RESEARCH ARTICLE

Determining Sexual Development and Size at Sexual Maturity of *Sardinella tawilis* and its Implications on Management

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ABSTRACT

Reproductive biology is important in formulating management interventions for fish stocks. Limits on catch size are established based on the identified size at first sexual maturity of the target fish species, which can be accurately determined through histological analysis of gonads. The study investigated the reproductive characteristics of the endangered *Sardinella tawilis* and determined the size at first sexual maturity based on histological analysis. Between 2017 and 2018, 312 fish samples with different lengths were collected in Taal Lake's northern and southern basins. The length-weight relationship of *S. tawilis* shows that the species exhibits negative allometric growth. Female *S. tawilis*, characterized by larger sizes, are significantly more abundant in our catches than male individuals (mean sex ratio $p<0.05$) and exhibit an asynchronous oocyte development. Histological analysis of gonads showed that the size at sexual maturity for both male and female *S. tawilis* were at 75 to 79 mm FL, which was smaller than the reported size at sexual maturity based on morphological analysis. Smaller average and maximum lengths, as well as the size at first sexual maturity, could suggest that *S. tawilis* has experienced growth overfishing and a slowly degrading lake environment through time. Results highlighted the importance of ensuring that immature *S. tawilis* can enter sexual maturity and contribute to the population through reproduction. It is also highly recommended that the size of *S. tawilis* to be targeted by fisheries are individuals above 100 mm FL, which exhibited the highest proportion of spawning capable individuals.

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1. INTRODUCTION

Sardinella tawilis (Order Clupeiformes, Family Clupeidae) is the only freshwater sardine in the Philippines that is endemic to Taal Lake, Batangas province. The species is relatively small, with a maximum observed length of 15.6 cm total length and a maximum weight of 35.9 grams (Mutia 2015, unpublished doctoral dissertation). Peak spawning is from March to May, and fecundity was estimated at 4,800 eggs for a fish with an average fork length of 9.9 cm and an estimated weight of 13.2 grams total weight (Mutia et al. 2011). Ecologically, *S. tawilis* is a significant second-level consumer in the lake, feeding on large-bodied adult copepods, ostracods, cladocerans, rotifers, and other protozoans (Papa et al. 2008; Magsino 2012). Its abundance, schooling behavior, and mobile nature are critical to Taal Lake's energy and nutrient exchange.

S. tawilis is one of only two commercially fished, endemic species in the country. The other species is *Mistichthys luzonensis*, locally known as "Sinarapan" and recognized as the smallest commercial fish in the world. Both species are considered two of the most important freshwater fish in the Philippines because of their uniqueness as a species, endemicity, and their contribution to the local fishery (Bagarinao 2001; Mutia et al. 2017). *S. tawilis* sustained the livelihood of numerous small-scale pelagic fishers in the vicinity of Taal Lake. However, as the demand for the fish increased, the population was subjected to an unsustainable exploitation rate, resulting in a marked decline in the current stock. A review of the estimated decline in *S. tawilis* catch showed an alarming trend. Fish catch data showed that from 1984 to 1988, S. *tawilis* catch dropped from 29,000 mt/year to less than 9,000 mt/year. Seven years later, the total fish catch was recorded at only 60 mt/year (Mutia 2001; Philippine Statistics Authority 1997-2015). Currently, the present trends showed no remarkable biomass recovery attributed primarily to the continued exploitation of the stock (Castillo 2005; Almazan 2010; Mutia et al. 2011). To arrest the further decline in *S. tawilis* population and prevent the collapse of the entire stock, the IUCN in January 2019 elevated the status of *S. tawilis* to the "Endangered" list due primarily to its declining population, limited distribution, and the presence of multiple threats.

In previous years, studies on the biology and ecology of *S. tawilis* have emerged as vital inputs in formulating conservation strategies to address its declining population. Despite its importance, basic information on the species' biology remains deficient, while others have become outdated. Among the data that require updating, one of the most critical to management is the size of the species at first sexual maturity. Size at sexual maturity is essential information necessary to effectively manage a population of a species under threat (Anderson et al. 1992). An accurate understanding of the timing of maturity is essential for effective fisheries management as the size and age at which fish become mature is a critical element of the species' life history (Roff 1982; Dieckmann and Heino 2007; King and McFarlane 2003; Midway and Scharf 2012). In addition, this parameter is also influenced by intense fishing pressure and thus is important to update it periodically.

Currently, information on the size at first sexual maturity is based on the modified five-point scale classification of the gonadal maturity stages of Laevastu (1965) (Mutia et al. 2011). In this study, sexual maturity was mainly based on the morphological and physical appearance of the gonad (i.e., color and opacity of the gonad, presence, and density of eggs and milt). However, the use of histological techniques in determining the size at different stages of sexual maturity has not been conducted on the species to determine key stages in the species' life history accurately. The study, using gonad histology, aims to: (1) determine the length (size) at first sexual maturity of S. *tawilis;* (2) determine sex ratio and sex frequency distribution in various size groups; and (3) describe gonadal development and differentiation in *S. tawilis*. The result of the study will add to existing life history information on the species and provide additional insights that could potentially improve or, at the least, support the existing management program of this iconic fish species.

2. MATERIALS AND METHODS

2.1 Study area and sample collection

Taal Lake (formerly known as Lake Bombon) is the third-largest lake in the Philippines. It is an active tropical volcanic lake with an area of 26,750 hectares, which includes a 2,493.6-hectare Volcano Island. Sample collection of *S. tawilis* were conducted in the lakeshore municipalities of Talisay, Tanauan, Cuenca, Santa Teresita, and Agoncillo (Figure 1). The collection of *S. tawilis* was done monthly from May 2017 to June 2018. Samples were collected in different sampling months across stations to cover the lake's wet and dry seasons and the reported peak spawning season of *S. tawilis* in March (Mutia et al. 2011). The fish samples were obtained by local fishers using gillnet ("pante"), beach seine ("pukot"), and motorized push nets ("suro"). Using active gears in sample collection

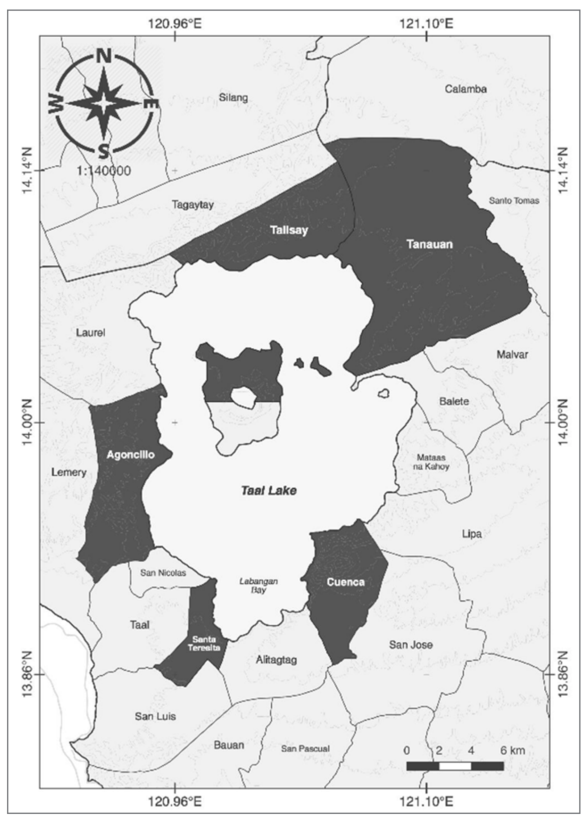

Figure 1. Taal Lake and the lakeshore municipalities. *S. tawilis* specimens were collected on landing sites located at the highlighted lakeshore municipalities.

is necessary to capture a wide range of sizes necessary to establish a good size and weight relationship. Fish samples were chosen randomly from the fish caught to avoid bias in size selection. A clearance (PAMB Resolution No. 37 Series of 2017) was acquired for collecting *S. tawilis* using beach seine and motorized push nets, as catching *S. tawilis* using these fishing gears is prohibited under the Unified Rules and Regulations on Fisheries (URRF) in Taal Lake.

2.2 Measurement of length and weight

The length and weight of the collected fish specimens were measured and recorded following standard protocols. The fork length (FL) was measured to the nearest millimeter by analyzing photographs of fish samples using ImageJ® software version 1.46 (Rasband 2008). On the other hand, body weight (BW) was measured to the nearest gram by weighing each fish sample in the Ohaus® analytical balance. Fish samples were pat dried with a paper towel before weighing to minimize water's effect on body weight. Four readings of length and weight measurement were done for each fish sample to ensure the accuracy of the derived values. The length and weight relationship of *S. tawilis* were estimated using the allometric equation, W= aLb, where W is the wet weight of the fish sample, L is the length of the fish, and a and b are the intercept and the slope of regression, respectively (Ricker 1975).

2.3 Identification of sex, sexual maturity, and stages of sexual development

Extraction of fish gonads was done by creating an incision on the ventral cavity, followed by removing the gut and other internal organs. Successfully extracted gonads were weighed following the previously mentioned protocol and preserved using 10% buffered formalin. The preserved gonad specimens were tagged, recorded, and sent to a third-party pathology laboratory for histological processing. The gonad samples were processed by following standard histological procedures to obtain multiple cross-sections at the mid-section of one gonad lobe. Sectioned gonad sections were stained with hematoxylin-eosin and embedded in paraffin. Analysis of histological sections was then conducted by examining the cellular characteristics of each gonad (e.g., the progression of vitellogenesis in oocytes, appearance of nuclei, and cytoplasm in spermatocytes) using a compound microscope. Analysis and determination of distinct histological features (e.g., stages of oocytes and spermatocytes) were conducted using multiple clupeid studies as references (Hay et al. 1987; Matsuyama et al. 1991a; Matsuyama et al. 1991b; Isaac-Nahum et al. 1998; Ganias et al. 2004; Shirafuji et al. 2007; Haslob et al. 2012; Hyle et al. 2014; Lajud et al. 2016). Identification of sex and establishment of sexual maturity stages for *S. tawilis* was based on the observations following the description of Brown-Peterson et al. (2011) (Table 1).

Table 1. Microscopic characteristics of phases in the reproductive cycle of male and female fishes (Brown-Peterson et al. 2011).

Phase	Histological Features	
	Male	**Female**
a. Immature - never spawned	Only Sg1 is present; no lumen in lobules	Only oogonia and PG oocytes are present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
b. Developing - testes beginning to grow and develop	Spermatocysts evident along lobules. Sg2, Sc1, Sc2, St, and Sz can be present. Sz is not present in the lumen of lobules or sperm ducts. GE continuous throughout.	PG, CA, Vtg1, and Vtg2 oocytes are present. No evidence of POFs or Vtg3 oocytes.
c. Spawning Capable - developmentally and physiologically	Sz in the lumen of lobules and/or sperm ducts. All stages of spermatogenesis (Sg2, Sc, St, Sz) can be present. Spermatocysts throughout testis, active spermatogenesis. Continuous GE along the periphery of the testis, discontinuous GE in lobules near the ducts	Vtg3 oocytes present. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of OM can be present.
d. Regressing - cessation of spawning	Residual Sz present in lumen of lobules and in sperm ducts. Widely scattered spermatocysts near periphery containing Sc2, St, and Sz. Little to no active spermatogenesis. Discontinuous GE in lobules throughout the testis.	Atresia (any stage) and POFs prominent. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
e. Regenerating - sexually mature but immature	No spermatocysts. Lumen of lobule nonexistent. Proliferation of spermatogonia throughout testes. GE continuous throughout. Small amount of residual Sz occasionally present in lumen of lobules and in sperm duct.	Only oogonia and PG oocytes present. Muscle bundles, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs may be present.

(Sg1 = primary spermatogonia, Sg2 = secondary spermatogonia, Sc1 = primary spermatocyte, Sc2 = secondary spermatocyte, St = spermatid, Sz = Spermatozoa, GE = germinal epithelium, PG = primary growth, CA = cortical alveolar, Vtg1 = primary vitellogenic, Vtg2 = secondary vitellogenic, Vtg3 = tertiary vitellogenic, POF = post-ovulatory follicles, OM = oocyte maturation

To generally classify *S. tawilis* samples based on sexual maturity (i.e., immature or mature), sexual development phases were generally categorized into Sexually Immature (pre-spawning) and Sexually Mature (spawning and post-spawning). Immature individuals are those characterized by continuing gonadal growth and gamete development and, thus, are not fully capable of reproduction. On the other hand, mature individuals are those under the spawning capable, regressing, and regeneration stages, as these are already capable of spawning and have fully functional gonadal structures. The size at sexual maturity was determined where more than 50% of the individuals were sexually mature on the proviso that larger and older classes had higher percentages of sexually mature individuals (Hilomen 1999).

Aside from determining sexual maturity, the mean sex ratio (F/M) was also computed in the study by determining the total number of male and female individuals in the samples collected. The chi-square goodness-of-fit test was then performed at the stats 3.5.3 package (R Core Team 2019) to determine the deviation of the mean sex ratio from the expected 1:1 ratio (Giora et al. 2014; Cao et al. 2009).

3. RESULTS

3.1 Length and weight

A total of 312 fish samples were collected in the study (Table 2). The recorded length of *S. tawilis* ranged from 30 to 124 mm FL, with an overall mean length of 87.5 mm ± 13.1 mm. Most individuals had sizes that ranged from 90 to 99 mm FL (74.2%). In terms of weight, the recorded wet body weight of *S. tawilis* ranged from less than 1 g to 22.7 g., where the majority (44.2%) had body weights that ranged from 8 to 11 g (n=138).

In terms of length and weight, the average size of *S. tawilis* recorded in this study was observed to be smaller than in previous reports (Table 3). Notably, since the unit of measurement for this study is in fork length (FL), the results could only be directly compared to the report of Aypa et al. (1991). The smaller sizes of fish can be attributed to the method of fish collection, which includes using active fishing gears like beach seine and motorized push nets. Smaller *S. tawilis* are more vulnerable to active fishing gears due to the mode of action, where the catching principle is based on chasing fish, along with the smaller mesh size of fish nets (up to 17k or 1.9 cm). Including smaller individuals in the samples reduced the overall mean size of the population. However, another factor to be considered is the historical high fishing pressure exerted on *S. tawilis* population, where exploitation rates go beyond sustainable levels (E > 0.5) (Villanueva et al. 1996; Mutia et al. 2011; Mutia et al. 2018). High exploitation of a fish population through time, alongside the use of unsustainable fishing gear, may result in growth overfishing (Pauly 1988). Growth overfishing occurs when fish are caught before they have time to grow (Pauly et al. 1989). Growth overfishing further translates to economic losses since fish are harvested before they reach the size where yield per recruit is optimized, and the weight and value of the catch may be reduced (Ben-Hasan et al. 2021).

Table 2. Number of *S. tawilis* specimens collected from Taal Lake, Batangas, Philippines (2017 to 2018).

Month	May-17	Jun-17	Jul-17	Aug-17	Dec-17	Feb -18	Mar-18	Jun-18
Samples (n)	47	45	38	25	22	39	29	67
Total (N)				312				

Table 3. Mean and maximum lengths and weights of *S. tawilis* in the present study and various literature.

	Castillo, B.B., A.S. Castillo, and C.L. Gonzales 1975 in Froese and Pauly 2019	Aypa et al. 1991	Mutia et al. 2011	Mutia et al. 2015	Present Study
Mean length	-	100 mm FL	111 mm TL	118 mm TL	87.5 ± 13 mm FL
Max. length	120 mm TL (M) 152 mm TL (F)	130 mm FL	118 mm TL	156 mm TL	101 mm FL (M) 122 mm FL (F)
Mean weight	-	-	13.2 g	14.9 g	9.9 ± 3 g
Max. weight	-	-	16.3 g	35.9 g	23.0 g

In terms of the length-weight relationship, results indicate that *S. tawilis* exhibit a negative allometric (hypo-allometric) relationship, as shown by the b value (b = 2.658) (Figure 2). A negative allometric growth implies that growth is towards the elongation of the body (length) rather than an increase in weight (Froese et al. 2011). *S. tawilis* are pelagic and are expected to have a slimmer and elongated body. This body shape favors their movement and dynamics in a pelagic environment. The calculated value of R2 indicates that 94% of the variation in weight is due to the linear relationship between length and weight.

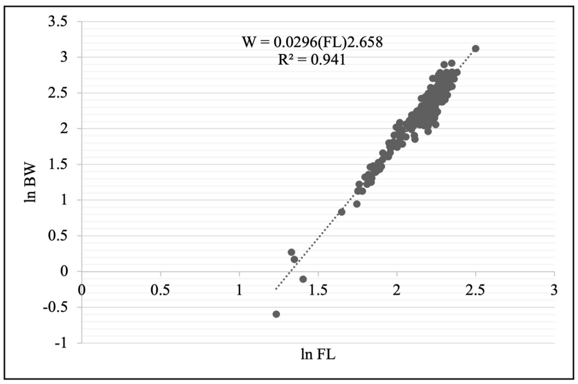

Figure 2. Length-weight relationship of *S. tawilis* (n=312) collected from Taal Lake, Batangas, Philippines (2017 to 2018).

3.2 Sex ratio and sex frequency distribution across length

Based on the analysis of gonad histological sections, *S. tawilis* exhibited a gonochoristic sexual pattern (i.e., individuals are distinctly male or female). This is consistent with what has been reported in the literature (Aypa et al. 1991; Catedral 2002, unpublished thesis; Mutia et al. 2011; Mutia 2015, unpublished doctoral dissertation). In addition, the gonochoristic sexual pattern of *S. tawilis* is consistent with the other species of Sardinella (*S. aurita*, *S. longiceps*, *S. brasiliensis*, *S. fimbriata*), which were also reported to exhibit a gonochoristic pattern (Tsikliras and Antonopoulou 2006; Deshmukh et al. 2010; Isaac-Nahum et al. 1988; Kudale and Rathod 2016). However, eight fish specimens were observed to have undeveloped gonads (i.e., tissue was too small, or the cavity was empty). These specimens were not subjected to either macroscopic or histological identification of sex. Instead, these were classified under the category "unsexed."

The overall mean sex ratio of *S. tawilis* was recorded at 0.79:1 (male:female). The abundance of female over male individuals was determined to be significant (p<0.05). The result was consistent with the previously reported sex ratios of *S. tawilis* at 0.95:1 (Catedral 2002, unpublished thesis) and 0.6:1 (Mutia 2015, unpublished doctoral dissertation), where females were more abundant than males. The greater abundance of female *S. tawilis* observed in the study was also consistent with the reported sex ratios of other Sardinella species, such as *S. aurita*, *S. longiceps*, *S. gibbosa*, and *S. fimbriata* (Tsikliras and Antonopoulou 2006; Deshmukh et al. 2010; Ghosh et al. 2013). In terms of size, females were observed to be larger than males. The sizes of males range from 55 to 104 mm FL, whereas females range from 50 to 124 mm FL (Figure 3). The higher proportion of females, as shown by the significant male-to-female sex ratio (p<0.05), with larger body sizes, suggests high population fecundity.

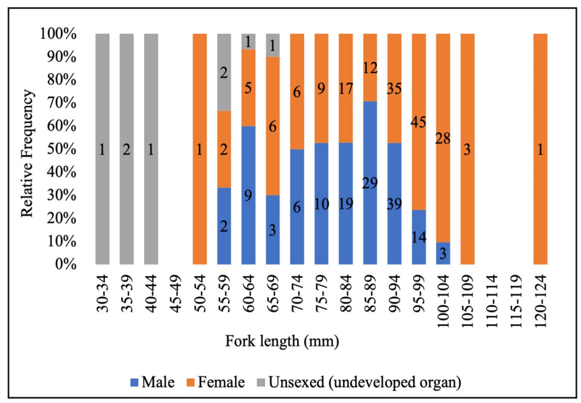

Figure 3. Sex frequency distribution per length class of *S. tawilis* (n = 312).

3.3 Sex ratio and sex frequency distribution across length

The spermatocyte and oocyte development stages of *S. tawilis* are described in Tables 4 and 5, respectively. The spermatogonia is the largest cell characterized by spherical nuclei and light granular cytoplasm among the spermatocytes. In contrast, primary and secondary spermatocytes, spermatids and spermatozoa, were characterized to have dense nuclei with minimal cytoplasm (Plate 1, left). As for the oocyte development of *S. tawilis*, it was observed that the production of oocytes is continuous, as shown by the overlapping sizes of oocytes across development stages (Table 5). Furthermore, an asynchronous oocyte pattern was observed wherein oocytes in many development stages co-occur in one gonad (Plate 1, right) (Macewicz et al. 1996). The asynchronous oocyte development pattern of females implied that *S. tawilis* is a batch spawner, capable of having a series of spawning over time (Brown-Peterson et al. 2011).

Table 4. Summary of spermatocyte development stages defined for *S. tawilis* collected from Taal Lake, Batangas, Philippines (2017 to 2018).

Spermatocyte Development Stage	Description	Size Range (μm)	Mean Size ± SD (μm)
1. Spermatogonia (Sg)	Largest spermatogenic cell with spherical nuclei and light granular cytoplasm	3.04 to 7.52	4.69 ± 0.88
2. Primary and Secondary Spermatocytes (Sc)	Nuclei are dense with partially indistinct cytoplasm	2.44 to 4.00	3.12 ± 0.38
3. Spermatids (St)	Dense nuclei with eosinophilic cytoplasm	1.10 to 1.95	1.45 ± 0.18
4. Spermatozoa (Sz)	Dark, round nuclei with minimal cytoplasm. Tails are not distinct.	0.63 to 1.44	1.23 ± 0.18

Table 5. Summary of the oocyte development stages defined for *S. tawilis* collected from Taal Lake, Batangas, Philippines (2017 to 2018).

Oocyte Development Stage	Description	Size Range (μm)	Mean Size ± SD (μm)
1. Chromatin-Nucleolus (CN)	Cytoplasm is strongly basophilic. Nucleus is about half the size of the oocyte.	7.89 to 47.56	3.12 ± 0.38
2. Perinucleolus (Pn)	Cytoplasm is strongly basophilic. Nucleus is about a third of the size of the oocyte.	21.54 to 69.35	44.11 ± 11.81
3. Cortical Alveoli (CA)	Cytoplasm is less basophilic. Yolk vesicles found in the mid to outer regions of the cytoplasm.	48.73 to 178.64	103.1 ± 28.95
4. Primary (Vtg1) and Secondary (Vtg2) Vitellogenic	Cytoplasm dominated by oil droplets. Yolk granules start to accumulate.	108.1 to 261.2	175.3 ± 40.12

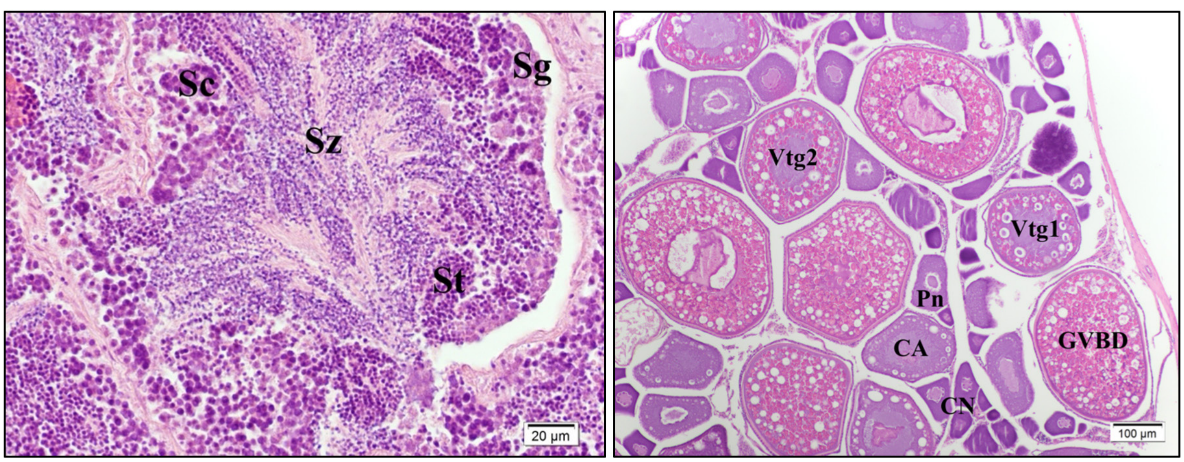

Plate 1. Different development stages of spermatocytes (left) and oocytes (right) in spawning capable *S. tawilis* (Sg = spermatogonia; Sc = spematocyte; St = spermatid; Sz = spermatozoa; CN = chromatin nucleus; Pn = perinucleolus; CA = cortical alveoli; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic; GVDB = germinal vesicle breakdown).

The sexual development stages of *S. tawilis* were categorized into immature, developing, spawning capable, regressing, and regenerating (Plates 2 and 3) based on the descriptions of Brown-Peterson et al. (2011). In this study, the different stages of sexual development were observed across length classes for female and male *S. tawilis* (Figure 4). Immature females were observed in individuals with sizes ranging from 50 to 79 mm FL. Developing females were observed among samples within sizes ranging from 60 to 84 mm FL, with the highest proportion observed within the size range of 70 to 74 mm FL. Spawning capable females comprised the largest proportion of individuals in the succeeding size ranges. Regressing

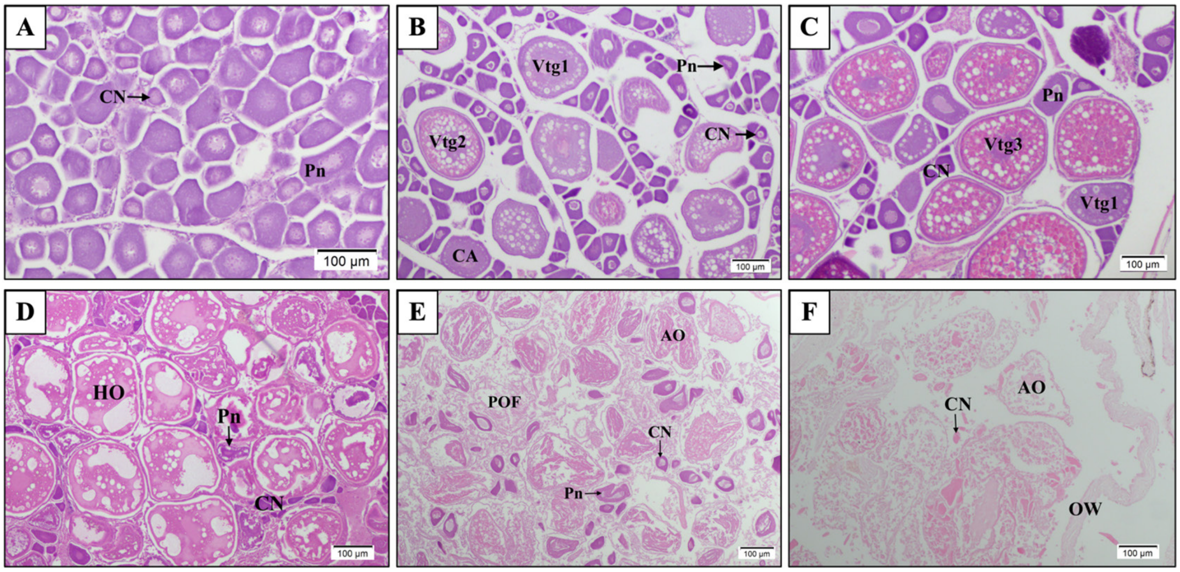

Plate 2. Stages of sexual development of female *S. tawilis*: Immature (A), Developing (B), Spawning Capable (Developed) (C), Spawning Capable (Ripe) (D), Regressing (E), and Regenerating (F). (CN = chromatin nucleus; Pn = perinucleolus; CA = cortical alveoli; Vtg1 = primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic; GVM = germinal vesicle migration; GVDB = germinal vesicle breakdown; HO = hydrated oocyte; POF = post-ovulatory follicle; AO = atretic oocyte).

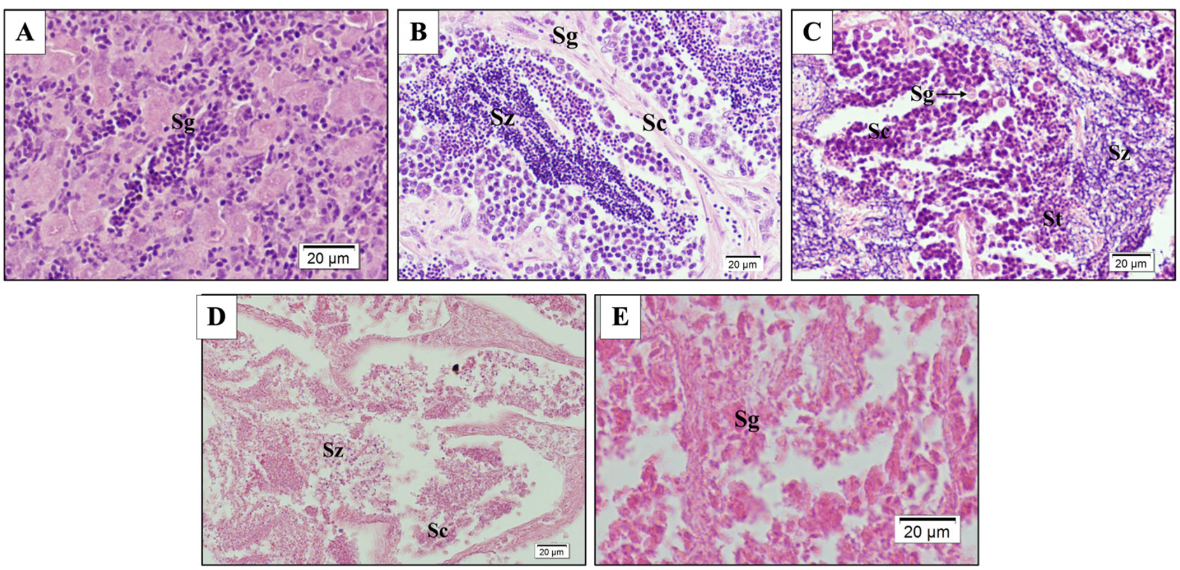

Plate 3. Stages of sexual development of male *S. tawilis*: Immature (A), Developing (B), Spawning Capable (C), Regressing (D), and Regenerating (E). (Sg = spermatogonia; Sc = primary and secondary spermatocytes; St = spermatid; Sz = spermatozoa).

females, on the other hand, were observed to occur on sizes where spawning-capable individuals were dominant. Finally, regenerating females were only observed in individuals with sizes ranging from 90 to 94 mm FL.

In male *S. tawilis,* immature individuals were observed within the size range of 55 to 69 mm FL. On the other hand, developing males were observed among samples with sizes ranging from 55 to 84 mm FL, with the highest proportions on sizes ranging from 55 to 74 mm FL. Furthermore, spawning capable and regressing males were observed in individuals with sizes ranging from 75 to 104 mm FL. Lastly, regenerating males were observed in individuals with sizes ranging from 75 to 99 mm FL. In this study, the proportion of regenerating males observed was greater than regenerating females.

Sexual development across length showed that males started to develop from the immature to developing stage at a smaller size (55 to 59 mm FL)

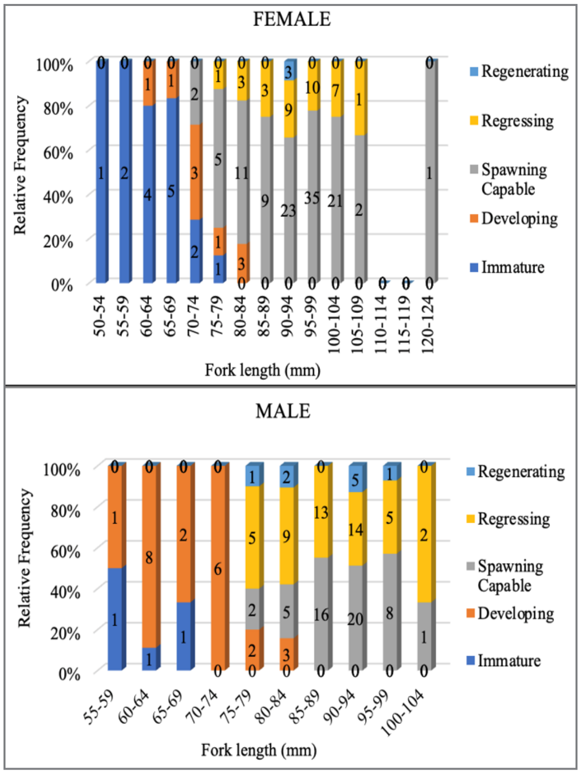

Figure 4. Stages of sexual development of *S. tawilis* per length class (upper graph: male = 134; lower graph: female = 170).

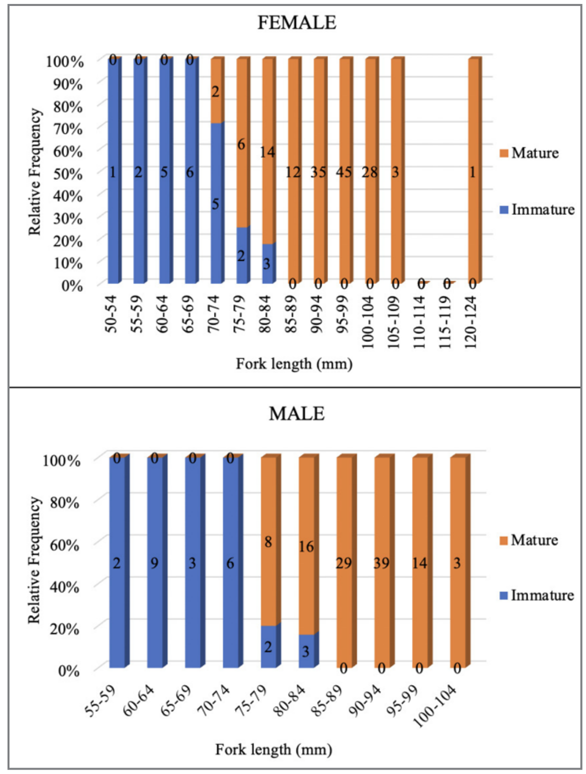

Figure 5. Immature and mature individuals per length class of *S. tawilis* (upper graph: male = 134; lower graph: female = 170).

than females (60 to 64 mm FL). However, advancement from developing to spawning capable stages started earlier in females (70 to 74 mm FL) compared to males (75 to 79 mm FL). This implies that some female individuals reach sexual maturity at a smaller size compared to males.

3.4 Size at sexual maturity

The general categorization of *S. tawilis* into sexually immature (pre-spawning) and sexually mature (spawning and post-spawning) stages showed that all female and male individuals within 50 to 69 mm FL and 55 to 74 mm FL, respectively, were sexually immature (Figure 5). On the other hand, all individuals with sizes greater than 85 mm FL were observed to be sexually mature. The length class where the proportion of mature individuals was greater than 50% of immature individuals was 75 to 79 mm FL for male and female individuals (Figure 5). Hence, this size range is the estimated size at sexual maturity of *S. tawilis*. This was smaller than the reported size at sexual maturity at 112 mm TL for males and 116 mm TL for females (Mutia 2015, unpublished doctoral dissertation).

4. DISCUSSION

Overall, the average size of *S. tawilis* collected for this study was smaller than in the previous reports. The smaller average size of samples caught for this study may have been greatly influenced by how the samples were collected. Samples of *S. tawilis* in this study were obtained from fishing gears with varying mesh sizes. The smaller mesh sizes and mode of action of the active fishing gears (i.e., chasing fish) may have favored the catch of smaller fish individuals. Furthermore, gonad histological analysis showed that more than 80% of the *S. tawilis* individuals analyzed are already classified as sexually mature, with the size at first sexual maturity at 75 to 79 mm FL for both sexes. A higher proportion of sexually mature individuals, when translated into the population level, may indicate that more individuals can also spawn for the population. However, it is notable that the post-spawning (regressing and regenerating) individuals collected in the study were only present in low frequencies. A high proportion of female spawning capable individuals accompanied by low regressing and regenerating individuals could indicate that these individuals are highly vulnerable to fishing before being given a chance to spawn. Growth overfishing in the *S. tawilis* population through time could also be reflected in the size at which *S. tawilis* attains the first sexual maturity. High fishing pressure may have drastically reduced the large and sexually mature individuals in a population where smaller individuals are left to adapt physiologically by reaching size at sexual maturity at smaller sizes to ensure continuous reproduction of the population (Lappalainen et al. 2016). The effects of high fishing pressure on the growth, age, and size at sexual maturity of fish have been well documented on the life history of commercially valuable fish (Ricker 1981; Trippel 1995; Taylor and McIlwain 2010; Magqina et al. 2020). In Pacific salmon stocks (*Oncorhynchus tshawytscha*), the excess removal of smaller, younger fish resulted in a depressed growth rate of fish individuals (Ricker 1981). The smaller size at sexual maturity of *S. tawilis* could be a response to the reported high exploitation rate in the previous years (Villanueva et al. 1996; Mutia et al. 2004), but not exclusively. However, since *S. tawilis* is a short-lived species and reproductive studies were limited prior to the drastic fish catch decline during the 1980s, it is also important to consider the effects of environmental factors such as annual variation in food type and abundance, which could be attributed to the existing spatio-temporal variations in the physico-chemical properties of the lake's water (Papa and Mamaril 2011).

The reproductive success of *S. tawilis* is crucial since it is endemic to Taal Lake, and no other sources of larvae can contribute to the recruits. Since *S. tawilis* was estimated to be short-lived, as shown by the high growth constant (K) reported at 0.98 cm yr-1 (Mutia 2015, unpublished doctoral dissertation), reproduction should be efficient to maximize the population's recruits. Allowing the fish to spawn before it is harvested will ensure that each fish will contribute to the stock's recruits and the population's genetic pool (Walters and Martell 2004). As observed from the study results, many spawning capable individuals were being included in the harvests, despite the advantages shown by the reproductive strategies (e.g., larger sizes of female individuals, asynchronous oocyte development, batch spawning) exhibited by *S. tawilis*. This indicated that a large proportion of the stock cannot spawn and does not further reach the regressing and regenerating (post-spawning) stages.

The endangered status of *S. tawilis* in the IUCN is imperative to the current threats to the survival and declining population of the fish species. The compounding impacts of different environmental variables operating in Taal Lake may have highly affected the survival, growth, and reproduction of *S. tawilis*. It has been cited that overfishing, introduction of alien species, and water quality deterioration are the primary negative drivers that impact the overall state of the *S. tawilis* population (Mutia et al. 2004; Willette et al. 2011). Biological parameters measured in the study support the growth overfishing of *S. tawilis* in Taal Lake. The continued use of illegal, active fishing gears (e.g., motorized push net or "suro," and beach seine or "pukot") indicates that heavy fishing pressure is sustained in the lake, contributing much to the observed population decline in *S. tawilis* population despite its efficient reproductive strategies. The use of active fishing gears is prohibited on the lake, as stated in the URR, and gillnet is the only fishing gear allowed to catch *S. tawilis*. The continued illegal use of active fishing gear with unregulated net mesh size contributes strongly to the unsustainable fishing of *S. tawilis* in the lake. Aside from heavy fishing pressure, Taal Lake, with its geographical location and existing environment, provides an excellent opportunity for the introduction of Non-Native Species (NNS) and the eventual establishment of their populations to become invasive alien species (IAS) (To et al. 2022). As proof, new records of introduced alien species have been recently noted in Taal Lake. These IAS are *Parachromis managuensis* (jaguar guapote), *Pangasianodon hypopthalmus* (pangasius), *Colossoma macropomum* (red-bellied pacu), *Ptergoplichthys disjunctivus* (janitor fish), and *Sarotherodon melanotheron* (black-chinned tilapia) (Mutia et al. 2017). To further emphasize the problem of invasives in Taal lake, IAS has also shown increased production since 2009 (Mutia et al. 2017). The negative impact of IAS cuts across the lake biodiversity, impacting trophic relationships, population interactions, and human health concerns, resulting in significant economic losses (Pimentel et al. 2005). Compounding those mentioned natural and anthropogenic predation of *S. tawilis* is the deterioration of the lake's water quality (Mamaril 2001; Mutia et al. 2004). The increasingly eutrophic condition of the lake (Papa and Mamaril 2011; Rosana et al. 2013) indicates the enhanced occurrence and dominance of cyanobacteria in the plankton communities of the lake. Cyanobacteria have long been considered a poor-quality food for primary consumers and are less preferred by large-bodied zooplankton (Ger et al. 2014; Ger et al. 2016). In turn, the strong preference of *S. tawilis* for large adult copepods (Papa et al. 2008) indicates that the continued eutrophication of lakes could impact the growth and reproductive output of *S. tawilis* (Papa et al. 2008). Overall, the study's findings implied that the species had signs of population decline despite its efficient reproductive strategies, which may have resulted from the compounding effects of various environmental and anthropogenic factors. In terms of fisheries, the continued illegal use of active fishing gear with unregulated net mesh size contributes strongly to the unsustainable fishing of *S. tawilis* in the lake.

5. CONCLUSION AND RECOMMENDATIONS

Overall, the analysis of reproductive traits in this study showed that *S. tawilis* exhibit an efficient reproductive strategy, as observed from the gonochoristic sexual pattern, larger body size of female individuals, and asynchronous oocyte development. However, despite the species' reproductive strategies, the current population is still under threat of decline primarily, but not exclusively, by overexploitation. In addition, other environmental factors, such as the proliferation of invasives and deteriorating water quality, were also recognized as significant factors that have negatively impacted the secondary production of *S. tawilis*. As a result of their synergistic effects, smaller sizes of fish were recorded, as well as a smaller size at first sexual maturity.

Among the contributors above to the decline in sardine productivity in general, uncontrolled direct extraction is considered the most concerning, especially when faced with the prospect of collapsing sardine stocks (Willette et al. 2011). Furthermore, overfishing has been consistently identified as a major driver of the population decline of *S. tawilis* (Mamaril 2001; Willette et al. 2011; Mutia et al. 2017). A decline in the mean length of fish caught over time is also primarily attributed to heavy fishing pressure (Lae et al. 2004). This suggests that the smaller sizes of fish recorded in this study could be attributed to the historical heavy fishing pressure on *S. tawilis*. Hence, regulating the *S. tawilis* fishery is essential in the conservation and stock revival of the species. Complementary implementation of a closed fishing season and regulated mesh size of fishnet is important to effectively manage the stock of *S. tawilis*. Strict implementation of a closed fishing season during the peak spawning months to address premature harvesting of spawning capable individuals is recommended to allow fish to spawn with minimal stress and mortality from fisheries. Since 2019, a closed fishing season for *S. tawilis* was implemented, covering the months of March and April. These months were reported to be the peak spawning months of *S. tawilis* (Mutia et al. 2015). Continued implementation of a closed fishing season during these months is predicted to lead to a higher fecundity through the years, resulting in a higher spawning rate of *S. tawilis*. Consequences of fishing on spawning individuals (e.g., forced delay in fertilization) that can lead to a decline in fertilization rates and deterioration of the quality of eggs can also be prevented by closed fishing season implementation (Overzee and Rijnsdorp 2015).

Moreover, the concerned fisherfolks should follow strict enforcement of the allowable fishing gear (i.e., passive fishing gear). For the non-peak spawning months, it is highly recommended that the size of *S. tawilis* to be fished are individuals above 100 mm FL. This size was delineated as the optimum size for spawning since this size exhibited the highest proportion of spawning-capable individuals. The URR of Taal Lake indicates that only passive fishing gear, such as gill net (mesh size of 10 to 12.5), is allowed to catch *S. tawilis*. A study by Alba et al. (2018) showed that gill nets with mesh sizes of 11k and 10k caught *S. tawilis* with mid-length sizes ranging from 95 mm TL to 135 mm TL, respectively, whereas gill nets with mesh sizes of 12.5k to 12k caught mid-length size ranging from 85 mm TL to 12.5 mm TL. Therefore, if the target fish to be caught is above 100 mm FL, it is more effective to use gill nets with mesh sizes 11k and 10k. By implementing this, the juveniles will be able to reach sexual maturity and will be able to reproduce prior to being harvested.

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AUTHOR CONTRIBUTIONS

Pardo KC: Conceptualization, Methodology, Visualization, Writing - Original draft preparation. **Ticzon V**: Supervision, Methodology, Writing - Reviewing, and Editing. **Camacho MA**: Supervision, Writing - Reviewing and Editing.

CONFLICTS OF INTEREST

To the best of our knowledge, no conflict of interest exists.

ETHICS STATEMENT

The authors obtained a clearance following the PAMB Resolution No. 37 Series of 2017 from the Protected Area Management Board of the Taal Volcano Protected Landscape (PAMB – TVPL), permitting the conduct of the study, including collecting juvenile *S. tawilis* individuals.

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