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Productivity in the East African Coastal Current under Climate Change

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Reproductive biology of the anchovy (Stolephorus commersonnii, Lacepède, 1803) and spotted sardine (*Amblygaster sirm*, Walbaum, 1792) from Tanga Region, Tanzania

Joseph S. Sululu^{1*}, Albogast T. Kamukuru², Baraka C. Sekadende¹, Shigalla B. Mahongo^{3,5}, Mathias M. Igulu⁴

- ¹ Tanzania Fisheries Research Institute, Dar es Salaam Centre, PO Box 78850, Dar es Salaam, Tanzania
- ⁴ WIOMSA, Mizingani Street, PO Box 3298, Zanzibar, Tanzania
- ² Department of Aquatic Sciences and Fisheries Technology, University of Dar es Salaam, PO Box 35064, Dar es Salaam, Tanzania
- ⁵ Lake Victoria Fisheries Organization, P.O. Box 1625, Jinja, Uganda
- ³ Tanzania Fisheries Research Institute, Institute Headquarters, PO Box 9750 Dar es Salaam, Tanzania.
- * Corresponding author: jsululu02@gmail.com

Abstract

The present study investigated the reproductive biology of *Stolephorus commersonnii* and *Amblygaster sirm* at two landing sites in Tanga on the northern coast of Tanzania. Fish samples were collected on a monthly basis from ringnets operated by artisanal fishers in the nearby coastal waters. Spawning seasons were determined using gonadosomatic index (GSI) and gonadal maturity stages. The size at first maturity was 57.7 mm and 66.2 mm total length for male and female *S. commersonnii* respectively. Male and female *A. sirm* were estimated to attain first maturity at 147.7 mm and 169.2 mm respectively. The spawning seasons of both species were protracted. *S. commersonnii* demonstrated a year round spawning cycle with peaks in August, October and January. The peak spawning season for male and female *A. sirm* was recorded in August and September respectively. Both species exhibited skewed size-dependent sex ratios with females predominating in the larger size classes. *A. sirm* had a higher fecundity rate with a maximum of 96,500 eggs in the largest female fish of 258 mm as compared to *S. commersonnii* (10,055 eggs) in the largest fish of 98 mm. The mean (±SE) total fecundity of *S. comersonnii* and *A. sirm* was 5,134.7 ± 136.9 eggs, and 47,029.03 ± 1,435.13 eggs in females of sizes 68 mm to 98 mm and 170 mm to 258 mm respectively.

Keywords: Anchovies, Clupeids, Reproduction, Tanga, Ringnet fishery

Introduction

Studies on the reproductive biology of fishes provide essential knowledge for stock management and conservation (King and McFarlane, 2003; Silva *et al.*, 2005). Most studies on fish reproduction rely on the classification of gonad maturity stages, which are critical for the accurate determination of the reproductive strategy of a species (Franco *et al.*, 2014). However, the gonadosomatic index (GSI) is used as an indicator for the sexual cycle of different fish species, through which spawning seasons can be determined (Nunes *et al.*, 2011). Further, the knowledge on spawning season and fecundity of a certain fish species helps to manage and maintain the fishery for such species as well as facilitate fishing plan strategies (Azza, 1992). The success of any species is eventually determined by the ability to reproduce successfully in fluctuating environments in order to maintain the population (Veerappan *et al.*, 1997). Therefore, a comprehensive knowledge of the maturation cycle assists in predicting the annual changes that the fish population undergoes.

Landings of Engraulidae and Clupeidae occupy the second and third places worldwide, respectively

(Zhang, 2001), providing the global human population with abundant and high-quality animal protein. The engraulid fishes, commonly known as anchovies, are widely distributed in both tropical and sub-tropical waters (Mcgowan and Berry, 1983). Clupeids are also widely distributed with about 65 genera and 214 species worldwide already confirmed (Meng *et al.*, 1995). Most engraulids, including *S. commersonnii*, spawn in coastal areas on the inner continental shelf and their recruitment frequently takes place in protected shallow areas that offer sufficient food and shelter from predators (Silva *et al.*, 2003).

Individuals of the anchovy, S. commersonnii Lacépède, 1803 (Engraulidae) are distributed globally from 27°N to 24°S and from 38°E to 155°E in waters with a depth of less than 50 m (Gao et al., 2016). Many species of anchovies are economically important in several regions (Franco et al., 2014); essentially, they are utilized throughout the tropical Indo-Pacific region for human consumption and as tuna bait (Andamari et al., 2002). Moreover, anchovies are known to form a vital part of marine food chains and form a link between the planktonic organisms and the predators such as carnivorous fishes, marine mammals, and birds. On the other hand, the clupeid A. sirm is more abundant in the Western Indian Ocean (WIO), South China Sea and in coastal waters of Papua New Guinea, Australia (Fischer and Bianchi, 1984), Indonesia, Philippines and Thailand (Chullarson and Martosubroto, 1986). The demand for A. sirm in the coastal states of the Indian Ocean is not only as a food fish, but also as a bait fish for the handline and longline fishery (Pradeep et al., 2014). Most clupeids and engraulids are reported to be multiple spawners, releasing many batches of eggs every year, hence producing batches of fecundity (Alheit, 1989). Some of the engraulids spawn batches of eggs every 2 - 10 days (Clarke, 1987).

Apart from being ecologically important through linking of planktonic organisms and predator fishes, S. *commersonnii* and *A. sirm* are also essential economically to fishers and coastal communities in Tanzania. Currently these species are in high demand in and out of the country as a human protein source and as animal food. Despite the ecological and economic significance of *S. commersonnii* and *A. sirm*, there is a paucity of information on the reproductive biology of these species from Tanzania and most of the WIO countries. However, a few reproductive biology studies have been reported in Tanzania for other non-small pelagic species (Kamukuru, 2009; Kamukuru and Mgaya, 2004; Lamtane *et al.*, 2007). The present study therefore examined the reproductive activity of *S. commersonnii* and *A. sirm* with the aim of establishing important biological information for conservation and management of these species.

Materials and methods

Study sites

The study was undertaken at two landing sites; namely, Sahare and Vyeru, which lie at 05° 05' S, 039° 07' E and 04° 57' S, 039° 08' E, respectively, in Tanga region in the northern part of Tanzania (Fig. 1). The criteria for choosing the two landing sites were based on their proximity to the East African Coastal Current (EACC) region in the Pemba Channel, and the associated upwelling, and their history within the small pelagic fishery, being one of the most productive areas for small pelagics in Tanzania

Specimens and data collection

Specimens for the study were obtained from ringnets operated by artisanal fishers during dark moons for a period of one year, from August 2016 to July 2017. Specimens of both S. commersonnii and A. sirm were collected from different fishing units at the two landing sites. The availability of specimens relied entirely on the catch of fishermen, while the frequency of sampling was three days per lunar month. However, individuals of A. sirm were not sampled in April 2017 at Vyeru due to their absence in the catch. During sampling, individuals of both species were identified using the field guide key by (Fischer and Bianchi, 1984). Altogether, 3631 and 1159 specimens of S. commersonnii and A. sirm respectively were collected. Each specimen of the two species was measured for total length (TL) on a measuring board to the nearest millimetre (± 0.1 mm), body length (BL), body weight (TW) and gonad weight (GW) to the nearest gram $(\pm 0.01g)$ using a sensitive digital balance.

The sex of each specimen was determined by macroscopic examination of the gonads. The gonadal maturity stages of males and females were assigned macroscopically according to the description of Athukoorala *et al.* (2015) based on five stages. Basically, external morphological criteria (shape, colour of testis and ovaries) were used to assign sex and maturity stages upon dissection.

The spawning seasons were established based on the analysis of two aspects: (i) gonadal maturity stages;

and (ii) gonadosomatic index (GSI), which was determined as: into an ogive function; a non-linear regression as described by Duponchelle and Panfili (1998):

$$GSI = (Gonad weight/ total fresh weight of fish) \times 100.$$

The length at first maturity (L_{M50}) was determined by computing the proportion of mature specimens in all size classes. Mature individuals at stage III and above were considered as mature for determination of L_{M50}

$$(L_{M50}) = (\% MF = \frac{1}{1 + e^{(-a(L - L_{M50}))}})$$

where %MF represents percentage of mature fish by size class, and L is the mid length of each size class, and a and L_{M50} are constants for the model. The pro-

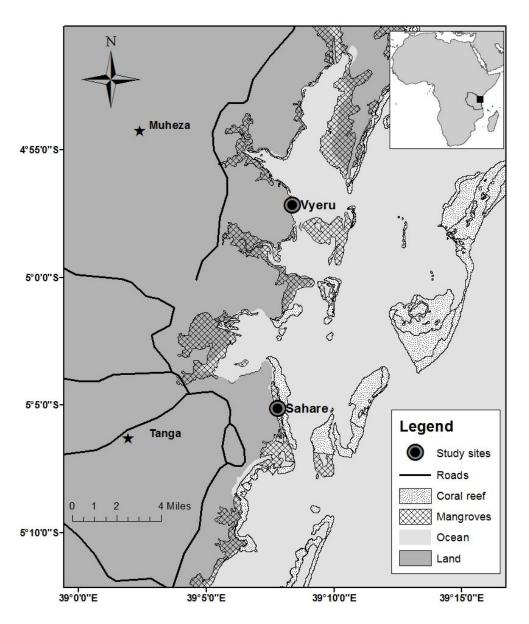


Figure 1. Location of sampling sites along the coast of Tanga Region.

of these species. The length at which 50% of individuals were found to be mature was considered as the size the species reaches maturity for the first time. The L_{M50} of both sexes was estimated at class intervals of 5 mm and 10 mm respectively and the data fitted portion of the two sexes comparative to one another was used to determine the sex ratio of the two species. Fecundity was determined by taking a pair of ovaries from mature female individuals (stages III and IV) and preserving these in plastic bottles containing Gilson's fluid. The sample of ovaries in bottles were kept at room temperature for three months, but were frequently and vigorously agitated to facilitate release of the eggs from the ovarian tissues.

The fecundity was determined by counting mature yolked oocytes of a ripe and gravid fish. The total fecundity of females of the two species was determined using a volumetric method, whereby plastic bottles containing ova and Gilson's fluid were repeatedly filled with tap water, and then the supernatant and remains of ovarian tissues decanted. Cleaned ova of S. commersonnii and A. sirm were diluted with tap water at a volume of 500 and 1000 ml, respectively. The mixture of eggs and tap water was transferred into a plastic jar of 90 mm diameter and 103 mm height, and then a plastic ruler was used to stir the mixture until the eggs were seen to be evenly distributed. A 1 ml subsample of the mixture (eggs and water) was quickly taken from the sample in the jar and then counted under a dissecting microscope at

X10 magnification. A total of five (5) subsamples were drawn per specimen, and the average from these subsample counts was considered as the number of ova in a mixture of specified volume (Murua *et al*, 2003). Total fecundity of each female of both species was estimated following the formula given by Holden and Raitt (1974) as follows:

$$F = nV/v$$

Where n = number of eggs in the subsample, V = volume to which the total number of eggs is made up, and v = volume of the subsample.

The relationship between size (length) and fecundity was derived from the equation:

where Y is fecundity, L is the total length of the fish in cm and a and b are constants as described by Madan and Velayudhan (1984).

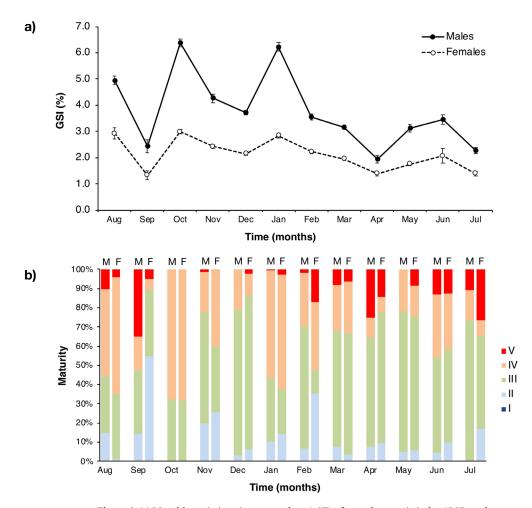


Figure 2. (a) Monthly variations in mean values (±SE) of gonadosomatic index (GSI), and (b) gonadal maturity stages of male (M) and female (F) *S. commersonii*.

Data analysis

The variation in the sex ratio of *S. commersonnii* and *A. sirm* was tested using the Chi-square test. The differences in GSI and condition factor (k) between sexes were tested using an independent t test. One way ANOVA was also applied to test GSI differences among months, and Tukey's *post-hoc* test was used for significance analyses in GSI values to determine which months were different from each other. Linear regression analysis was used to test the correlation between total length of female mature individuals of both species and their fecundity. All statistical data analyses were performed using SPSS analytical software. A 0.05 significance level was used for all tests.

Results

Mean monthly GSI values of *S. commersonnii* ranged from 1.93% to 6.38% in males and 1.34% to 3.00% in females, whereas in *A. sirm* they ranged from 0.25% to 2.68% and from 0.27% to 3.19% respectively (Fig. 2a & 3a). Findings of this study revealed that spawning in both

species is protracted. More importantly, it was observed that *S. commersonnii* spawned throughout the year, as gravid gonads (capable spawning individuals in stage IV) of this species were observed during all months.

The highest GSI values and percentages of gravid gonads of both sexes of *S. commersonnii* were recorded in October and January with females extending to August indicating peak spawning during these months (Fig. 2a & b). In *A. sirm*, spawning occurred between August and July for males and between September and July for females. The highest GSI values of male and female *A. sirm* in August and September respectively corresponded to higher proportions of individuals with ripe gonads (Stages IV) signifying that peak spawning occurs within these months (Fig. 3 a & b).

One-way ANOVA revealed that GSI values varied significantly among months in both species, with F $_{(11, 1727)}$ = 81.2; P< 0.001 and F $_{(11, 1416)}$ = 22.2; P<0.001 in males and females of *S. commersonnii* respectively.

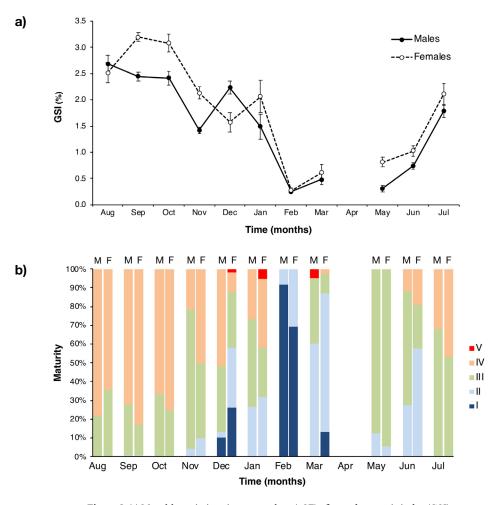


Figure 3. (a) Monthly variations in mean values (±SE) of gonadosomatic index (GSI), and (b) gonadal maturity stages of male (M) and female (F) *A. sirm*.

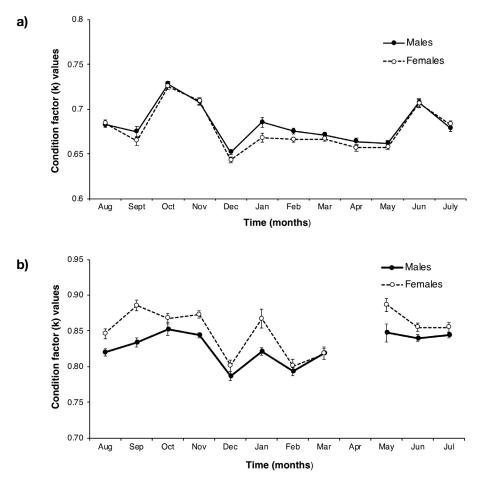


Figure 4. Monthly variations in the condition factor (K) of (a) *S. commersonnii*, and (b) *A. sirm* from both Sahare and Vyeru sites.

In *A. sirm* the GSI values were found to be F_(9, 398) = 39.5; P<0.001 for males and F_(10, 484) = 41.8; P < 0.001 for females. The GSI values in peak spawning months of males (October and January) and females (August, October and January) of *S. commersonnii* were significantly higher compared to other months (Tukey *post-hoc* test, P < 0.001). On the other hand, the peak GSI values of male and female *A. sirm* during August and September were significantly higher than all other months, with the exception of August and December (Tukey *post-hoc* test, P = 0.000). The GSI showed significant difference between sexes in both *S. commersonnii* (*t* test, t =26.3, P < 0.001) and *A. sirm* (*t* test, t = - 3.7, P < 0.001).

Condition factor

The monthly condition factor (K) for *S. commersonnii* revealed similar high values in both males and females between October (0.73) and November (0.71) respectively. This was followed by a decline through to December, an increase through to January and then a decline from February to May and picked again in June in both sexes (Fig. 4a). The monthly K values for both males and females of *A. sirm* were higher between May and October (0.85) and in May (0.88). A very sharp declining trend from November to December was noticed in both sexes of this species (Fig. 4b). Months where higher K values were recorded for both species as stated above, indicate that fish were in a better condition during these months compared to any other period in the present study (Fig. 4a & b). The condition factor (K) revealed significant differences between sexes in both species; *S. commersonnii* (*t* test, t = 2.99; P < 0.05) and *A. sirm* (*t* test, t = -9.09; P < 0.001).

Size at first maturity

Males of both species attained first sexual maturity (L_{M50}) at a small size compared to female individuals. The size at first sexual maturity for male and female of *S. commersonnii* were estimated to be 57.7 mm and 66.2 mm respectively (Fig 5a). For *A. sirm*, the sizes were 147.7 mm for males 169.2 mm for females (Fig. 5b).

The monthly sex ratio in *S. commersonnii* indicated that males dominated the catch for more than six

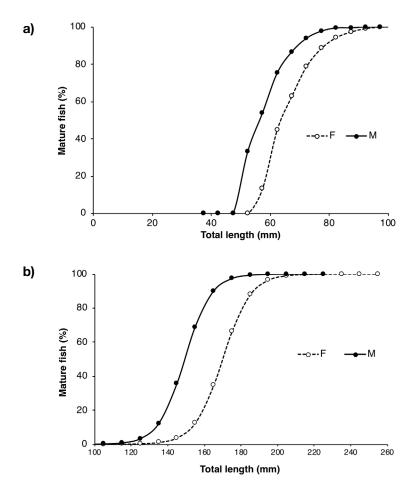


Figure 5. Size at first sexual maturity of (a) *S. commersonnii*, and (b) *A. sirm* from both Sahare and Vyeru sites.

months with a peak in August. The highest percentage of females was in September. Undetermined (UD) specimens were found almost throughout the study period, although in small numbers compared to males and females of this species. The highest proportion of UD specimens was recorded in September. The overall sex ratio of S. commersonnii was 1:0.9, being significantly in favour of females ($\chi 2 = 5.9$; df = 1; p < 0.05) (Table 1). In A. sirm, the predominance of males was observed from August to December and February, peaking in August. Females of A. sirm were more abundant in January, March, May and July with the highest percentage in May. UD specimens of this species were not recorded in most of the months except in January, February and March, with the highest proportion in February (Table 2). The overall sex ratio of A. sirm was 1:0.98 and a Chi-square test showed no significant difference from a normal ratio of $1:1(\chi 2)$ = 0.06; df = 1; p > 0.05).

The length frequency distribution are shown in Fig. 6 a and b. The total length of *S. commersonnii* and *A. sirm*

in the fishery varied from 47 mm to 102 mm and from 65 mm to 255 mm, respectively. Variations in sex ratio with size revealed that females of *S. commersonnii* predominated in larger size classes between 91 and 105 mm TL ($\chi 2 = 4.4 df = 1$; p < 0.05) while males dominated in smaller size classes between 61 and 90 mm TL ($\chi 2 = 7.7$; df = 1; p < 0.01). A similar trend was observed in *A. sirm*, where the dominance of females was in size classes between 181 and 260 mm TL ($\chi 2 = 66.3$; df = 1; p < 0.001), while males were more abundant in size classes between 150 and 180 mm TL ($\chi 2 = 63.8 df = 1$; p < 0.001).

The total fecundity ranged from 850 ova in a specimen of *S. comersonnii* of 68 mm and 1.9 g to 10,055 ova in a large *S. comersonnii* of 98 mm and 6.9 g, whereas in *A.sirm* it ranged from15,700 ova in a small fish of 170 mm and 35.7 g to 96,500 ova in a large fish of 258 mm and 94.5 g. The mean (\pm SE) fecundity of *S. comersonnii* and *A. sirm* was 5, 134. 66 \pm 136.94 ova and 47,029.03 \pm 1,435.13 ova, respectively. The relative fecundity of *S. comersonnii* ranged from 459.5 to 1448.8 ova per gram

| Months | Total no. of specimens | UD | Male No. | % | Female No. | % | Sex ratio (M:F) | Chi-square values |
|---------|------------------------|----|----------|------|---------------|------|--------------------|----------------------|
| Aug. 16 | 331 | 1 | 187 | 56.7 | 143 | 43.3 | 1:0.76 | 5.87* |
| Sept | 252 | 24 | 98 | 43.0 | 130 | 57.0 | 1:1.33 | 4.49* |
| Oct | 271 | 0 | 151 | 55.7 | 120 | 44.3 | 1:0.79 | 3.55 |
| Nov | 311 | 11 | 154 | 51.3 | 146 | 48.7 | 1:0.95 | 0.21 |
| Dec | 513 | 4 | 280 | 55.0 | 229 | 45.0 | 1:0.82 | 5.11* |
| Jan. 17 | 280 | 1 | 138 | 49.5 | 141 | 50.5 | 1:1.02 | 0.03 |
| Feb | 331 | 3 | 155 | 47.3 | 173 | 52.7 | 1:1.12 | 0.99 |
| Mar | 344 | 11 | 188 | 56.5 | 145 | 43.5 | 1:0.77 | 5.55* |
| Apr | 165 | 8 | 77 | 49.0 | 80 | 51.0 | 1:1.04 | 0.06 |
| May | 302 | 9 | 159 | 54.3 | 134 | 45.7 | 1:0.84 | 2.13 |
| Jun | 265 | 13 | 131 | 52.0 | 121 | 48.0 | 1:0.92 | 0.39 |
| Jul | 266 | 10 | 122 | 47.7 | 134 | 52.3 | 1:1.10 | 0.56 |
| Pooled | 3631 | 95 | 1840 | 52.0 | 1696 | 48.0 | 1:0.92 | 5.86* |

Table 1. Monthly variation in sex ratio of S. commersonnii collected from Sahare and Vyeru landing sites from August 2016 to July 2017.

*Significant at 0.05 level of error or 95% confidence

Table 2. Monthly variation in sex ratio of A. sirm collected from Sahare and Vyeru landing sites from August 2016 to July 2017.

| Months | Total No. of specimens | UD | Male No. | % | Female No | % | Sex ratio (M:F) | Chi-square values |
|---------|------------------------|----|-------------|------|--------------|------|--------------------|----------------------|
| Aug. 16 | 85 | 0 | 58 | 68.2 | 27 | 31.8 | 1: 0.47 | 11.31** |
| Sept | 300 | 0 | 144 | 48.0 | 156 | 52.0 | 1 :1.08 | 0.48 |
| Oct | 50 | 0 | 26 | 52.0 | 24 | 48.0 | 1:0.92 | 0.08 |
| Nov | 136 | 0 | 74 | 54.4 | 62 | 45.6 | 1:0.84 | 1.06 |
| Dec | 124 | 8 | 59 | 50.9 | 57 | 49.1 | 1 : 0.97 | 0.03 |
| Jan. 17 | 34 | 0 | 15 | 44.1 | 19 | 55.9 | 1: 1.27 | 0.47 |
| Feb | 99 | 63 | 23 | 63.9 | 13 | 36.1 | 1 :0.57 | 2.78 |
| Mar | 89 | 24 | 24 | 36.9 | 41 | 63.1 | 1 :1.71 | 4.45 * |
| Apr | | | | | | | | |
| May | 27 | 0 | 8 | 29.6 | 19 | 70.4 | 1: 2.38 | 4.48 * |
| Jun | 154 | 0 | 77 | 50.0 | 77 | 50.0 | 1 :1.0 | - |
| Jul | 61 | 0 | 28 | 45.9 | 33 | 54.1 | 1:1.18 | 0.41 |
| Pooled | 1159 | 95 | 536 | 50.4 | 528 | 49.6 | 1: 0.98 | 0.06 |

*Significant and ** very significant at 0.05 level of error or 95% confidence

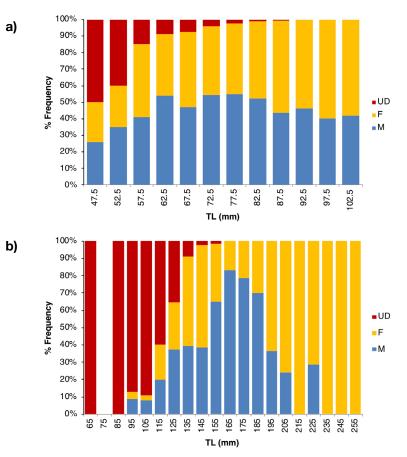


Figure 6. Length-frequency distribution of male, female and undetermined (a) *S. commersonnii*, and (b) *A. sirm.*

of fish with a mean (\pm SE) of 1047.01 \pm 14.2 ova per gram of fish; whereas in *A.sirm* it ranged from 374.4 to 1075.8 ova per gram of fish and averaged (\pm SE) at 723.5 \pm 14.6 ova per gram of fish.

The power function revealed a significant correlation between total length (TL) of fish and total fecundity (Y), with allometric growth in both species (Y= 0.000003TL^{4,77}, r = 0.76, df = 144, P< 0.001 in *S. comersonnii* (Fig. 7a); and Y = 0.0000007 TL^{4,72}, r = 0.68, df = 123, P< 0.001 (Fig. 7b) in *A. sirm*). The correlation between fish weight and total fecundity in both species showed a positive linear relationship; Y= - 4004.7 + 1916.8 TW, and a strong correlation coefficient (r = 0.9, F= 6.82, df = 144, P < 0.001) in *S. comersonnii*, and Y= - 17757.5 + 1014.6, r = 0.9, F= 6.82, df = 144, P < 0.001 in *A. sirm*.

Discussion

The findings of this study revealed that the two species exhibit protracted spawning. Moreover, mature individuals of both male and female *S. commersonnii* with ripe gonads were collected throughout the sampling period, which suggests that the species spawns throughout the year on the Tanzanian coast. This pattern agrees with other studies on *Stolephorus* species; for instance Basilone *et al.* (2006) and Rohit and Gupta (2008) reported similar spawning behaviour in stolephorid anchovies and *Stolephorus waitei*. On the other hand, extended spawning in *A. sirm* has also been reported elsewhere in the world; for instance Conand (1991), Veerappan *et al.* (1997), and Authukoorala *et al.* (2015).

A prolonged spawning period for several months or during the entire year is a character of an indeterminate serial spawning fish (George, 1998). Serial spawners (including anchovies and most clupeids) are known to produce more eggs compared to total spawners (eg. eels - Anguilla spp). Most serial spawners, especially anchovies, are small in body size and normally do not have sufficient space in their body cavities to accommodate the total amount of eggs produced per year at the same time; therefore they need to spawn in batches for long periods (Maack and George, 1999). Palomera (1992) related random spawning over time in clupeids to a strategy that enables at least some batches of larvae to encounter favourable environmental conditions to enhance individual survival. The scattered spawning peaks (Fig. 2a & 3a) observed

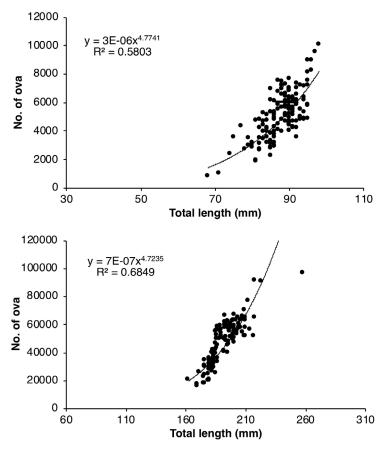


Figure 7. Length-fecundity relationship of a) *S. commersonnii* (N=145), and b) *A. sirm* (N = 124).

in the present study support the point that S. commersonnii and A. sirm are serial spawners.

The peak spawning period of S. commersonnii during this study falls virtually at the same time as that of Stolephorus devisi as reported by Rohit and Gupta (2008). This similarity could probably be attributed to the fact that the two species share many morphological and ecological similarities, hence their life histories do not differ much. However, the peak spawning seasons of S. commersonnii reported during this study are partially comparable to that of Luther et al. (1992) who found that this species exhibited two spawning peaks; February - October and March - May. Such variations suggest flexibility in S. commersonnii to regulate their reproductive period according to environmental factors, of which nutrient availability, photoperiod and temperature have been reported as the main factors affecting reproduction of engraulids in coastal waters (Silva et al., 2003; Araújo et al., 2008). Several studies have also reported different spawning seasons in anchovies (engraulidae) in tropical and sub-tropical waters, including Kim et al. (2013) and Andamari et al. (2002).

The condition factor (K) is another aspect widely used in studies on reproductive biology of different fish species, predicting that individuals with higher K values are in better physiological condition (Rodrigues-Filho et al., 2011). The present study showed that K values for both sexes of S. commersonnii were higher in one of the peak spawning periods (October) (Fig. 4a) and then exhibited a declining trend in the other two peak periods (January and August). A similar trend was observed in A. sirm where the highest K value (0.89) seemed to correspond with the peak spawning period (September) in females, and a slightly lower value (0.82) in the peak spawning period (August) for males, as compared to the values recorded in May and October (Fig. 4b). The slight decline in K values observed during peak spawning of these two species indicates high energy expenditure during spawning (Rodrigues-Filho et al., 2011) which probably resulted in poor fish health condition as K values lower than 1 implies the fish is in poor health (Bhattacharya and Sree, 2012). This could result in minor effects on newly fertilized eggs, rates of hatching and larval survival of these species (Souza-Conceição et al., 2005).

The size at first maturity of male and female S. commersonnii in the present study are comparable to that reported by Alba et al. (2016) for unsexed individuals at 71 mm, but lower than those (110 mm and 109 mm) reported by Luther (1979) and Andamari et al. (2002), respectively. In addition, the sizes that were obtained for both sexes of A. sirm during this study almost concur with those reported by Veerappan et al. (1997) at 150 mm and 160 mm for males and females, respectively. However, Conand (1991) found sizes at first maturity for A. sirm to be higher (between 175-179 mm in males and 180-184 mm in females) as compared to the ones observed in the present study. This signifies that fishes that belong to the same species may attain first maturity at different sizes depending on the condition of the environments they inhabit and other associated factors. This is in agreement with other scientists who suggested that the growth of fish could be retarded by environmental conditions and food resources (Wootton, 1990) and pressure exerted from fishing activities (Baali et al., 2017).

Moreover, changes in size at first maturity may be ascribed to the different strategies utilised by fish in different environments to better adapt to environmental conditions (Baali *et al.*, 2017). This study also demonstrated that males of both species attained first sexual maturity at smaller sizes than females. This could either be due to variations in the quantity of energy reserves available for gonad development, as a direct effect (Morgan, 2004), or due to changes in growth, which influence the onset of gonadal maturation, as an indirect effect (George and Mikko, 2004). The males of *S. commersonnii* and *A. sirm* matured earlier than the females, probably because they required less energy reserves for gonadal maturation.

The overall sex ratio observed in *S. commersonnii* during this study concurs with the observation by Rohit and Gupta (2008), who reported a sex ratio of 1:07 in *Stolephorus insularis* along the Manglore-Malpe coast of India. Furthermore, the current study showed an insignificant difference from the expected population ratio of 1:1 in *A. sirm*. A similar trend was found in other clupeid species like *Sardinella lemuru* in Western Australia (Gaughan and Mitchell, 2000), and *Sardinops sagax* (Gaughan *et al.*, 2008), but differed from that reported by Jayasuriya (1989) and Veerappan *et al.* (1997) who found a predominance of females in the overall sex ratio of *A. sirm* in Sri lanka and India.

S. commersonii and A. sirm revealed a skewed size-dependent sex ratio with females dominating in larger size classes during this study. This was also evident in other tropical and sub-tropical waters for Stolephorus hetrolobus (Milton et al., 1990), and anchovies like Engraulis encrasicolus (Baali et al., 2017) and A. sirm (Veerappan et al., 1997). This could be ascribed to a number of factors including faster growth of females resulting in them becoming vulnerable to fishing gear, and displaying different migratory movements as compared to males (Abderrazik et al., 2016), and natural mortality differing between the sexes (Turner et al., 1983). The most likely hypothesis in the case of the present study could be migration. Anchovies and clupeids of the same cohort are known to move in large schools over long distances (hundreds of kilometres) searching for food and spawning. These types of movements are very common in these fishes as a mechanism to increase survivorship by diminishing detection by predators (Swartzman, 1991), and confusing predators by complex coordinated manoeuvres (Eshel, 1978) while looking for food and undertaking other activities. It is probable that this kind of spatial movement affected all size classes of both sexes and species during this study.

The monthly deviation in sex ratio observed in both species during this study could be explained by migration or behavioural differences between the sexes which allow one sex to be more easily caught than the other. A similar variation in sex ratio in other anchovies has been found off California (Klingbeil, 1978) and in Peru (Alheit et al., 1984). This deviation has also been reported in other cluipeids such as Sardinella longiceps along the coast of Ratnagiri off Maharashtra in India (Deshmukh, et al., 2010). It has been indicated that such variations in the sex ratio are difficult to describe, but some authors have this to a combination of factors including availability of the food in the region, as found by Nikolsky (1969) who reported that when food is abundant in a particular area, females predominate, and the situation changes where food is limited. The spatial segregation of spawning and non-spawning fish is another factor that has been observed to cause variation in some anchovy and clupeid species (Williams and Clarke, 1983). Females of these families tend to separate either by depth or area from the non-spawners, migrating with predominantly males to establish spawning schools (Alheit et al., 1984). The observed monthly variation in sex ratio of the two species investigated in the present study could be attributed to one or a combination of all these factors.

The present study found a direct proportional relationship between size (total length and weight) and

fecundity of mature and gravid females in both species. These findings comply with Rao (1988) in Stolephorus spp and Veerappan et al. (1997) in A. sirm. Other species in the family Clupeidae have also shown this kind of relationship; for instance Zaki et al. (2012) reported the fecundity of Sardinella longiceps to increase with increase in size (ranging from 22,456 ova at 159 mm TL and 36 g, to 61, 867 ova at 187 mm TL and 54 g). This relationship was found in both S.commersonni and A. sirm during this study, and could be explained by the fact that as the fish increases in size (length and weight) more space is created for accommodating eggs. This makes sense in that an increment in body size tends to increase the size of the body cavity, and ensures availability of more energy for the production of many eggs (Jonsson and Jonsson, 1997; Singh et al., 1982). Moreover, this study found the fecundity of S. commersonnii and A. sirm to range between 850 at 68 mm TL - 10055 eggs at 98 mm TL, and 17500 at 170 mm TL - 96,500 eggs at 258 mm TL respectively; being higher than the ranges of S. devis (162 eggs to 3166 at a size between 61-96 mm TL) and slight lower than that of A. sirm (21,800 eggs at 121 mm TL to 124, 800 at a size of 226 mm TL) as reported by Rao (1988) and Veerappan et al (1997). Such variation in fecundity could be attributed to differences in environmental conditions that may influence food availability in the area, but also to high fishing pressure which can stress the fish and affect reproduction processes.

Conclusion

This study has confirmed that both species are multiple spawners. Moreover, intensive spawning of both sexes of *S. commersonnii* occurred in August, October and January while in *A. sirm* this occurred during August and September for males and females respectively. Taking this into consideration, it is recommended that the responsible authorities start practicing management measures such as seasonal closures during peak seasons to reduce growth overfishing of these species. However, most emphasis should be put on *S. commersonnii*, which is the most abundant small pelagic species from Tanga coastal waters. This species faces continual heavy exploitation pressure due to high demand in and outside the country.

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