RESEARCH ARTICLE

Age Determination and Body Length Relationship of Two-Spot Red Snapper (*Lutjanus bohar*)

Maybelle A. Fortaleza • Cleto L. Nañola Jr. ✉
University of the Philippines Mindanao, PHILIPPINES

Abstract

Otolith study on fifty two-spot red snappers (*Lutjanus bohar*) in Davao Gulf, Philippines, was conducted to describe their growth pattern, determine the age structure, and estimate their age at sexual maturity. Fish samples were obtained from Toril and Bankerohan Public Markets in Davao City from February to June 2015 where fish morphometrics, otolith extraction, and age determination followed. Length-weight relationship showed that *L. bohar* follows isometric growth pattern (b = 3.0015). Somatic and otolith morphometrics gave significant correlations where otolith length and total length relationship had the highest R^2 value (R^2 = 0.9382). Out of fifty fish samples, twenty-one of the sagittal otoliths had ages ranging from three to seven years old. The parameters obtained from the age-at-length data fitted to von Bertalanffy growth function were K = 0.81 and L_∞ = 28.9 cm, with an estimated age at maturity of six years old. The growth performance index (φ = 2.83) also revealed that *L. bohar* in Davao Gulf has faster growth rate compared to other locations. Faster growth rate leading to earlier maturity and smaller size-at-maturity may indicate the compounded effects of environmental factors and fishing pressure to slow-growing fishes. Thus, we recommend studying the population ecology of *L. bohar* in Davao Gulf and considering a larger sample size in future researches.

Keywords: age • growth • length-weight relationships • Lutjanidae • *Lutjanus bohar* • otolith • two-spot red snapper

Correspondence: CL Nañola Jr. Department of Biological Sciences and Environmental Studies, College of Science and Mathematics, University of the Philippines Mindanao, Mintal, Tugbok District, Davao City 8022, Philippines. Telephone: +63 82 293 0302. Email: clnanola1@up.edu.ph

Author Contribution: MAF conceptualized the study, gathered and analyzed the data, and wrote and revised the submitted paper. CLN provided supervision during the conduct of the study, acquired funding and provided resources, and wrote and revised the submitted paper.

Editor: Eufemio T. Rasco, Academician, National Academy of Science and Technology, PHILIPPINES

Received: 26 March 2016 **Accepted:** 15 December 2016 **Published:** 10 May 2017

Funding Source: Partial funding support from the Department of Environment and Natural Resources – Biodiversity Management Bureau (DENR-BMB) under the National Coral Reef Visualization and Assessment (CoRVA) Program and the "Sustainable Development of the Philippine Tuna Value Chain" research program of the Higher Education Regional Research Center (HERRC)–University of the Philippines Mindanao funded by the Commission on Higher Education (CHED).

Competing Interest: The authors have declared no competing interest.

Citation: Fortaleza MA, Nañola Jr. CL. 2017. Age determination and body length relationship of two-spot red snapper (*Lutjanus bohar*). Banwa B. 12:res003.

Age Determination and Body Length Relationship of Two-Spot Red Snapper (*Lutjanus bohar*)

Maybelle A. Fortaleza • Cleto L. Nañola Jr.
University of the Philippines Mindanao

Introduction

Reef fishes are found to be abundant in the tropical region with the highest biodiversity concentration at the Coral Triangle (Carpenter and Springer 2005). Among these reef fishes that have both ecological and economic significance is the family of tropical snappers or the family Lutjanidae. These tropical snappers are important in the trophic ecology as crepuscular predators (Moyle and Cech 2000). Nelson (1994) described the family Lutjanidae as having more than 125 species with five subfamilies. They are highly abundant in the Indo-Pacific region (Allen 1985; Wright et al. 1986) and are harvested in different quantities (Marriott and Mapstone 2006).

The species of interest, the two-spot red snapper (*Lutjanus bohar*) belongs to the subfamily Lutjaninae, the largest among other subfamilies (Morallana 2013). It is a long-lived reef fish reaching around 60 cm in terms of fork length (L_F) and has a maximum estimated age of more than fifty-five years old (Marriott et al. 2007). The slow-growing and late-maturing nature of *L. bohar* identifies them to have a K-selected life history (Marriot et al. 2007), which makes them vulnerable to overfishing (Morallana 2013). To date, *L. bohar* remains unevaluated in relation to exploitation level while the other representative species under family Lutjanidae were already classified as vulnerable (IUCN 2015).

Age-based studies are used to investigate the life history of reef fishes (Choat and Robertson 2002), and these are necessary in ameliorating stock assessments (Grandcourt 2005). As fishing can greatly influence reef fish ecology, studying the life history traits of reef fishes can help determine how they respond to such exploitation (Jennings et al. 1999; Jennings et al. 2001). One of the many ways to conduct an age-based study on fishes is through otolith science (Thorrold and Hare 2002; Miller et al. 2010).

Otoliths are hard structures made of calcium carbonate, which are embedded in a proteinaceous matrix (Victor 1982; Jobling 1995). These so-called "ear stones" are responsible for sound reception and balance (Campana 2004; Rodriguez Mendoza 2006). Unlike other calcified structures (e.g., scales and bones), otoliths lack resorption—i.e., the minerals deposited in it are not utilized even during starvation periods (Thorrold and Hare 2002; Rodriguez Mendoza 2006). For most teleosts, otoliths come in three sets, namely, sagitta, astersicus, and lapillus (Miller and Simenstad 1994; Cailliet et al. 2001), and the largest and most commonly used among the three is the sagittal otolith (Miller and Simenstad 1994; Choat and Robertson 2002; McBride et al. 2010). Periodic growth increments pertain to the concentric rings found in the otolith microstructure, and these are relatively important for age determination (Campana 2001). The ages of both juvenile and adult reef fishes can be determined based on otolith increments that are deposited daily and/or annually (Fowler 1990).

Age-based studies of *L. bohar* in Kenya (Talbot 1960) and Papua New Guinea (Wright et al. 1986) used scales and length frequency analysis, respectively, to determine its growth parameters. Despite various methods in determining age and growth rates, Campana (2001) emphasized the accuracy in measuring the age of fishes using otoliths, which is also best suited for tropical fish species (Brothers et al. 1975). Loubens (1980) and Marriot et al. (2007) were among those who have conducted otolith studies for *L. bohar* in New Caledonia and Australia, respectively. Given the significant impacts of *L. bohar* in marine ecology and fisheries, it is important to investigate their life history through otolith studies. Hence, this study is directed to determine the age structure and body length relationship of *L. bohar* in the Philippine setting, particularly in the Davao Gulf (Figure 1).

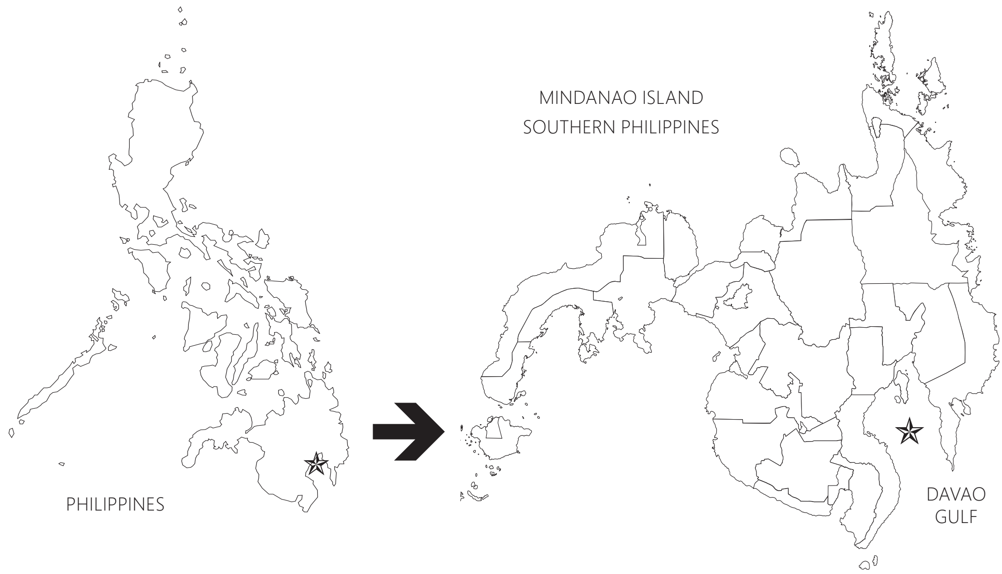

FIGURE 1 Location of the Davao Gulf in Mindanao, Southern Philippines

Materials and Methods

Time and Place of Study

Market surveys were carried out in Bankerohan and Toril Public Markets in Davao City with fifty *L. bohar* individuals collected from February until June 2015. These were favorable months considering that spawning aggregations of *L. bohar* along with other lutjanids in Indo-West Pacific region occurs from mid-May to June (Martinez-Andrade 2003). The market surveys were done from six to eight o'clock in the morning to secure fresh fish samples from traditional catches. According to the market peddlers, most of their catch comprised of lutjanids, lethrinids, and few serranids obtained through spearfishing and use of gill nets. The fish samples were kept in a styrofoam container with ice to preserve their freshness. Labeling and morphometric procedures were performed in the laboratory immediately.

Fish Morphometrics

The total length (L_T) of the fish was measured from the anterior-most part of the fish to the tip of its longest caudal fin ray (Anderson and Neumann 1996). Length measurements were done using a measuring board and the wet weight of the fish samples was determined using a weighing scale. All measurements were expressed in metric scale: centimeter (cm) for the total length and gram (g) for the fish weight.

Otolith Extraction and Morphometrics

Otolith extraction was done following the open-the-hatch method described by Secor et al. (1992). The otolith length (OL) and otolith width (OW) were measured in millimeters using a digital caliper. Otolith length was measured from the rostrum to the postrostrum (Secor et al. 1992) while the otolith width was measured perpendicularly to otolith length (Morales-Nin 1992). The otolith mass (OM) was obtained using a digital weighing scale (ALC210.4 Acculab). All extracted pair of sagittal otoliths were kept in Eppendorf tubes containing 95% ethanol for proper storage.

Otolith Preparation and Reading of Growth Increments

Right sagittal otoliths were used, and if broken, the left ones work as substitute given that the growth rings in either of the two otoliths are the same (Morales-Nin 1992). The mounting and embedding procedure of the otolith was adapted from the method of Robbins and Choat (2002). Right sagittal otoliths were used, grinded, and polished on wet sandpaper (#600 and #1000, respectively). The ground area was checked under the microscope from time to time to avoid overgrinding or hitting the nucleus. Age estimation was done by counting the annual growth increments or the concentric rings that can be observed under the microscope (Miller and Simenstad 1994). Following the age estimation method described by Marriott and Mapstone (2006), otolith increments were identified as opaque bands and counted under scanner objective (Ken-A-Vision). Counting of annual instead of daily growth increments is the preferred age estimation method for long-lived reef fishes like *L. bohar*.

Data Analyses

The relationship between the total length and the fish weight of *L. bohar* was determined using scatter plot graph. The formula $W = aL^b$ was used to determine the length-weight relationship, where a and b are constants determined by linear regressions (Karachle and Stergiou 2012). Anderson and Neumanns's (1996) interpretation of b values were used to describe the pattern of growth of *L. bohar* as either allometric or isometric.

The relationship between fish and otolith morphometrics was interpreted in a scatter plot graph through simple linear regression. Furthermore, the age estimates of *L. bohar* were verified using age and otolith mass relationship where the two variables are expected to be linearly correlated (Robbins and Choat 2002). The von Bertalanffy growth curve of *L. bohar* was obtained using Paleontological Statistics (PAST), where the age-at-length data was fitted to the von Bertalanffy growth function (VBGF) model at 95% level of confidence. The growth performance equation, adapted from Pauly and Munro (1984), was used to compare the data regarding the growth of *L. bohar* gathered in different locations.

Results and Discussion

Of the fifty fish samples collected, twenty-nine were males and twenty-one were females. The predominance of male *L. bohar* individuals is attributed to their spawning behavior where several males would follow a female (Domeier and Colin 1997). Moreover, fishes thriving in warmer water temperature were observed to have approximately 75% males in the brood (Moksness et al. 2008). *L. bohar* is among the favored targets of fishermen in the Philippines and usually harvested with serranids and lethrinids (Russ and Alcala 1989). Spearfishing and the use of gill nets are two of the most common methods used in fishing lutjanids in the Davao Gulf. In the Indian Ocean, *L. bohar* are caught using traps, hooks, and driftnets (Druzhinin 1972), whereas in Papua New Guinea, they are mainly caught using hook-and-line and sometimes with the use of spear or gill nets (Wright et al. 1986).

Length and Weight Relationship

The minimum values observed for the standard length (L_S) and total length (L_T) of *L. bohar* were 10.3 and 13.4 cm, respectively (Table 1). The maximum lengths recorded were 23.8 cm for L_S and 30.4 cm for L_T. Mean L_S is 17.81 cm while the mean L_T is 22.46 cm. The wet

TABLE 1 Summary of the minimum, maximum, and mean values for the fish and otolith morphometrics of *Lutjanus bohar* (n = 50)

Morphometric measurements / Unit	Minimum value	Maximum value	Mean value
Standard length (L_S); cm	10.30	23.80	17.81±3.21
Total length (L_T); cm	13.40	30.40	22.46±4.03
Fish weight (FW); g	42	460	208
Otolith length (OL); mm	6.79	14.13	10.36±1.64
Otolith width (OW); mm	5	10.02	7.43±1.08
Otolith mass (OM); mg	43	379.60	153.20
Otolith age (OA); years	3	7	5.80

weight of the fish samples was observed to range from 42 to 460 g with a mean weight of 208.26 g.

The logarithmic relationship of the L_T and FW has an R^2 value of 0.986 (Figure 2), which means that there is a strong relationship between the body length and weight measurements of *L. bohar*. The computed *a* and *b* values for L_T and FW relationship were 2×10^{-5} and 3.0015, respectively. The obtained *b* value ($b = 3.0015$) indicates that the growth of *L. bohar* is isometric, which means that the same body form is maintained as the fish grows older (Karachle and Stergiou 2012; Renán et al. 2015). The b value may not be necessarily equal to 3 because the disparity of values is associated with habitat, season, and reproductive activity (Alicli et al. 2012) of two-spot red snappers in their environment.

Furthermore, the b value of *L. bohar* in the Davao Gulf (b = 3.0015) is close to the b value presented in the summary of length-weight relationships of New Caledonian lagoon fishes (Kulbicki et al. 2005). *L. bohar* in New Caledonia has a b value of 3.059 and classified as cylindrical in terms of shape. This may denote an isometric growth given that the shape classes were either compressed or elongated if not identified as cylindrical. Isometric growth was also observed in other members of the family Lutjanidae (Table 2). In a study conducted by Renán et al. (2015) in Southern Gulf of Mexico, isometric growth was observed for *L. synagris* (b = 2.634) and *Ocyurus chrysurus* (b = 2.795). Govinda Rao et al. (2014) also reported isometric growth pattern for *L. lutjanus* (b = 3.0113) in Visakhapatnam, middle east coast of India.

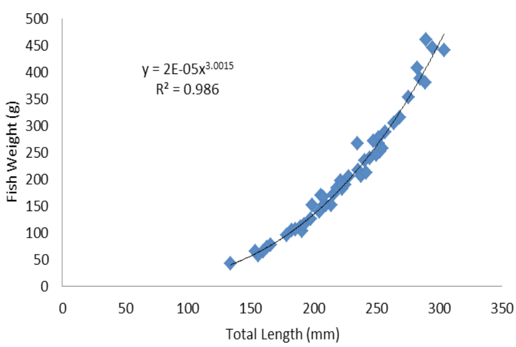

FIGURE 2 Relationship between the total length and fish weight of *Lujtanus bohar*

Relationship of Fish and Otolith Morphometrics

High R^2 values were observed for all fish length and otolith morphometric relationships, denoting strong correlations. Among the otolith measurements, otolith length (OL) showed the strongest relationship to L_T with an R^2 value of 0.9382 (Figure 3a). A significant correlation was also observed for otolith width (OW) (Figure 3b) and otolith mass (OM) (Figure 3c) with R^2 values of 0.9002 and 0.7971, respectively. Waessle et al. (2003) reported that otolith length and otolith mass are good predictors of standard length and fish weight (Corral et al. 2013). The OL showed the highest R^2 value (0.9382) among other otolith measurements, which means that OL is the best predictor of fish size for *L. bohar*.

Otolith Age

The age structure of *L. bohar* is from three to seven years old, with highest age frequency observed among five-year old individuals (n = 6). The otolith microstructure of *L. bohar* is characterized by a series of dark bands after the nuclear region, which are identified as annual increments (Figure 4). The opaque bands were more perceivable from the sulcus and then fainting as it encompasses the sectioned otolith microstructure. Hence, deposition of mineral causes the otolith microstructure to grow more in width (OW) than in length (OL) as the fish grows older. Moreover, the relationship between the age

TABLE 2 Length-weight parameters of other lutjanid species with isometric growth pattern

Lutjanid species	Range of total length (mm)	n	Log a	b	Growth
Lutjanus lutjanus (Govinda Rao et al. 2014)	89–240	526	−4.8635	3.0113	Isometric
Lutjanus synagris (Renán et al. 2015)	185–459	412	−1.3300	2.6340	Isometric
Ocyurus chrysurus (Renán et al. 2015)	244–504	727	−1.7140	2.7950	Isometric

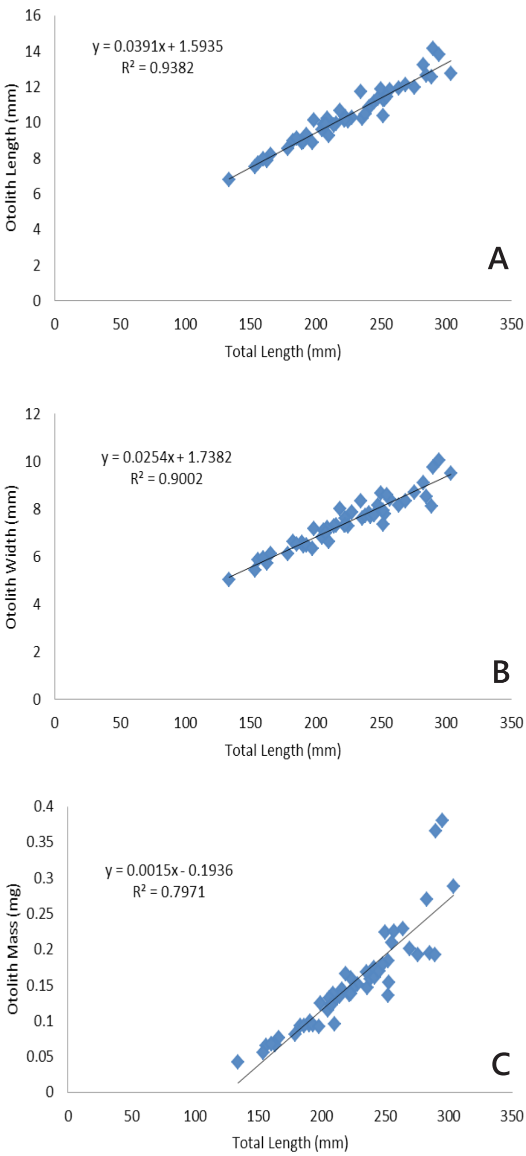

FIGURE 3 (A) Relationship between the total length and otolith length, (B) total length and otolith width, and (C) total length and otolith mass of *Lutjanus bohar* samples

and otolith mass of *L. bohar* revealed a strong correlation with an R^2 value of 0.7903 ($p < 0.0001$) (Figure 5). Although there were only few samples used in age determination, the verification method indicates that the quality of age estimates is acceptable.

Growth and Age-at-Length Data of *Lutjanus bohar*

The growth curve for *L. bohar* collected from the Davao Gulf was determined using the von Bertalanffy growth function (VBGF) fitted at 95% level of confidence (Figure 6). The top and bottom curves represent the upper and lower limits of the 95% confidence interval while the middle curve is the resulting growth curve given by the equation $L_T = 289.3\ (1\text{-}7.157\ e^{(-0.8124x)})$. The steep part of the growth curve, which is from three to four years shows a period of rapid growth. This result coincides with the study conducted by Marriott et al. (2007), where the rapid growth phase of *L. bohar* in the Great Barrier Reef, Australia, was observed between three to five years. As the growth curve approaches the plateau, the energy allocated for growth has shifted towards reproductive purposes (Ross and Biagi 1991). The life stage and existing environmental conditions (Ross and Biagi 1991) such as water temperature (Kausar and Salim 2006) and change in maturation schedules due to fishing pressure (Jennings et al. 1999; Woods et al. 2003) are some of the factors contributing to varying growth periods of fishes. This emphasizes the need to determine the range of maturation schedule.

Comparing the growth parameters of *L. bohar* studied in different locations, it appears that fish collected from the Davao Gulf has smaller average maximum length (L_∞) compared to studies done in New Caledonia and in the

TABLE 3 Comparison on the growth parameters of *Lutjanus bohar* in different locations (Martinez-Andrade 2003; Marriott et al. 2007)

Source	Method	Location	L_∞ (cm)†	K (cm)‡	φ (cm)§	L_m (cm)**
Loubens (1980)	O*	New Caledonia	62.0 L_T	0.11	2.63	34.0
Marriott et al. (2007)	O	Great Barrier Reef, Australia	63.0 L_F	0.10	2.60	24.8
This study (2015)	O	Davao Gulf, Philippines	28.9 L_T	0.81	2.83	20.8

NOTES: *Otolith sections †Average maximum length ‡Asymptotic length §Growth performance **Length at maturity

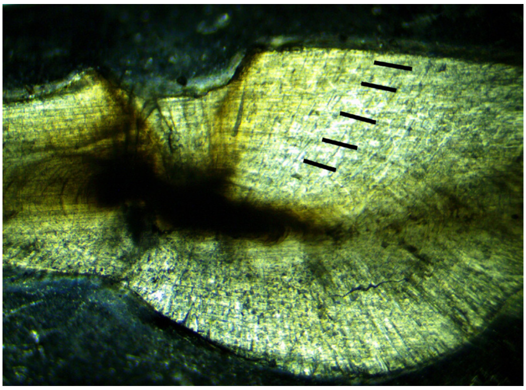

FIGURE 4 Transverse section of a five-year-old *Lutjanus bohar* (L_T = 210 mm) otolith showing the nucleus and alternating opaque and translucent bands

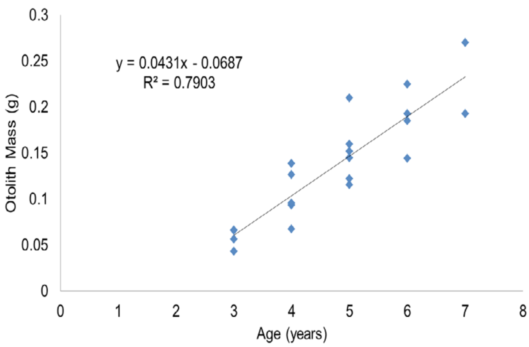

FIGURE 5 Otolith age and mass relationship for *Lutjanus bohar*

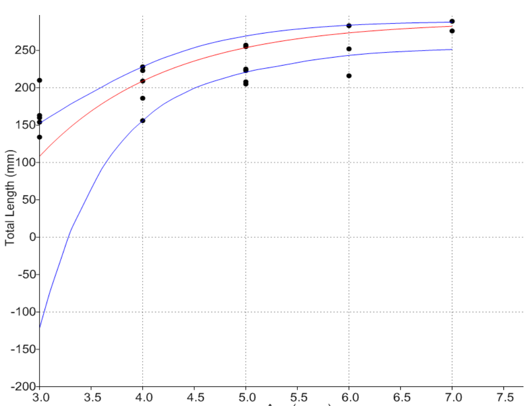

FIGURE 6 Fitted von Bertalanffy growth model of *Lutjanus bohar* collected in Davao Gulf from February to June 2015

Great Barrier Reef, Australia (Table 3). *L. bohar* are bottom-oriented predators (Jobling 1995) and the fishing methods used by local fishermen may be limited as larger and older individuals are found in deeper waters (Martinez-Andrade 2003; Marriott et al. 2007). Marriot et al. (2007) also reported that the *L. bohar* individuals used in their study were obtained through commercial deep fishing and recreational spearfishing; hence, their samples were large and many. Large sizes of *L. bohar* are often feared for ciguatera poisoning (Marriott et al. 2007). As mentioned, the most common fishing methods used to catch this species are spearfishing aided with compressor and gill nets, and these factors may also account for the low number of mature and larger *L. bohar* specimens obtained during the entire sampling period.

Furthermore, the asymptotic length and growth performance index of *L. bohar* in the Davao Gulf showed higher values, where K = 0.81 and φ = 2.83. The resulting growth parameters of *L. bohar* mean faster growth rate compared to that of New Caledonia and the Great Barrier Reef, Australia. While warmer temperature is an evident environmental factor associated with faster growth rate, the existing fishing pressure in the Davao Gulf can also contribute to the changes in the growth rate and maturity of *L. bohar*. This has been reported in several other tropical reef studies where heavy exploitation has caused the decrease of relative abundance of certain fish species, resulting to decreased average size (Russ and Alcala 1989), earlier maturity, and smaller size-at-maturity (Jennings et al. 1999).

Increase in growth rate results to earlier maturation, and this is a manifestation of a decrease in abundance of a population (Sadovy 1996). Coral reef fisheries tend to take out the large and slow-growing species first among others (Jennings and Polunin 1996; Friedlander et al. 2010). Since slow-growing fishes are vulnerable to overfishing, their size and age at maturity will eventually shift in response to exploitation (Jennings et al. 1999; D'Alessandro 2010). Moreover, life history characteristics are heritable, and it is probable that *L. bohar* have inherited these responses to exploitation (Sadovy 1996; Jennings et al. 1999).

In temperate regions, Obrien (1999) observed the same results where warmer temperature during autumn may have caused the faster growth and earlier maturation of *Gadus morhua* stocks in the Georges Bank compared to those in the Gulf of Maine. Exploitation has also caused the decrease in size and age at maturity among *G. morhua* stocks. This trend was also observed in other lutjanid species where Zhao and McGovern (1997) found out that there was a decrease in both age and length of maturation of vermilion snapper (*Rhomboplites aurorubens*) stocks in the South Atlantic Bight. They concluded that the decrease in size and maturation of vermilion snappers was due to intense overfishing, which heightened in 1980s.

Age at Maturity of *Lutjanus bohar*

Lutjanids mature from three to eight years (Secretariat of the Pacific Community Information Sheet 2011), and their maturation schedule is influenced by fishing pressure, predator and prey abundance, stock composition, and other biotic and abiotic factors (Wooton 1990). Based on the outputs of VBGF, the age at maturity of *L. bohar* in the Davao Gulf is approximately six years old, referring to the point where the growth curve starts to plateau (Figure 4). This marks the transition from rapid growth of the fish to eventual flattening of the curve, where energy reserves dedicated for growth are shifted towards reproductive purposes (Ross and Biagi 1991).

The estimated age at maturity of *L. bohar* caught in the Davao Gulf means that they are maturing at an earlier time and smaller size compared to *L. bohar* in Australia and in other locations. Earlier sexual maturation is attributed to prevailing environmental factors such as warmer water temperature where fishes in the tropics would have faster metabolic rates (Kausar and Salim 2006). However, genotypic and environmental factors can also influence the changes in maturation schedule (Sadovy 1996). These environmental factors include the effects of intense fishing pressure, which can lead to increased growth rate and consequent decrease in mean maximum size, size at maturity, and age at maturity (Russ and Alcala 1989; Sadovy 1996; Jennings et al. 1999).

Pet et al. (2005) added that the decrease in the average fish size is a result of fishing spawning aggregations. Their compensatory response to their declining population is to mature at an earlier time and at a smaller size (Trippel 1995). Maturing at an earlier age allows individuals to spawn over extended periods to increase the probability of producing recruits that will eventually reach settlement (Munro 1983). Although long-lived fish populations such as *L. bohar* can have several age classes, it is necessary that they will be buffered against potential recruitment failure (Jennings and Lock 1996; Marriott et al. 2007). Fishing is among the most exploitative activities on coral reefs (Russ and Alcala 1989), and if not prevented, the overexploitation of coral reef fishes may cause their perpetuation to fail.

Summary and Conclusion

The otolith study on two-spot red snappers (*L. bohar*) in the Davao Gulf, Philippines, was conducted to determine the age structure and estimate the age at sexual maturity of these commercially important coral reef fish. The body length and weight relationship revealed that the growth pattern of *L. bohar* is isometric. Growth performance equation (adapted from Pauly and Munro 1984) was used to compare the growth parameters of *L. bohar* in different locations. Results show that *L. bohar* in the Davao Gulf have faster growth rate and earlier maturation compared to those in New Caledonia (Loubens 1980) and the Great Barrier Reef, Australia (Marriott et al. 2007). The age truncation observed in *L. bohar* accompanied by decrease in size and earlier maturation may be attributed to prevailing environmental conditions, but it can also suggest their compensatory response to existing fishing pressure in the Davao Gulf.

Additional samples of aged *L. bohar* can help establish the entire growth curve, thus providing a concrete explanation on the effects of fishing pressure. Environmental parameters such as chlorophyll-*a* and sea surface temperature should be obtained with respect to the sampling period to describe how food availability and temperature influence their growth rate. Sex-specific data are necessary as reproductive behavior may vary between males and females. While conservation efforts have been made for small pelagic fishes in the Davao Gulf, similar attention is needed for commonly harvested reef fishes in the area such as snappers, groupers, rabbitfishes, and parrotfishes. Further studies regarding the harvest rates and reproductive biology of *L. bohar* should be made to instigate efforts on fisheries management of these long-lived and highly exploited fish species in the Davao Gulf.

Acknowledgment

This paper is the undergraduate thesis of the primary author. We extend our gratitude to Ms. Merlene Elumba for her assistance in conducting statistical analyses and to Asst. Prof. Fritzie Ates-Camino and Asst. Prof. Marion John Michael Achondo for their comments as review panelists in the preparation of this paper.

References

Alicli TZ, Oray IK, Karakulak FS, Kahraman AE. 2012. Age, sex ratio, length-weight relationships and reproductive biology of Mediterranean swordfish, *Xiphias gladius* L., 1758, in the eastern Mediterranean. Afr J Biotech. 11(15):3673–3680.

Allen GR. 1985. Snappers of the world: an annotated and illustrated catalogue of lutjanids species known to date [FAO species catalog]. Rome (IT): FAO Fish Synop. 6(125):208.

Anderson RO, Neumann RM. 1996. Length, weight, and associated structural indices. In: Murphy BR, Willis DW, editors. Fisheries techniques. Bethesda (MD): American Fisheries Society.

Brothers EB, Mathews CP, Lasker R. 1975. Daily growth increments in otoliths from larval and adult fishes. Fish Bull. 74(1).

Cailliet GM, Andrews AH, Burton EJ, Watters DL, Kline DE, Ferry-Graham LA. 2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Exp Gerontol. 739–764.

Campana SE. 2001. Review paper on accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J Fish Biol. 59:197–242.

Campana SE. 2004. Photographic atlas of fish otoliths of the Northwest Atlantic Ocean. Ottawa (Ontario): NRC Research Press.

Carpenter KE, Springer VG. 2005. The center of marine shore fish biodiversity: the Philippine Islands. Environ Biol Fish. 72:467–480.

Choat JH, Robertson DR. 2002. Age-based studies on coral reef fishes. In: Sale PF. Coral reef fishes: dynamics and diversity in a complex ecosystem. Orlando (FL): Elsevier Science.

Corral JM, Soliman VS, Yamaoka K. 2013. Otolith and body length relations in the spiny siganid (*Siganus spinus* Linnaeus 1758). Asia Life Sci. 22(1):303–311.

D'Alessandro EK. 2010. Early life dynamics in tropical Western Atlantic and Carribean snappers (Lutjanidae) and barracudas (Sphyranidae) [dissertation]. [Coral Gables (FL)]: University of Miami.

Domeier ML, Colin PL. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci. 60(3):698–726.

Druzhinin AD. 1972. The distribution of Lutjanidae and Sciaenidae (Pisces) in the Indian Ocean. Ind J Fish. 18:52–65.

Fowler AJ. 1990. Validation of annual growth increments in the otoliths of a small, tropical coral reef fish. Mar Ecol Prog Ser. 64:25–38.

Friedlander AM, Sandin SA, DeMartini EE, Sala E. 2010. Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. Mar Ecol Prog Ser. 410:219–231

Govinda Rao V, Krishna NM, Sujatha K. 2014. Length weight relationship and length groups of two species of snappers (Pisces Lutjanidae) represented in the catches of Visakhapatnam, Middle East Coast of India. J Exp Zool Ind. 17(1):127–132.

Grandcourt E. 2005. Demographic characteristics of selected epinepheline groupers (Family: Serranidae; Subfamily: Epinephelinae) from Aldabra Atoll, Seychelles. Atoll Res Bull. 539:200–216.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron. 4(1):9.

IUCN [International Union for Conservation of Nature and Natural Resources]. 2015. The IUCN Red List of Threatened Species. Cambridge (UK): IUCN. [accessed 2015 January 27]. http://www.iucnredlist .org

Jennings S, Reynolds JD, Polunin NVC. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conserv Biol. 13(6):1467–1475.

Jennings S, Kaiser MJ, Reynolds JD. 2001. Marine fisheries ecology. Oxford (UK): Blackwell Science Ltd.

Jennings S, Polunin NVC. 1996. Effects of fishing effort and catch rates upon the structure and biomass of Fijian reef fish communities. J Appl Ecol. 33:400–412.

Jennings S, Lock JM. 1996. Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM, editors. Reef fisheries. London (UK): Chapman & Hall.

Jobling M. 1995. Environmental biology of fishes. London (UK): Chapman & Hall.

Karachle PK, Stergiou KI. 2012. Morphometrics and allometry in fishes. In: Wahl C, editor. Morphometrics. New York (USA): Cornell University.

Kausar R, Salim M. 2006. Effect of water temperature on the growth performance and feed conversion ratio of *Labeo rohita*. Pak Vet J. 26(3):105–108.

Kulbick M, Guillemot N, Amand M. 2005. A general approach to length-weight relationships for New Caledonian lagoon fishes. Cybium. 29(3):235–252.

Loubens G. 1980. Biologie de quelques espèces de poissons du lagon Néo-Calédonien. II. Sexualité et reproduction. Cah Indo-Pac. 2:41–72.

Marriott RJ, Mapstone BD. 2006. Geographic influences on and the accuracy and precision of age estimates for the red bass, *Lutjanus bohar* (Forsskal 1775): a large tropical reef fish. Fish Res. 80:322–328.

Marriott RJ, Mapstone BD, Begg GA. 2007. Age-specific demographic parameters, and their implications for management of the red bass, *Lutjanus bohar* (Forsskal 1775): a large, long-lived reef fish. Fish Res. 83:204–215.

Martinez-Andrade F. 2003. A comparison of life histories and ecological aspects among snappers (Pisces: Lutjanidae) [dissertation]. [Baton Rouge (LA)]: Louisiana State University.

McBride RS, Hauser JW, Sutherland SJ, editors. 2010. Brodeur's guide to otoliths of some Northwest Atlantic fishes. North Fisheries Science Center Reference Document 10-04. Woods Hole (MA): National Oceanic and Atmospheric Administration.

Miller JA, Simenstad CA. 1994. Otolith microstructure preparation, analysis, and interpretation: procedures for a potential habitat assessment methodology. Seattle (WA): Fisheries Research Institute.

Miller JA, Wells BK, Sogard SM, Grimes CB, Cailliet GM. 2010. Introduction to proceedings of the 4th International Otolith Symposium. Environ Biol Fish. 89:203–207.

Moksness E, Kjørsvik E, Olsen Y, editors. 2008. Culture of cold-water marine fish. Oxford (UK): Blackwell Publishing.

Morales-Nin B. 1992. Determination of growth in bony fishes from otolith microstructure. Rome (IT): Food and Agriculture Organization.

Morallana JM. 2013. Regional connectivity, differentiation and biogeography of three species of the genus *Lutjanus* in the Western Indian Ocean [thesis]. [Grahamstown (ZA)]: Rhodes University.

Moyle PB, Cech Jr. JJ. 2000. Fishes: an introduction to ichthyology. 4th ed. Upper Saddle River (NJ): Prentice-Hall.

Munro JL. 1983. Epilogue: progress in coral reef fisheries research. 1973–1982. In: Carribean Coral Reef Fishery Resources. ICLARM Stud. Rev. 7. ICLARM, Manila, Philippines. p. 276.

Nelson JS. 1994. Fishes of the world. 3rd ed. New York (USA): John Wiley & Sons.

Obrien L. 1999. Factors influencing the rate of sexual maturity and the effect on spawning stock for Georges Bank and Gulf of Maine Atlantic Cod *Gadus morhua* Stocks. J Northw Atl Fish Sci. 25:179–203.

Pauly D, Munro JL. 1984. Once more on the comparison of growth in fish and invertebrates. ICLARM Fishbyte. 2:21. [Qtd in: Bilgin S, Bal H, Taşçi B. 2012. Length based growth estimates and reproduction biology of whiting, *Merlangius merlangus euxinus* (Nordman, 1840) in the Southeast Black Sea. Turk J Fish Aquat Sc. 12:871–881.]

Pet JS, Mous PJ, Muljadi AH, Sadovy YJ, Squire L. 2005. Aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National Park, Indonesia: monitoring and implications for management. Environ Biol Fish. 74:209–218. [Qtd. in: Robinson J, Samoilys M, editors. 2013. Reef fish spawning aggregations in the Western Indian Ocean: research for management. WIOMSA Book Ser. 13. Nairobi (KE): WIOMSA, CORDIO.]

Polunin NVC, Roberts CM, editors. 1996. Reef fisheries. London (UK): Chapman & Hall.

Randall JE. 1979. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. Fish Bull. 78(2):201–249.

Renán X, Trejo-Martinez J, Caballero-Arango D, Brulé T. 2015. Growth stanzas in an Ephinephelidae-Lutjanidae complex: considerations to length-weight relationships. Rev Biol Trop. 63(1):175–187.

Robbins WD, Choat JH. 2002. Age-based dynamics of tropical reef fishes: a guide to processing, analysis and interpretation of tropical fish otoliths [technical manual]. Townsville (AU): James Cook University.

Rodriguez Mendoza RP. 2006. Otoliths and their applications in fishery science. Ribartsvo 64(3):89–102.

Ross MR, Biagi RC. 1991. Recreational fisheries of coastal New England. Amherst (MA): University of Massachusetts Press.

Russ GR, Alcala AC. 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar Ecol Prog Ser. 56:13–27.

Sadovy YJ. 1996. Reproduction of reef fishery species. In: Polunin NVC, Roberts CM, editors. Reef fisheries. London (UK): Chapman & Hall. pp. 15–59

Sale PF. 2002. Coral reef fishes: dynamics and diversity in a complex ecosystem. Orlando (FL): Elsevier Science.

Secor DH, Dean JM, Laban EH. 1992. Otolith removal and preparation for microstructural examination. In: Stevenson DK, Campana SE, editors. Otolith microstructure examination and analysis. Can Spec Publ Fish Aquat Sci. pp. 19–57

Secretariat of the Pacific Community Coastal Fisheries Programme. 2010. Noumea (NC): Pacific Community [accessed 2015 February 01]. http://www.spc.int/

Talbot FH. 1960. Notes on the biology of the Lutjanidae (Pisces) of the east African coast with special reference to *Lutjanus bohar* (Forsskal). Ann S Afr Mus. 1:549–579. [Qtd. in: Marriott RJ, Mapstone BD, Begg GA. 2007. Age-specific demographic parameters, and their implications for management of the red bass, *Lutjanus bohar* (Forsskal 1775): a large, long-lived reef fish. Fish Res. 83:204–215.]

Thorrold SR, Hare JA. 2002. Otolith applications in reef fish ecology. In: Sale PF, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. Orlando (FL): Elsevier Science. p. 243.

Trippel E. 1995. Age at maturity as a stress indicator in fisheries. BioScience. 45:759–771.

Victor BC. 1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar Biol. 71:203–208.

Waessle JA, Lasta CA, Favero M. 2003. Otolith morphology and body size relationships for juvenile Sciaenidae in the Rio de la Plata estuary (35-36˚S). Scientia Marina. 67(2):233–240. [Qtd.in: Corral JM, Soliman VS, Yamaoka K. 2013. Otolith and body length relations in the spiny siganid (*Siganus spinus* Linnaeus 1758). Asia Life Sci. 22(1):303–311.]

Woods MK, Fischer AJ, Cowan Jr. JH, Nieland D. 2003. Size and age at maturity of female red snapper *Lutjanus campechanus* in the Northern Gulf of Mexico. GCFI:54.

Wooton RJ. 1990. Ecology of teleost fishes. New York (NY): Chapman and Hall.

Wright A, Dalzell PJ, Richards AH. 1986. Some aspects of the biology of the red bass, *Lutjanus bohar* (Forsskal), from the Tigak Islands, Papua New Guinea. J Fish Biol. 28:533–544.

Zhao B, McGovern JC. 1997. Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens* in the South Atlanatic Bight. US Fish Bull. 95:837–848.