new information is closer to historical reports of fish living 90–100 years and weighing over 270 kg (Fitch and Lavenberg, 1971), and some even as large as 360 kg (Holder, 1910).

Giant Sea Bass can be found in semi-predictable, large aggregations during the summer for 1–2 months, although recent studies suggest a longer aggregation time (House et al., 2016; Clark and Allen, 2018). Fishers have often targeted these spawning aggregations (Myers and Worm, 2003), landing high catches (Crooke, 1992) of up to 255 large fish in three days (Domeier, 2001). Due to their massive size, they have historically been targets for both recreational and commercial fishers since the 1800s (Pondella and Allen, 2008). Catches of the once economically important fishery began to fall dramatically in the early 1900s. In 1934, the commercial catches were close to 114,000 kg until a rapid decline to less than 15,000 kg not more than two years later (Pondella and Allen, 2008). In 1981, the California State Legislature created a moratorium prohibiting the recreational take and limiting commercial take of GSB, which came into effect in 1982. This essentially closed the commercial and recreational fisheries, except for a two-fish per trip bycatch allowance for commercial fishers, later amended to one in 1988. Additionally, Prop 132 (the Marine Resources Protection Act) was passed in 1994 to close the gill and trammel net fisheries near shore, and eventually the GSB were placed on the International Union for Conservation of Nature red list as critically endangered species (Cornish, 2004). While the GSB population remains protected but depressed, the population appears to be recovering slowly (Pondella and Allen, 2008; House et al., 2016). Estimates of their effective population size remain around 500 (Chabot et al., 2015). They have been observed more frequently in the last 15 years (Pondella and Allen, 2008), with juveniles continuously being caught and released in the recreational fisheries (Baldwin and Keiser, 2008).

Giant Sea Bass are thought to reach sexual maturity at about 11–13 years of age (Fitch and Lavenberg, 1971), but no systematic studies have confirmed this estimate. They are

[1] California State University, Northridge, Department of Biology, 18111 Nordhoff Street, Northridge, California 91330; Email: (LGA) larry.allen@csun.edu. Send reprint requests to LGA.
Submitted: 7 February 2018. Accepted: 15 March 2018. Associate Editor: K. Martin.
 DOI: 10.1643/CE-18-021 Published online: 14 June 2018

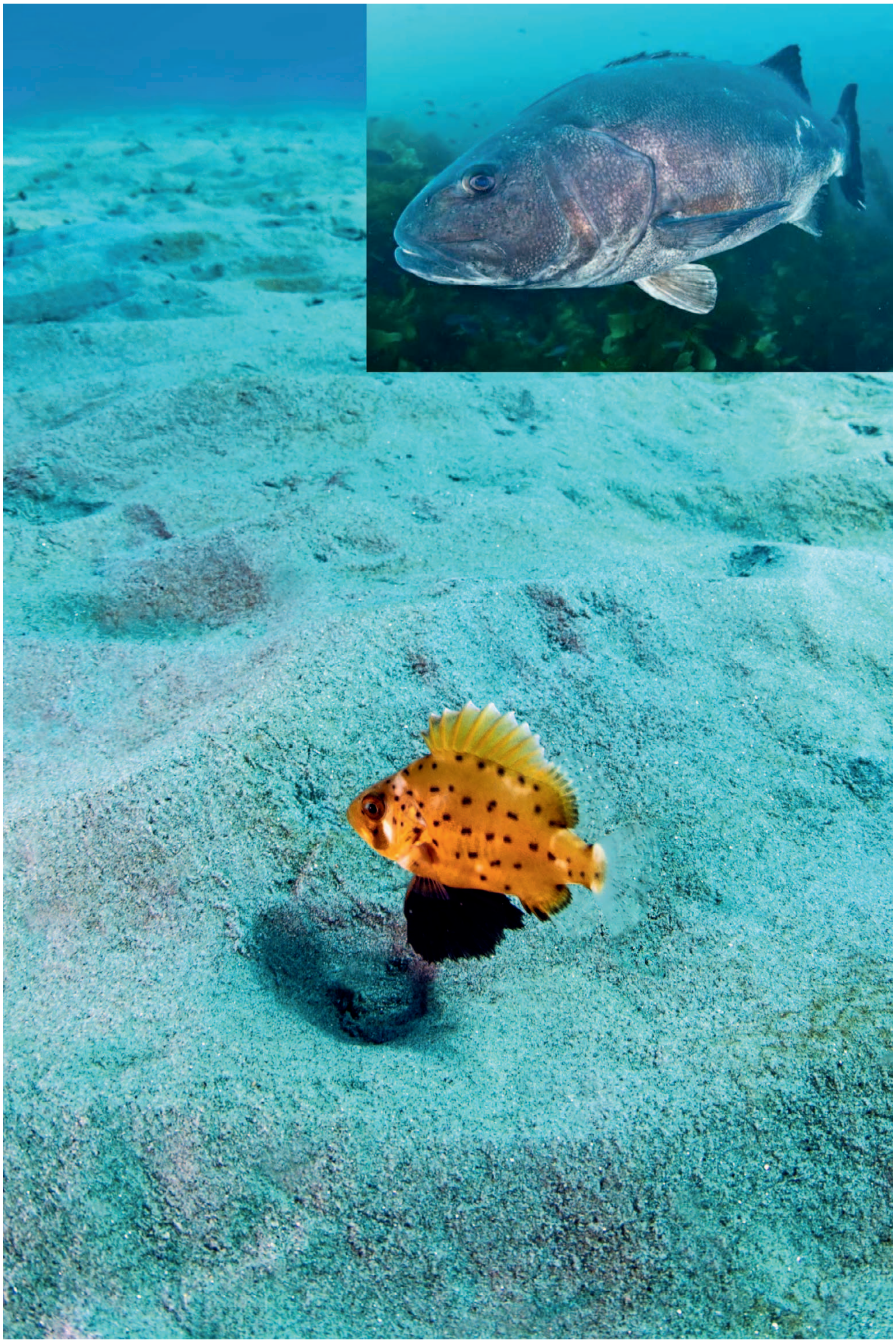

Fig. 1. A YOY Giant Sea Bass photographed over a typical, nearshore, sandy bottom off the Southern California coast. Inset top: an adult Giant Sea Bass, *Stereolepis gigas,* estimated at 2 m in total length photographed off Catalina Island, California. Photo credit: Mike Couffer.

oviparous, broadcast spawners with planktonic eggs (Crooke, 1992; Moser, 1996). They spawn during the warmer water months (Peres and Klippel, 2003), and recent evidence suggests that they do so in pairs (Clark and Allen, 2018). The larvae remain in the plankton until they transform and recruit to nearshore areas as young-of-the-year (YOY; Love, 2011). Prior to the present study, we knew very little about this species at this early age. Young-of-the-year GSB undergo several morphological changes during the first few months after recruitment and are almost unrecognizable as a GSB (Moser, 1996; Love, 2011). Furthermore, previous to this study, no information existed either on the growth rates in the first year of life or their planktonic larval duration (PLD) that can directly yield inferences into temporal scales of their spawning periods prior to this study. Finally, Shane et al. (1996) provided limited information on larval transformation on GSB reared in captivity, estimating metamorphosis at around 12.4 mm TL, but estimates on daily growth rate in the wild were largely lacking. Because of these gaps of information spanning their first year of life, the goals of this study were to: 1) determine the distribution and recruitment dynamics for YOY GSB populations off Southern California, 2) estimate growth rates based otolith analysis, 3) determine pelagic larval duration (PLD) based on settlement checks in these otoliths, and finally 4) examine the general temporal scale of the GSB spawning period off Southern California in 2014 and 2015.

MATERIALS AND METHODS

Field surveys.—Twenty beaches in Southern California were chosen as potential GSB nursery sites based on the availability of low sloping bottoms off sandy beaches where YOY GSB had been previously reported and photographed. Once the beaches had been surveyed at each of the 20 locations during the preliminary surveys, we chose the five sites that yielded the highest probability of locating these juvenile giants on a regular basis. These five sites all had the prerequisite soft sandy bottoms with little to no rock bottom nearby and usually had some evidence of sand dollar beds in the area. These sites included: Zuma Beach in Malibu (34°1′14.56″N, 118°49′54.01″W); Veterans Park in Redondo (33°50′10.42″N, 118°23′30.06″W); Cabrillo Beach in San Pedro (33°42′27.73″N, 118°16′53.83″W); Big Corona Del Mar State Beach in Newport Bay (33°35′29.70″N, 117°52′30.39″W); and La Jolla shores in San Diego (32°51′19.63″N, 117°15′45.03″W). The Big Corona site was moved up the shore to the Newport Beach Pier (33°36′26.63″N, 117°55′54.80″W) after early investigation yielded higher abundances directly ashore of the head of the Newport Submarine Canyon. During the last year of data collection, we focused only on the two sites off Veterans Park in Redondo Beach and the Newport Pier in Newport Beach, California.

A total of 150 surveys were conducted from July 2013 through September 2016. SCUBA transects were conducted every one to three weeks at rotating locations as weather and conditions allowed. Transects were run along isobaths at various depths, ranging from 2–18 meters, with depths being randomly chosen for typically three, 100-meter transects at relatively “shallow” (2–5 m), “mid” (6–8 m), and “deep” (8–10 m) strata. SCUBA transects consisted of two divers swimming 2 meters apart recording individuals seen within approximately 2 meters on each side of the diver covering 400 m^2 each. GoPro© Hero3 video cameras recorded each of the SCUBA transects. These video records were later analyzed in the lab and used to estimate YOY abundance and distribution. Sizes were estimated using a metric ruler in the field and/or compared to known measurements recorded on the GoPro© camera. In addition to intensively surveying submarine canyon sites, we also surveyed the immediate areas (within 2 km) north and south of each of the canyon locations measuring the distance from the closest head of these submarine canyons. GPS coordinates were taken for 75 individual YOY whose locations could be determined with the use of Google Earth. Depth at which each fish was sighted was also recorded.

Determination of growth rates.—Thirty individuals were collected for growth rate analysis. Fourteen individuals were collected by hand net during SCUBA surveys from off Newport Beach and 16 from Redondo Beach. Two more were taken by trawl net off the Palos Verdes peninsula plus one each from off the coast of Santa Barbara and in Los Angeles Harbor. Specimens were placed on ice for euthanization. In the laboratory, each fish was weighed, measured, and photographed before dissection. The sagittal otoliths were then removed as described in Craig et al. (1999). Otoliths were weighed to the nearest 0.001 gram, length measured from the longest axis parallel to the sulcus, and width measured from the widest point perpendicular to the sulcus. Otoliths were mounted on slides sanded first with 3M® Wet/Dry 500 grit sandpaper, then 3M® Wet/Dry 1000 grit, and finally polished with Fandeli® 1500 grit sandpaper. When available we compared both the left and right otolith to ensure consistency in reads between the two respective otoliths. After polishing, these were photographed at 100x under oil immersion using an Olympus BX51 compound microscope. Twenty-three otoliths were judged readable. The images were then analyzed using ImageJ software (Schneider et al., 2012). A line was drawn from the center of the nucleus of each otolith to the outermost edge to ensure the accuracy of the ring count. Thereafter, the image under the line was processed and plotted in a grayscale XY plot. By counting the number of distinct valleys in the grayscale plot, we were able to establish an age (in days) for each individual collected. Planktonic Larval Duration (PLD) was determined by counting the number of daily rings out to the settlement check (where the first obvious differentiation in width occurred). This band represents the time of settlement from the plankton that is accompanied by a drastic change in temperature, or a significant change in diet. We added four days to the settlement count for each otolith to account for the two days to hatching plus two days until yolk absorption and first feeding (Cordes and Allen, 1997).

RESULTS

Only 160 YOY GSB were sighted in 150 transects covering the three-year period (Figs. 1, 2). Among these YOY, three distinct color phases were observed; black, brown, and orange. The black phase follows the planktonic phase and is the smallest of the three phases, occurring just after the larval stage ranging in size from 10–21 mm TL (Fig. 2A). In this phase the body is round with short snout, and the laterally compressed body has a faint lateral line running the length of the body. There are also a number of white blotches surrounding the face and a few scattered blotches down the body. The pectorals, anal, and rounded caudal fin are transparent; the dorsal fin fades from black to dark brown out onto the fin, and the enlarged pelvic fins are solid black. The brown phase is slightly larger ranging from 23–33 mm TL (Fig. 2B) and is similar in shape to the black phase. The white blotches remain around the face and body, and black spots that vary in pattern can now be seen sporadically covering the body, with the background color changing to dark brown. The pectorals, anal, and caudal fin remain transparent, as does the dorsal fin fading from black to dark brown, and the pelvic fins remain enlarged and a solid black. The largest of the three YOY phases is the orange phase with fish ranging in size from 41–185 mm TL (Fig. 2C). It has a similar body shape to the two previous phases, maintaining the very round body shape as it grows in length. The body of the fish varies from bright orange to reddish in color, with the white and black spots remaining. The transparent fins begin to fill in with a color matching the rest of the body, in a slow and systematic fashion.

Despite the fact that we conducted surveys throughout all months of 2014, the YOY GSB were only found from July through February, with peak abundances occurring in the late summer months from August through October (Fig. 3). The presence of the smallest, black phase indicated that settlement occurred multiple times roughly about one month apart throughout the summer and fall months of

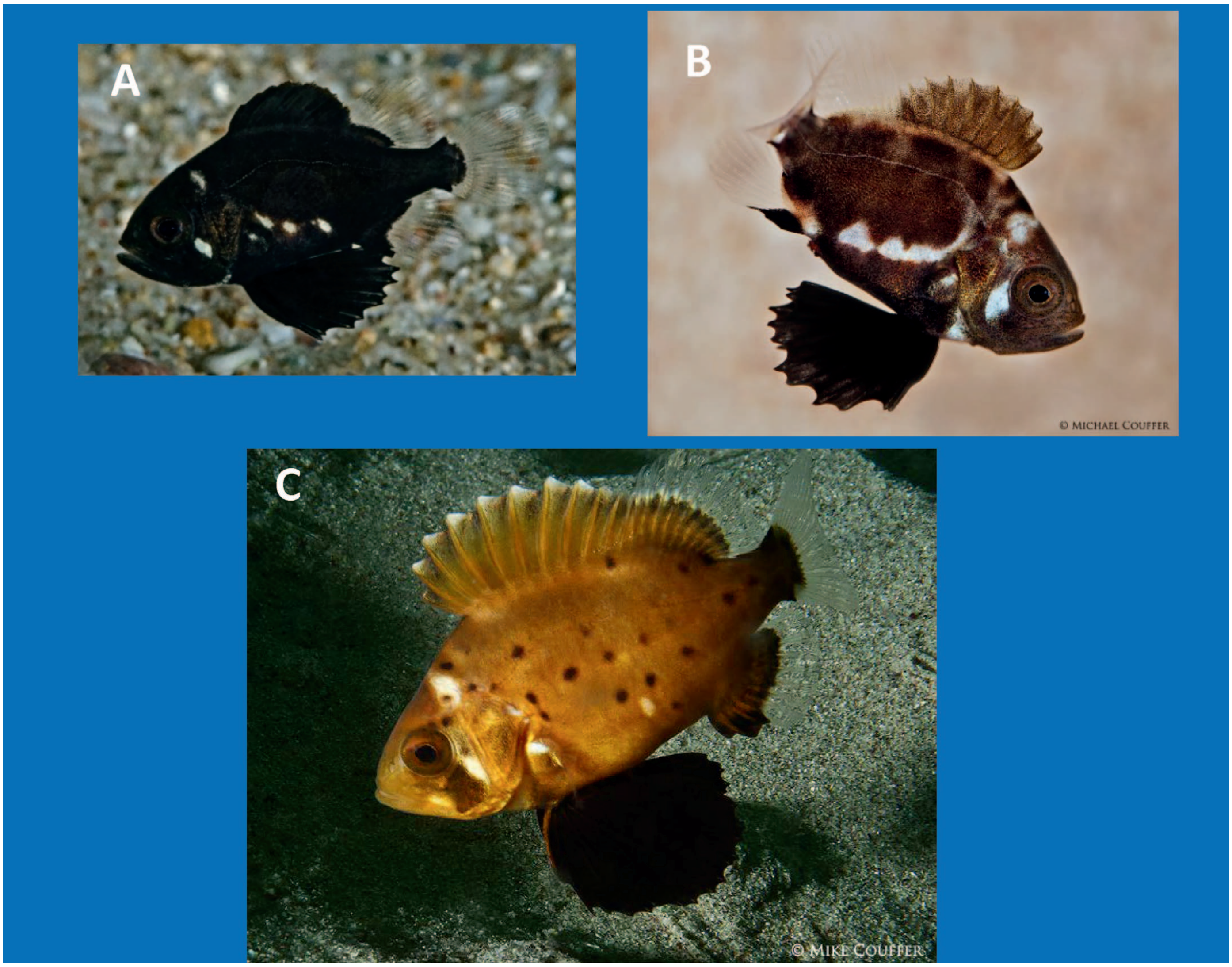

Fig. 2. (A) Photograph of a young-of-the-year Giant Sea Bass in the black phase that ranged from 10–21 mm in total length. (B) Brown phase that ranged in size from 23–33 mm TL. (C) Orange phase that ranged in size from 41–186 mm TL. Photo credit: Mike Couffer.

both 2014 and 2015, thus extending the possible spawning times for GSB from June through October, at least during the years of our study.

Distribution.—Young-of-the-year GSB were found at six of the original 20 survey sites. In the 2014–2015 surveys, densities of YOY GSB were significantly higher (Kruskal-Wallis test: $H_{19,350} = 31.3$; $P = 0.04$) at the six sandy beach locations nearest the heads of submarine canyons (Fig. 4). The highest densities of YOY GSB were found at Redondo Beach (#40/ha), followed by Newport Beach (#33/ha) and La Jolla (#33/ha) off Southern California (Fig. 5). Geographically, YOY GSB were distributed exclusively along the coast where the 100 m depth contour line comes closest to shore where the heads of underwater canyons ended abruptly at shallow sandy beach ecosystems (Fig. 5). In fact, the large majority of the occurrences (73%) of YOY GSB were within 500 m of the submarine canyon heads (Fig. 6).

We found YOY GSB throughout the survey area at depths from 2 m to almost 10 m. The smallest black YOY were found throughout this depth range; however, the largest, orange individuals were almost exclusively in the 6 to 10 m depth range. Overall, size of the YOY GSB was significantly correlated ($r = 0.40$, df $= 155$, $P < 0.001$) to depth in this shallow sand riffle zone (Fig. 7).

Growth rates and PLD.—Based on daily ring counts, total length (mm TL) and age (d) for YOY GSB ($n = 23$) were significantly correlated ($r = 0.95$, df $= 22$, $P < 0.0001$) and best described by the following linear equation for length-at-age: $y = 1.23x - 18.49$ ($R^2 = 0.91$), where $x =$ age (d) and $y =$ length (mm TL; Fig. 8). The length-at-age slope predicts a growth rate of 1.23 mm/day. The collected YOY GSB ($n = 23$) ranged from 31 to 84 days old. Planktonic larval duration was calculated to be 26.8 ± 2.4 days based on the presence of the first settlement check. We estimated the size at settlement to be 14.4 ± 3.0 mm TL (10.6 ± 2.5 mm standard length [SL]).

DISCUSSION

Young-of-the-year GSB were relatively rare and recruitment restricted to relatively few areas. The occurrence of these YOY along the Southern Californian coast in 2014–2015 corresponded strongly with the presence of submarine canyons, suggesting that the presence of submarine canyons may increase recruitment success in Giant Sea Bass. The soft sandy benthos inshore of these underwater canyon areas represent

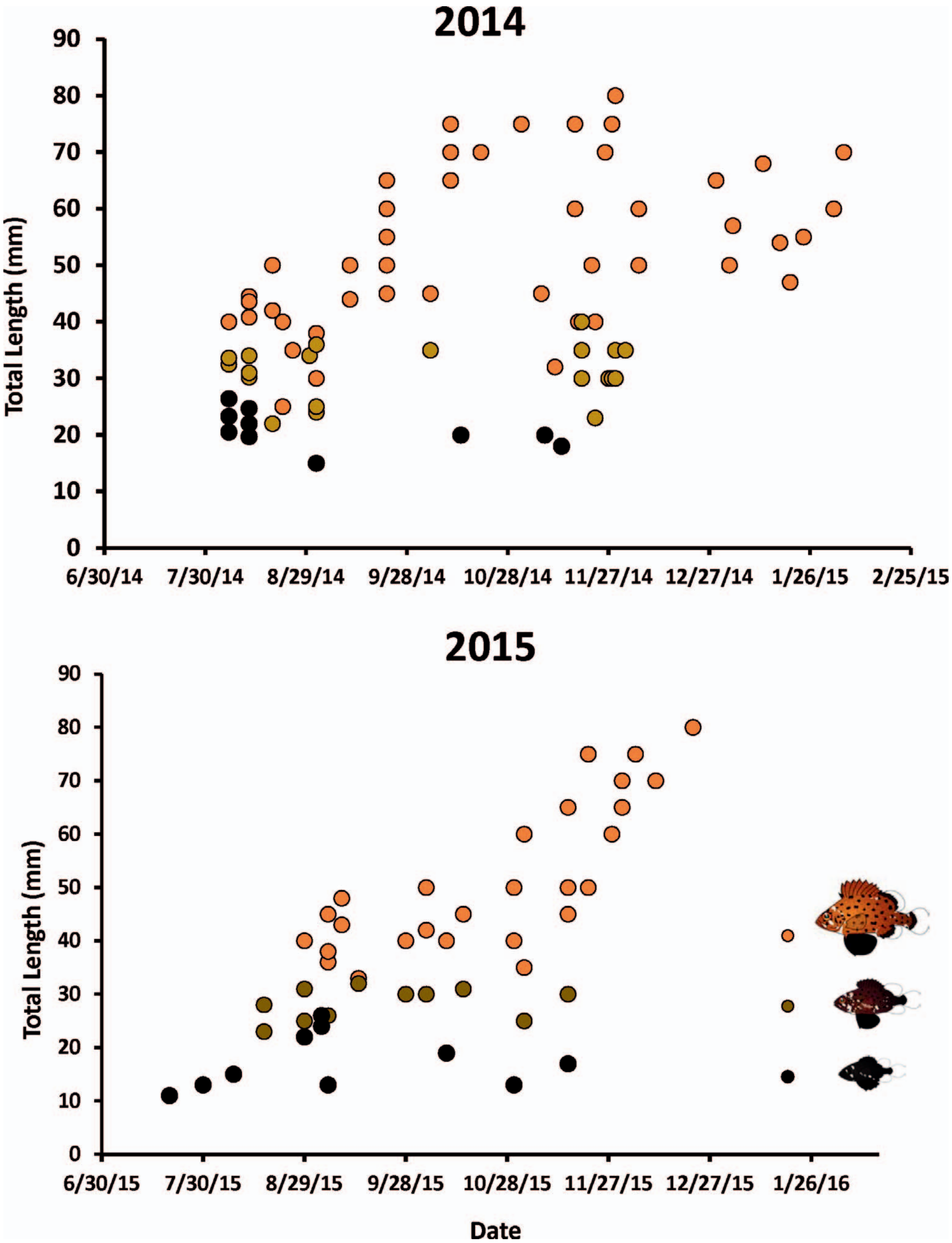

Fig. 3. The size (mm TL) and color phase of young-of-the-year *Stereolepis gigas* observed by date in surveys conducted in 2014 (top) and 2015 (bottom).

successful nursery grounds for GSB. This may be because sandy benthos areas, in general, contain a high abundance of food (Dahl, 1952) and are relatively devoid of predators (McLachlan, 1990), especially when compared to nearby kelp forests and rocky reefs. Furthermore, submarine canyons typically support high abundance of organisms due to the internal waves and alongshore currents causing upwelling from the canyon, providing cold nutrient rich waters that increase primary productivity (Shea and Broenkow, 1982; Pai et al., 2016). Because these nutrients increase the mean biomass of algal primary producers and, in turn, primary consumers, including mysids, these areas provide ample resources for secondary consumers such as recruiting GSB. Those same internal waves and currents that bring nutrients could also facilitate the dispersal of the YOY GSB by channeling the late larvae up to the head of the canyon and the surrounding shallow sandy beach areas where they settle.

YOY GSB grew quickly in their first few months of life compared to other nearshore, predatory fishes off Southern California that settle in relatively shallow and warm habitats. The growth rate of 1.23 mm/d found in the current study is high compared to those previously found for California Halibut (*Paralichthys californicus*) at 0.85 mm/d (Allen, 1988), White Sea Bass (*Atractoscion nobilis*) at 0.35 mm/d (Donohoe, 1997), and Kelp Bass (*Paralabrax clathratus*) at 0.41 mm/d (Findlay and Allen, 2002). On the other hand, the sand basses, Barred Sand Bass (*P. nebulifer*) and Spotted Sand Bass (*P. maculatofasciatus*), have comparable, higher YOY growth rates than GSB at 1.28 and 1.13 mm/d (Allen and Block, 2012).

Planktonic larval duration, age, and size at settlement for the YOY GSB found in the current study were remarkably similar to those estimated for the aforementioned sea basses. Like GSB, all three species of *Paralabrax* are summer spawners and have a PLD of approximately one lunar month (28 d), with size at settlement centered on 10 mm SL. Interestingly,

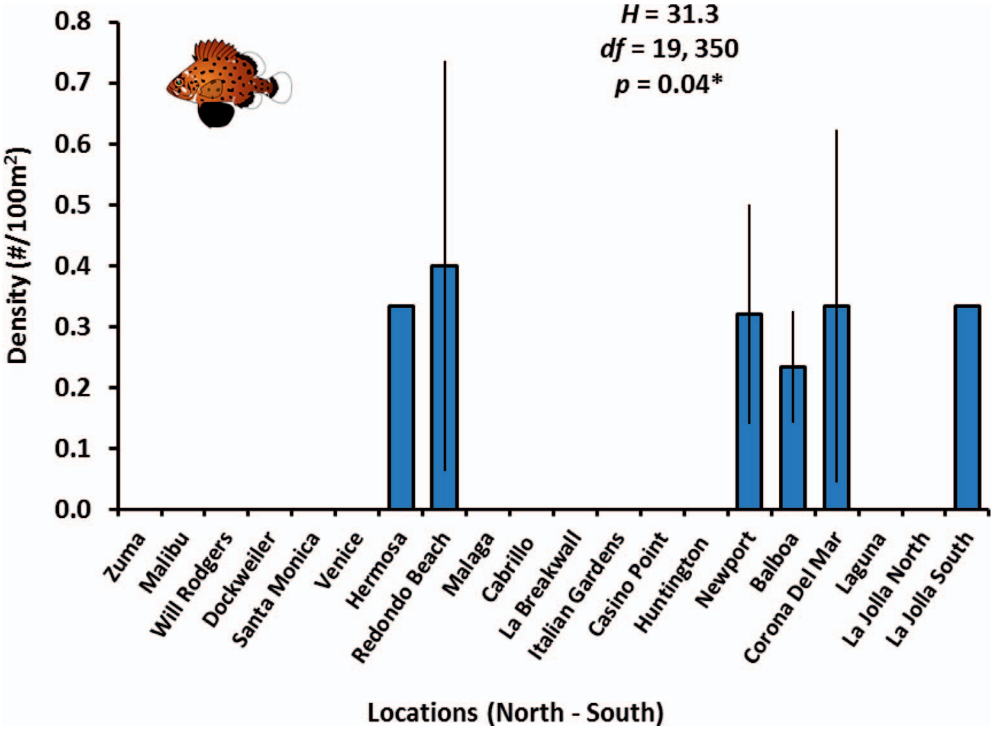

Fig. 4. The mean density (number of individuals/m^2 ± 1 SD) found in transects by location of the GSB from north to south in the Southern California Bight from 2013 to 2015. Densities at the non-zero locations were indistinguishable from one another statistically.

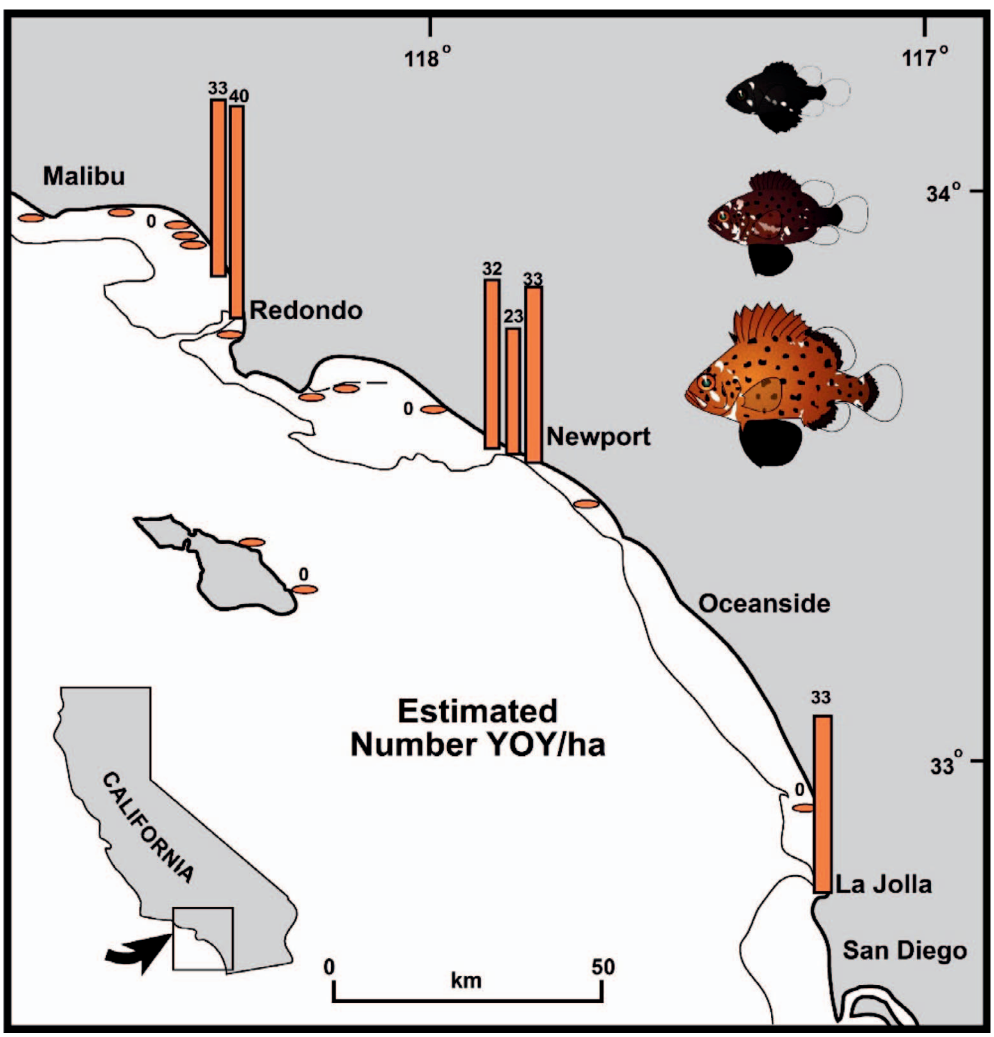

Fig. 5. Distribution map of young-of-the-year GSB observed off Southern California. The bars represent the densities of individuals seen (# per ha). Ovals represents sites surveyed which had zero sightings. The line represents the depth contour line where submarine canyons meet shallow sandy beach areas.

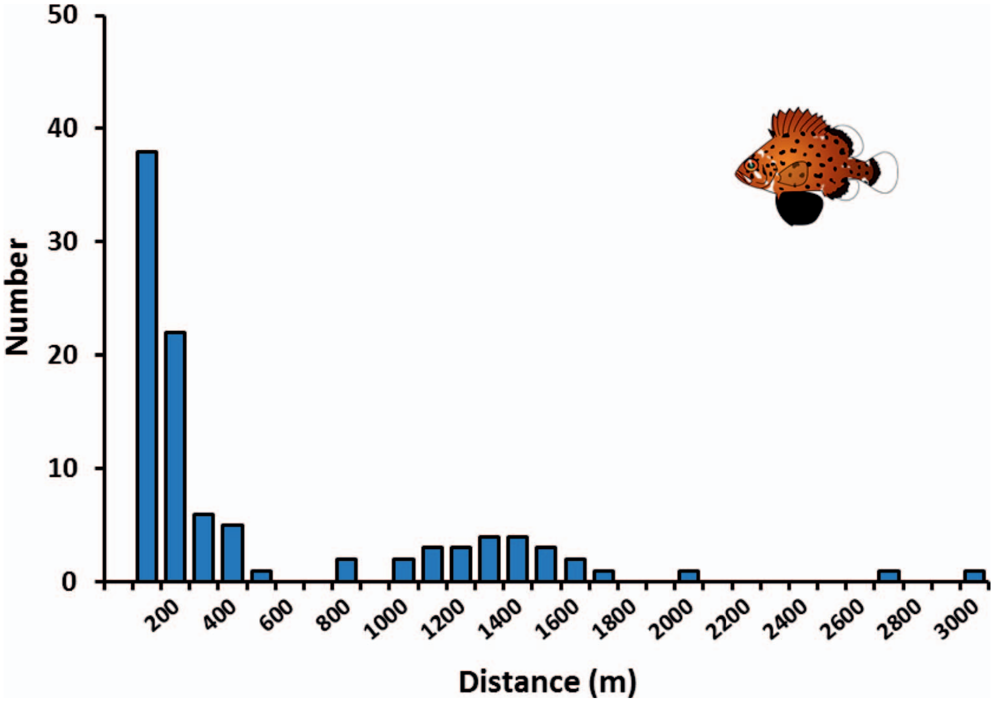

Fig. 6. Numbers of individual YOY GSB observed and their estimated distance (m) from the head of a submarine canyon off the coast of Southern California.

two additional economically important, broadcast spawning fishes from Southern California also have a PLD at or near the lunar month and similar sizes at settlement. The PLD and size at settlement for California Halibut (*Paralichthys californicus*) were estimated at 28 d and 10.6 mm SL (Sears-Hartley, 1994), while those of White Seabass (*Atractoscion nobilis*) were found to be 29 d and 6–9 mm SL, respectively (Donohoe, 1997).

Moreover, our findings regarding PLD of YOY GSB hindcast the adult population spawning from July through November, which extends the season cited in Crooke (1992). We conducted our study during the 2014–2015 El Niño period that produced unseasonably warm weather and water surface temperatures. An increase in the surface temperature would predictably cause an increase in the metabolic rate, directly increasing the growth rates (Mosegaard et al., 1988). We observed recruitment well into November, since the waters remained warmer, and spawning might have occurred later in the year. Therefore, the temporal scale of the spawning period could exhibit a longer duration during an El Niño year.

The discovery of the temporal scale of the PLD is vital for inferences on their spawning periods, without having to be present in the water to confirm mating, since this can be ineffective, inefficient, and time consuming. Based on the age of these individuals we can estimate the duration of the mating periods, which until now have only been speculated on through aggregation sightings. Clark and Allen (2018)

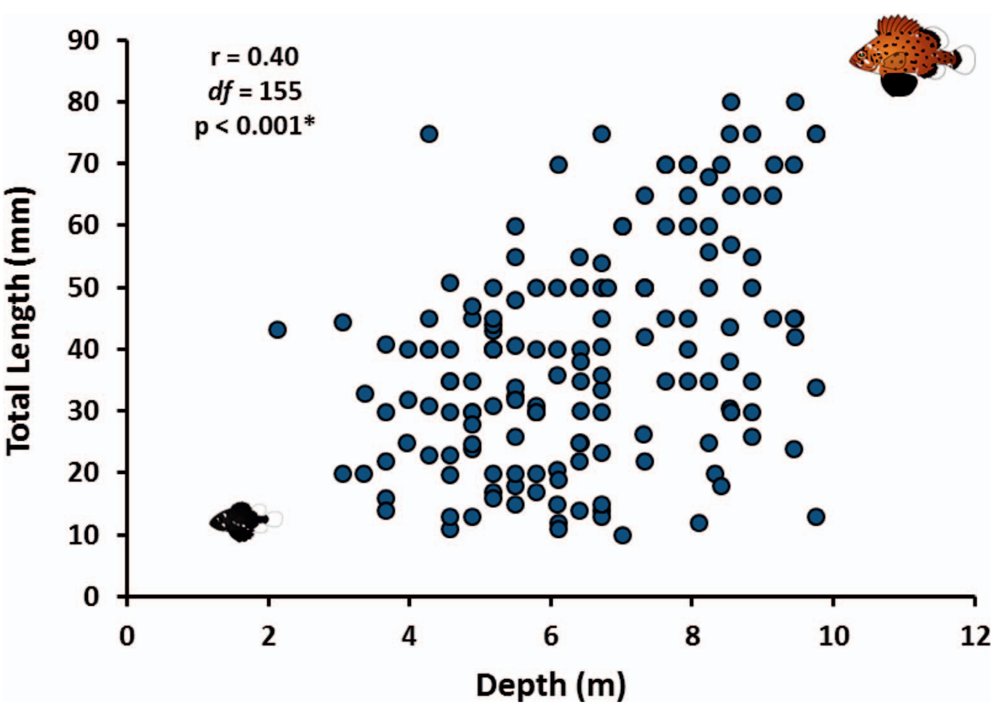

Fig. 7. Total length (mm) of the YOY GSB individuals observed by depth (m) of occurrence from 2013–2016.

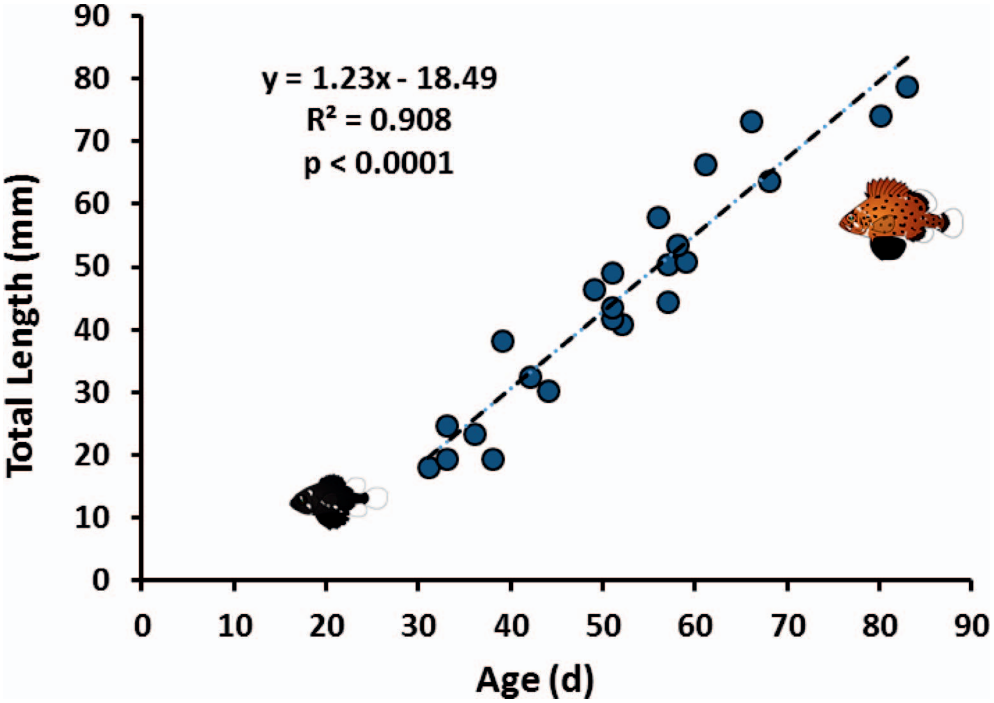

Fig. 8. Observed age in days at total length (mm) for *Stereolepis gigas* ($n = 23$) taken from Southern California based on daily ring counts.

documented that mating occurs primarily in the summer months, but our data suggest that some degree of spawning was occurring later than previously thought during both 2014 and 2015.

Population estimates and other early life history information are essential to aid in the recovery of any overfished species. The potential management of the fishery needs to have as much detailed information as possible to properly asses the current and future populations. These estimates can help inform policy makers about predicted populations and, therefore, whether or not the current catch allowance is sustainable. Direct effects of fishing can alter community compositions that can be detected, but the indirect effects of fishing on marine communities can take decades to determine (Estes et al., 2001; Daan et al., 2005; Babcock et al., 2010).

If the nursery area of a species is found to be limited or endangered by development, future populations may be at risk compared to a species that recruits more broadly. Obviously, the future population of GSB will be dependent on the survival of their YOY that are, in turn, reliant on these sandy beach areas adjacent to submarine canyons. Occasionally for human recreational purposes, sandy beaches are replenished in these areas using sediment dredged up from these submarine canyons (Mike Couffer, pers. comm.). These sand replenishment events might have a deleterious impact on the recruitment success of the YOY of GSB. Protecting these nursery areas may be a key component to help manage future GSB populations.

Knowledge of early developmental processes and recruitment patterns are crucial not only to our understanding of the completion of the life history for any species but also allows us to make increasingly intelligent decisions about current fisheries management policies and future conservation efforts. Our study is the first of its kind to examine the YOY of this endangered species (Cornish, 2004). For the first time, this study was able to identify the nursery habitat, recruitment patterns, the PLD, and growth rate of the young-of-the-year of Giant Sea Bass, *Stereolepis gigas,* off Southern California, thereby adding to the baseline of life history information for this endangered and understudied species.

ACKNOWLEDGMENTS

We give special thanks to Mike Couffer (Grey Owl Pictures, Inc., Corona del Mar, CA) for the many hours he spent underwater assisting with observations and surveys. We also extend our gratitude to Richard Yan for countless hours of otolith work. Mark Steele and Mike Franklin provided facilities and guidance throughout the project. Todd Anderson and Milton Love both provided valuable comments on an earlier draft of this paper. The PADI Foundation, the International Women's Fishing Association, the Office of Graduate Studies, and the Nearshore Marine Fish Research Program (NMFRP), Department of Biology, California State University Northridge all supported this research. All collecting and handling of the animals followed CSUN's Animal Care Protocol, and specimens were collected under California State Fish and Wildlife Collecting Permit #13028.

LITERATURE CITED

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay-Long Beach Harbor, 1983–1985. Bulletin of the Southern California Academy of Sciences 87:19–30.

Allen, L. G., and A. H. Andrews. 2012. Bomb radiocarbon dating and estimated longevity of Giant Sea Bass (*Stereolepis gigas*). Bulletin of the Southern California Academy of Sciences 111:1–14.

Allen, L. G., and H. E. Block. 2012. Planktonic larval duration, settlement, and growth rates of the young-of-the-year of two sand basses (*Paralabrax nebulifer* and *P. maculatofasciatus*: fam. Serranidae) from Southern California. Bulletin of the Southern California Academy of Sciences 111:15–21.

Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences of the United States of America 107:18256–18261.

Baldwin, D. S., and A. Keiser. 2008. Giant sea bass, *Stereolepis gigas*. Status of the Fisheries Report, California Department of Fish and Game.

Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78:699–714.

Cailliet, G. M., M. S. Love, and A. W. Ebeling. 1996. Fishes: Their Structure, Identification and Natural History. Waveland Press, Long Grove, Illinois.

Chabot, C. L., H. W. Hawk, and L. G. Allen. 2015. Low contemporary effective population size detected in the Critically Endangered Giant Sea Bass, *Stereolepis gigas*, due to fisheries overexploitation. Fisheries Research 172:71–78.

Clark, B. L. F., and L. G. Allen. 2018. Courtship behavior of the Giant Sea Bass, *Stereolepis gigas*. Copeia 106:171–179.

Cordes, J. F., and L. G. Allen. 1997. Estimates of age, growth, and settlement from otoliths of young-of-the-year Kelp Bass (*Paralabrax clathratus*). Bulletin of the Southern California Academy of Sciences 96:43–60.

Cornish, A. (Grouper & Wrasse Specialist Group). 2004. *Stereolepis gigas*. The IUCN Red List of Threatened Species. www.iucnredlist.org

Craig, M. T., D. J. Pondella, II, and J. C. Hafner. 1999. Analysis of age and growth in two eastern Pacific groupers (Serranidae: Epinephelinae). Bulletin of Marine Science 65: 807–814.

Crooke, S. J. 1992. History of giant sea bass fishery, p. 153–157. *In:* California's Marine Resources and Their Utilization. W. S. Leet, C. M. Dewees, and C. W. Haugen (eds.). California Sea Grant Extension Publication UCSGEP-92-12, Sea Grant Extension Program, Department of Wildlife and Fisheries Biology, University of California, Davis, California.

Daan, N., H. Gislason, J. G. Pope, and J. C. Rice. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science: Journal du Conseil 62:177–188.

Dahl, E. 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4:1–27.

Domeier, M. L. 2001. Giant sea bass, p. 201–211. *In:* California's Living Marine Resources: A Status Report. W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson (eds.). California Department of Fish and Game, Sacramento, California.

Donohoe, C. J. 1997. Age, growth, distribution, and food habits of recently settled white seabass, *Atractoscion nobilis*, off San Diego, California. Fishery Bulletin 95:709–721.

Estes, J. A., K. Crooks, and R. Holt. 2001. Predators, ecological role of, p. 857–878. *In*: Encyclopedia of Biodiversity. Vol. 4. S. Levin (ed.). Academic Press, San Diego, California.

Findlay, A. M., and L. G. Allen. 2002. Settlement patterns of a temperate reef fish, the kelp bass (*Paralabrax clathratus*), at Santa Catalina Island, CA. Marine Ecology Progress Series 238:237–248.

Fitch, J. E., and R. N. Lavenberg. 1971. Marine Food and Game Fishes of California. California Natural History Guides: 28. University of California Press, Berkeley, California.

Hawk, H., and L. G. Allen. 2014. Age and growth of the Giant Sea Bass, *Stereolepis gigas*. CalCOFI Report 55:128–134.

Holder, C. F. 1910. The Channel Islands of California: A Book for the Angler, Sportsman, and Tourist. A.C. McClurg and Co., Chicago.

House, P. H., B. L. F. Clark, and L. G. Allen. 2016. The return of the king of the kelp forest: distribution, abundance, and biomass of Giant Sea Bass (*Stereolepis gigas*) off Santa Catalina Island, California, 2014–2015. Bulletin of the Southern California Academy of Sciences 115:1–14.

King, J. R., and G. A. McFarlane. 2003. Marine fish life history strategies: applications to fishery management. Fisheries Management and Ecology 10:249–264.

Love, M. S. 2011. Certainly More Than You Want to Know about the Fishes of the Pacific Coast: A Postmodern Experience. Really Big Press, Santa Barbara, California.

McLachlan, A. 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. Journal of Coastal Research 6:57–71.

Miller, D. J., and R. N. Lea. 1972. Guide to coastal marine fishes of California. California Department of Fish and Game, Fish Bulletin 157:1–235.

Mosegaard, H., H. Svedang, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Canadian Journal of Fisheries and Aquatic Sciences 45:1514–1524.

Moser, H. G. (Ed.). 1996. The Early Stages of Fishes in the California Current Region. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33, Allen Press Inc., Lawrence, Kansas.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280–283.

Pai, S.-C., C.-L. Wei, S. Lin, L.-S. Wen, and C.-M. Tseng. 2016. Observation of internal tide-induced nutrient upwelling in Hungtsai Trough, a submarine canyon in the northern South China Sea. Continental Shelf Research 120:59–67.

Peres, M. B., and S. Klippel. 2003. Reproductive biology of southwestern Atlantic wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae). Environmental Biology of Fishes 68:163–173.

Pondella, D. J., II, and L. G. Allen. 2008. The decline and recovery of four predatory fishes from the Southern California Bight. Marine Biology 154:307–313.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Sears-Hartley, J. 1994. Age, growth, and early life history of *Paralichthys californicus* derived from otolith microstructure. Unpubl. Master's thesis, California State University, Northridge, California.

Shane, M. A., W. Watson, and H. G. Moser. 1996. Polyprionidae: Giant sea basses and wreckfishes, p. 873–875. *In:* The Early Stages of Fishes in the California Current Region. H. G. Moser (ed.). California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33, Allen Press Inc., Lawrence, Kansas.

Shea, R. E., and W. W. Broenkow. 1982. The role of internal tides in the nutrient enrichment of Monterey Bay, California. Estuarine Coastal Shelf Science 15:57–66.