ASPECTS OF THE FECUNDITY OF THE BLACK-CHINNED TILAPIA SA-ROTHERODON MELANOTHERON IN THE FOSU LAGOON, GHANA

T. QUARCOOPOME* AND S. A. OWIREDU CSIR-Water Research Institute, P. O. Box AH 38, Achimota *Corresponding author's email – qpome@yahoo.com

Abstract

The black-chinned tilapia, Sarotherodon melanotheron (Pisces: Cichlidae), which dominated the Fosu Lagoon fishery, was exposed to pollution, siltation, fishing pressure, destructive fishing methods, and climate change. Samples of black-chinned tilapia were obtained with cast net, drag net and gill net, out of which 441 gravid specimen were randomly selected and dissected to remove eggs which were then counted. The absolute fecundity varied from 20 eggs to 370 eggs with mean of 78 ± 33 eggs. Fish that had fecundity below and above the reported minimum of 200 eggs constituted 98.86 per cent and 1.14 per cent of total sample, respectively, indicating that fecundity is below the minimum number of eggs the species is reportedly capable of producing. Positive, linear, weak and significant relationships were found between absolute fecundity and body parameters indicating that absolute fecundity is independent of body parameters, and could be influenced by biological, environmental, or anthropogenic factors. Condition factor ranged between 2.26 SL and 10.63 SL. Length at first maturity was 4.8 cm SL and 6.4 cm TL, respectively, confirming the precocious reproductive habit of the species. The size structure of the S. melanotheron population is dominated by small-sized fish of SL 7.0 - 7.9 cm (44.90 %) and 6.0 - 6.9 cm SL (32.65 %) ranges, which together accounted for 77.55 per cent of the total sample. It is recommended that the fecundity and other reproductive parameters of the species be investigated during the dry and wet seasons in order to determine the reproductive potential and strategies for survival of the species.

Introduction

The black-chinned tilapia, *Sarotherodon melanotheron* occurs naturally and abundantly in the coastal waters of western Africa from Senegal to DR Congo (Trewavas, 1983; Trewavas & Teugels, 1991). In Ghana, *S. melanotheron* is one of the socioeconomically important and most abundant indigenous cichlid fish species found mostly in brackish water ecosystems which comprise over 90 lagoons and estuaries along the 550 km coastline (Falk, Abban & Villwock, 1999; Abban *et al.*, 2000). The dominance of *S. melanotheron* in coastal waters where it forms between 65 per cent and over 90 per cent of commercial catches, and has culture potential (Pauly, 1976; Mensah, 1979; Blay & Asabere-Ameyaw, 1993; Falk, Abban & Villwock, 1999; Abban *et al.*, 2000) is attributed to its resilience and prolific reproductive habits typically reported for cichlids (Fryer & Iles, 1972). S. melanotheron is, however, threatened by pollution, siltation, overfishing, destructive fishing methods as well as habitat degradation and destruction in many lagoons (Abban *et al.*, 2000), including Fosu lagoon.

Fecundity is one of the most important parameters for estimating reproductive potential which has direct bearing on fish production, exploitation and management. King (1978) indicates that fecundity is important in determining the reproductive life history of fish and understanding various aspects of fish biology. Fecundity, however, is not a constant feature but fluctuates with variations in environmental factors such as food abundance, availability and consumption, water temperature, fish density, biomass index (Trippel, 1998; Lambert *et al.*, 2003; Kamler, 2005) and biological factors such as female fish size, trade-off between egg size and egg number, reproductive strategy and spawning pattern of the species (Lambert, 2008).

This study was undertaken against the backdrop of paucity of information on the fecundity of S. melanotheron, and its strategic adaptation and survival in Ghanaian brackish water environments. This is coupled with the observed high number of gravid fish harvested during the Fosu Lagoon Renaturation and Restoration Project as well as the exposure of the species to pollution, fishing pressure and climate change. The objective of the study, therefore, was to provide information on aspects of the fecundity of S. melanotheron to enhance the determination of its production potential, and understanding of its reproductive survival strategies for effective and sustainable management of fish in the Fosu lagoon for sustainable development.

Experimental

Study area

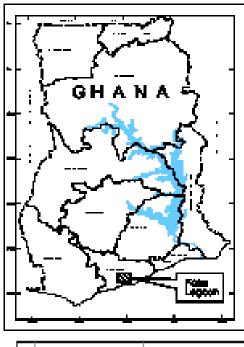
Fosu Lagoon is located in Cape Coast, in the Central Region of Ghana, and lies between latitude 5° 06' N – 5° 07' N and longitude 1° 15' W – 1° 16' W (Fig. 1). It is a 'closed' coastal lagoon separated from the sea (Gulf of Guinea) by a sand bar, and occasionally

breached during heavy rainfall or manually by sand winning activities or as part of rituals during the Fetu festival in the region. Fosu lagoon is a shallow lagoon with a surface area of 0.61 km² (61 ha) and mean depth of 1.5 m (CSIR-WRI, 2013). The lagoon is surrounded by many sites that act as point sources for discharge of contaminants. These include households, transport garages, mechanical workshops, educational institutions, a hospital, refuse dumps and sewages. Human activities in the study area are immense resulting in massive sedimentation and consequent invasion of aquatic macrophytes, especially in the more populated northern section (CSIR-WRI, 2013).

The study area is located within the littoral anomalous zone of Ghana which experiences less rainfall than the interior part of Ghana. Generally, the region is humid, experiencing high temperatures and two wet seasons in a year. The Antem stream and wetlands nearby contribute flow into the Fosu lagoon. Due to developments such as schools, hospitals etc. at the periphery of Fosu lagoon, ephemeral streams that used to drain into marshes and wetlands near the lagoon have been destroyed (CSIR-WRI, 2013).

Data collection

Fish samples from the Fosu lagoon were obtained from hired fishermen using cast nets, gill nets and two-man drag nets during the Fosu Lagoon Renaturation and Restoration Project in 2013. For each fishing gear, the fishermen sampled for specific periods in all different sections of the lagoon. The standard size of gill net was 91.4 m whilst 5.5 m (100 yds \times 6 yds), whilst that of the



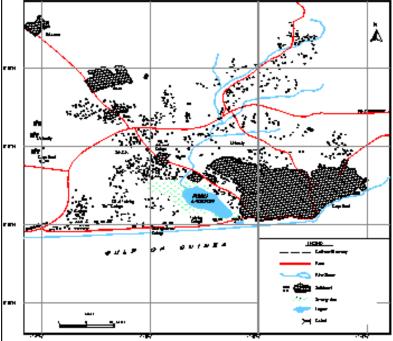


Fig. 1 Map of Ghana showing Fosu lagoon

cast net was 34 m long and 6.6 m base diameter with mesh size (stretched) of both nets being 12.7 mm ($\frac{1}{2}$ inch). The two-man drag net measured 15. 8 m \times 12.3 m with a mesh size of 5.0 mm. The specimens were randomly selected and preserved in formalin in the field, and washed under running tap water in the laboratory to get rid of the preservative before measurements were taken. The standard length (SL) and total length (TL) of each specimen were measured to the nearest 1.0 mm and 0.1 cm, respectively, on a fish measuring board, whilst the body weight (W) was measured to the nearest 0.1 g using a beam balance (KERN, EMB 500, Kern & Sohn, GmbH, Germany).

Each fish was dissected and gonads inspected visually to determine the maturity stage (Bagenal & Braum, 1968). A total of

> 441 specimens at stages three and four were selected randomly for fecundity analysis, by taking out the ovaries with the help of forceps and weighing with a beam balance (KERN, EMB 500, Kern & Sohn, GmbH, Germany). Females at maturity stage three had orange-reddish ovaries with eggs clearly discernible and ovaries occupying about two-thirds of the ventral cavity. For females at maturity stage four, the ovaries filled the ventral

cavity, whilst eggs were completely round and fell from ovaries with little pressure. Eggs were then separated from the ovarian tissues by placing them in modified Gilson fluid to harden the eggs, and help in breaking the ovarian tissue and liberating the individual eggs for counting.

Data analyses

Absolute fecundity (F) is the total number of eggs in the ovaries of a fish prior to spawning (Bagenal, 1978). Relative fecundity was determined with respect to various body parameters as follows: Body Weight: RF = AF/BW; Standard Length: RF = AF/SL; Total Length: RF = AF/TL (Biswas, 1993) where RF is the relative fecundity, AF is absolute fecundity, BW is body weight, SL is standard length and TL is total length.

To establish the relationship between absolute fecundity and body parameters, scatter diagrams of absolute fecundity against standard, total length, body weight and gonad weight separately as well as gonad weight against body weight were drawn, and a linear regression line fitted on each scatter diagram which was of the equation Y = a +bx where Y = fecundity, X = body parameters namely standard length (SL) and Total length (TL) in cm, body weight (BW) and gonad weight (GW) in g, constant a = intercept and constant b = slope.

Condition factor was computed using the formula $CF = 100 \times W/L^3$ (Ricker, 1975) where W was weight in g and L was total length in cm. The Mean condition factor for the population of gravid fish was calculated.

Length-weight relationship was established using the equation $W = a L^b$ where W was the weight (g) of fish and L was total length (cm) a and b were constants namely intercept and slope of graph, respectively. Data analyses were performed with Microsoft Excel version 2010 which was also used to generate relevant graphs. Analysis of Variance (ANOVA) was performed to determine whether there were any significant differences between the absolute fecundity and body parameters.

Results and discussion

Length frequency

Total length for gravid *S. melanotheron* from Fosu lagoon ranged from 4.0 to 14.0 cm. Length frequency group 7.0 - 7.9 cm accounted for 44.90 per cent of the total sample followed by the 6.0 - 6.9 cm length group, which made up 32.65 per cent with the 8.0 - 8.9 cm length group accounting for 12.93 % (Fig. 2). The difference in maximum length (14.0 cm TL) recorded in the study and that of 15.9 cm reported by Blay & Asabere-Ameyaw (1993) for the same lagoon, could be attributed to differences in sampling duration, environmental parameters such as pollution, and anthropogenic factors such as overfishing.

Length-weight relationship

The length-weight relationship of gravid *S. melanotheron* from the Fosu lagoon is represented by the equation $W = 0.026 \text{ TL}^{2.81}$ ($r^2 = 0.931$) (Fig. 3) which is similar to $W = 0.025 \text{ TL}^{2.78}$ ($r^2 = 0.928$) reported by CSIR-WRI (2013). The exponent 2.81 indicates that the growth pattern of gravid *S. melanotheron* is negatively allometric, meaning that increases in length and weight of the fish is not equal during growth resulting in fish becoming slender as they grow.

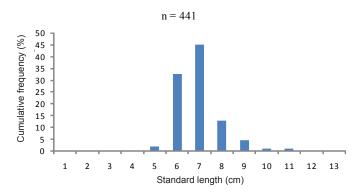


Fig. 2. Length frequency distribution of gravid *S. melanotheron* from Fosu lagoon

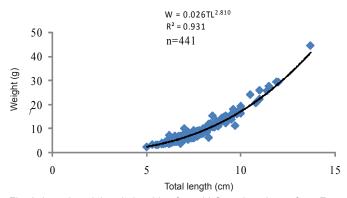


Fig. 3. Length-weight relationship of gravid *S. melanotheron* from Fosu lagoon

Condition factor

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The condition factor of a fish is a measure of the physiological 'well-being' or 'fatness' of the fish species, and gives an indication of the suitability of the aquatic environment for the growth of the species. The condition factor of gravid *S. melanotheron* population based on standard length varied from 2.26 to 10.63. This means that fish, which had condition factor of 2.26, was poorer in condition, whilst fish in better condition had a condition factor of 10.63. The mean condition factor of 3.75 for the population is typical of cichlids and indicates that the aquatic

environment of the Fosu lagoon is favourable for the growth of S. melanotheron. The mean condition factor was slightly lower than 3.9 reported by CSIR-WRI (2013) for all sexes combined, suggesting that some energy is being diverted into reproductive activities by the gravid individuals. About 43 per cent of the sampled fish had a condition factor greater than the mean population value indicating that almost half of the gravid S. melanotheron population in the Fosu lagoon is in good condition.

Length at first maturity

The size at first maturity for gravid *S. melanotheron* from Fosu lagoon was 4.8 cm and 6.4 cm for standard length and total length, respectively (Fig. 8), indicating precocious repro-

ductive habit. Among the reasons accounting for the precocious reproductive habit in the study, is the intense fishing pressure and the high numbers of gravid fish caught by fishermen. Intense fishing pressure is a selective pressure for fish to become reproductively mature at smaller sizes such as was reported from the Keta and Songor lagoons in Ghana (Dankwa *et al.*, 2004). The size at first maturity obtained in the study is lower than the value of 6.0 cm for male and female separately reported for the same lagoon by CSIR-WRI (2013) and Blay & Asabre-Ameyaw (1993) but higher than 4.0 cm SL for mature females (Eyeson, 1983). Length at first maturity of 6.4 cm TL was higher than 6.0 cm TL reported by CSIR-WRI (2013) and lower than 6.9 cm SL for brooding female reported by Trewavas (1983). These results were, however, far below that of Legendre (1983) who reported female *S. melan*- measured were below the minimum of 200 eggs reported by Trewavas (1983), leaving only five individuals representing 1.14 per cent having fecundity above the reported minimum. This indicates that the fecundity of *S. melanotheron* from Fosu lagoon is be-

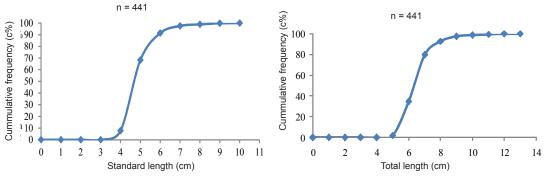


Fig. 4. Length at first maturity for gravid female S. melanotheron from Fosu lagoon

otheron size at first maturity of 13.4 cm from the Niger Delta in Nigeria. The findings indicate progressively decreasing size at which female *S. melanotheron* become mature in the Fosu lagoon.

Absolute fecundity

The absolute fecundity of *S. melanotheron* from the Fosu lagoon varied from 20 eggs for a fish measuring 4.7 cm SL, 5.8 cm TL and weighing 3.9 g to 370 eggs for a fish of length 9.3 cm SL, 12.0 cm TL and weighing 29.3 g. The egg of the biggest fish did not give the highest weight neither did the egg of the smallest fish give the least weight, indicating that fish of the same size or weight had variable fecundities. The mean absolute fecundity for 441 fish samples was 78 ± 33 eggs, whilst the most frequently observed absolute fecundity was 65 (Table 1). The results showed that 436 fish specimens representing 98.86 per cent of all gravid fish

low the minimum range of eggs the species is capable of producing.

The fecundity of 107 to 580 eggs reported for T. melanotheron in the Lagos lagoon in Nigeria by Fagade (1979) is slightly better than that reported in the study, possibly due to the effect of environmental factors such as pollution, fishing pressure and siltation occurring in the Fosu lagoon. The differences observed in the study compared with what was reported is in agreement with Withames et al. (1995) who stated that within a given species, fecundity may vary as a result of different adaptations to environmental habitat. Horwood, Bannister & Howlett (1986), Rijnsdorp (1991) and Kjesbu et al. (1998) indicated that even within a stock, fecundity is known to vary annually and undergo long term changes. Fagade et al. (1984) suggested that, variation in fecundity may be due to differential abundance of food, whilst Fawole & Arawomo (2000) indicated that wide

Parameter	Min	Max	Mean	Std dev	Mode
Standard length	4.0	10.5	58.03	8.26	55.0
Total length	5.0	13.7	73.54	10.26	72.0
Weight	2.3	44.5	7.69	4.0	6.0
Gonad weight	0.1	2.9	0.62	0.36	0.7
Abs. fecundity	20	370	78.0	32.75	65.0
Rel. fecundity (SL)	0.38	4.17	1.32	0.41	1.09
Rel. fecundity (TL)	0.32	3.26	1.04	0.32	1.0
Rel. fecundity (Wt)	2.70	28.73	10.71	2.95	10.0
Condition factor (SL)	2.26	10.63	3.75	0.55	3.67
Condition factor (TL)	1.08	3.02	1.84	0.19	1.72

 TABLE 1

 Descriptive statistics of fecundity parameters of gravid S melanotheron from Fosu Jagoo

fluctuations in fecundity could be attributed to differential feeding success as observed in *S. galileus* from Opa reservoir in Nigeria.

Bala & Abdullahi (2011) reported on the mean fecundity and egg range, respectively, of related species namely *O. niloticus* (1465; 222 – 9642) and *S. galileus* (1110; 197 – 4414) from the Sabke reservoir in Nigeria.

Relative fecundity

Fecundity relative to standard length, total length and body weight are shown in Table 1.

Relationships between absolute fecundity and body parameters

Relationships between absolute fecundity and various body parameters of *S. melanotheron* from the Fosu lagoon are presented in Figs 5 – 9. The equations for the body parameters studied were significant (P < 0.05), indicating that the differences are not due to chance but could be influenced by some environmental, bio-

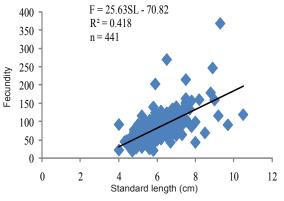


Fig. 5 Relationship between Absolute fecundity and Standard length for gravid *S. melanotheron* from Fosu lagoon

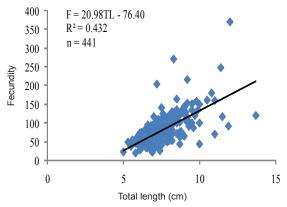


Fig. 6 Relationship between Absolute fecundity and Total length for gravid *S. melanotheron* from Fosu lagoon

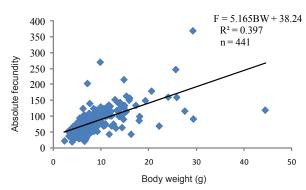


Fig. 7. Relationship between Absolute fecundity and Body weight for gravid S. melanotheron from Fosu lagoon

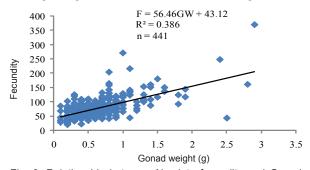


Fig. 8. Relationship between Absolute fecundity and Gonad weight for gravid *S. melanotheron* from Fosu lagoon

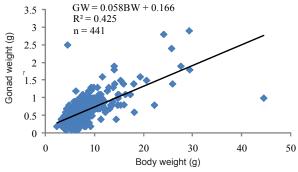


Fig. 9. Relationship between gonad weight and Body weight for gravid *S. melanotheron* from Fosu lagoon

logical or anthropogenic factors, but would need further research. The r^2 values ranged between 0.386 and 0.425 indicating weak correlation between absolute fecundity and body parameters. This means that absolute fecundity is independent of the body parameters for gravid *S. melanotheron* in the Fosu lagoon.

According to Gueye et al. (2012), S. melanotheron exhibited different reproductive strategies in different ecosystems. One of the reproductive strategies for the survival of gravid S. melanotheron in Fosu lagoon in the face of pollution, fishing pressure and climate change was impaired growth or stunting manifested by reduced sizes. Early sexual maturity or precocious reproductive habit evidenced by reduced sizes at first maturity could be a reproductive strategy for the gravid fish as corroborated by CSIR-WRI (2013) for combined sexes. The survival of S. melanotheron is being undermined by the observation that, fishing with drag nets removed more smaller-sized fish (below 6.0 cm) as well as more gravid fish than the other fishing gears.

Conclusion and recommendations

The absolute fecundity of gravid *S. melanotheron* population from the Fosu lagoon varied from 20 to 370 eggs with a mean of 78 ± 33 eggs. The fecundity is below the minimum number of eggs the species is reported to be capable of producing, with 98.86 per cent of the fish having fecundity below the reported minimum of 200

eggs, whilst 1.14 per cent of them had fecundity above the minimum. Positive, linear, weak and significant relationships were found between absolute fecundity and body parameters namely body weight, standard length, total length and gonad weight. It is recommended that the fecundity and other reproductive parameters of the species be investigated in one annual cycle during both the dry and wet seasons, to unravel the reproductive potential and reproductive strategies for survival of the species for proper management to ensure the sustainability of *S. melanotheron* in the Fosu Lagoon. Further research areas for investigation include the effect of anthropogenic, environmental and climatic factors on the fecundity of *S. melanotheron* as well as the effect of fishing gears on the survival of the species.

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References

- ABBAN, E. K., CASAL, C. M. V., FALK, T. M. & PULLIN, R. S. V. (2000) Biodiversity and sustainable use of fish in the coastal zone. *ICLARM Conf. Proc.* 63, 71 pp.
- BAGENAL, T. B. (1978) Methods for assessment of fish production in fresh water. Blackwell Scientific Publications, Oxford, London. 365 pp.
- BAGENAL, T. B. & BRAUM, E. (1968) Eggs and life history. In *Methods for assessment of fish* production in freshwaters (Ricker, W. E. ed). 1st edn. International Biological Programme Handbook, London No 3. Blackwell Scientific Publications. Oxford. Edinburg. pp 159 – 181.
- BALA, U. & ABDULLAHI, S. A. (2011) Aspects of the reproductive biology of fish of commercial importance in Sabke reservoir, Katsina State, Bayero. *Journal of Pure and Applied Sciences* 4(2), 178 – 181.
- BISWAS, S. P. (1993) Manual of methods in fish biology. Delhi, South Asian Publishers Pvt. Ltd., New Delhi International Book Co., Ab-

secon Highlands, New Jersey. pp. 65 – 91.

- BLAY, J. JR & ASABERE-AMEYAW, A. (1993) Assessment of the fishery of a stunted population of the cichlid, *Sarotherodon melanotheron* (Rüppel), in a closed lagoon in Ghana. *Journal of Applied Ichthyology* 9, 1 – 11.
- CSIR-WRI (2013) *Restoration and Renaturation* of Fosu lagoon. CSIR, Water Research Institute report prepared for Cape Coast Municipal Assembly, Cape Coast. 134 pp.
- DANKWA, H. R., SHENKER, J. M., LIN, J., OFORI-DANSON, P. K. & NTIAMOAH-BAIDU, Y. (2004) Fisheries of two coastal tropical lagoons in Ghana, West Africa. *Fisheries Management* and Ecology 11, 379 – 386.
- EYESON, K. N. (1983) Stunting and reproduction in pond-reared *Sarotherondon melanotheron*. *Aquaculture* **31**, 257 – 267.
- FAGADE, S. O. (1979) Observations on the Biology of Two Species of Tilapia from Lagos Lagoon, Nigeria. Bulletin d'LFAN T41 Ser. A No. 3.
- FAGADE, S. O., ADEBISI, A. A. & ATANDA, A. N. (1984) The breeding cycle of *Sarotherodon* galileus in the IITA lake, Ibadan, Nigeria. *Arch. Hydrobiol.* 100, 493 – 500.
- FALK, T. M., ABBAN, E. K. & VILLWOCK, W. (1999) Population genetic analysis of the haemoglobins of the black chinned tilapia Sarotherodon melanotheron (Teleostei, Cichlidae). Journal of Fish Biology 55, 233 – 242.
- FAWOLE, O. O. & ARAWOMO, G. A. O. (2000) Fecundity of *Sarotherodon galileus* (Pisces: Cichlidae) in the Opa reservoir, Ile-Ife, Nigeria. *Rev. Biol. Trop.* 48, 201 – 204.
- FRYER, G. & ILES, T. D. (1972) The cichlid fishes of the Great Lakes of Africa. Their biology and evolution. Oliver & Boyd, Edinburgh. 641 pp.
- GUÈYE, M., TINE, M., KANTOUSSAN, J., NDIAYE, P., THIAW, O. T. & ALBARET, J-J. (2012) Comparative analysis of reproductive traits in blackchinned tilapia females from various coastal marine, estuarine and freshwater ecosystems.

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PLoS ONE 7(1); e29464, dol:10.1371/journalpone0029464.

- HORWOOD, J. W., BANNISTER, R. C. A., & HOWLETT, G. J. (1986) Comparative fecundity of North sea Plaice (*Pleuronectes platessa* L.). *Proc. R. Soc. Lond. B.* 228, 401 – 431.
- KAMLER, E. (2005) Parent-egg-progeny relationships in teleost fishes: An energetics perspective. *Rev. Fish. Biol. Fish* **15**, 399 – 421. *Doi:10,1007/s11160-006-0002-y.*
- KING, R. P. (1978) Length-fecundity relationship of Nigeria fish populations. *NAGA*, *ICLARM* 20(1), 717 – 724.
- KJESBU, O. S., WITTHAMES, P. R., SOLEMDAL, P. & GREER WALKER, M. (1998) Temporal variations in the fecundity in the Norwegian cod (*Gaddus morhua.*). *Can. J. Fish. Aquat. Sci.* 53, 303 332.
- LAMBERT, Y., YARAGINA, N. A., KRAUS, G., MAR-TEINSDOTTIR, G. & WRIGHT, P. J. (2003) Using environmental and biological indices as proxies of egg and larval production of marine fish. J. Northw. Atl. Fish. Sci. 33, 115 – 159. doi: 10,2960/J.v33.a7.
- LAMBERT, Y. (2008) Why should we closely monitor fecundity in marine fish populations? J. Northw. Alt. Fish. Sci. 41, 93 - 106. doi 10:2960/J.v41.m628.
- LEGENDRE, M. (1983) Observations préliminaires sur la croissance et le comportement en élevage de Sarotherodon melanotheron (Ruppel, 1852) et de Tilapia guineensis (Bleeker 1862) en lagune Ebrie (Cote d'Ivoire) Doc. Sc. Cent. Rech. Oceanogr. Abidjan Vol. XIV; No. 2, 1–36.

- MENSAH, M. A. (1979) The hydrology and fisheries of the lagoons and estuaries of Ghana. *Marine Fishery Research Report No. 7. Fishery Research and Utilization Branch. Tema.* 14 pp.
- PAULY, D. (1976) The biology, fishery and potential for aquaculture of *Tilapia melanotheron* in a small West African lagoon. *Aquaculture* 7, 33 – 49.
- RICKER, W. E. (1975) Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* **191**, 209–210.
- RIJNSDORP, A. D. (1991) Changes in fecundity of female north sea ploaice (*Pleuronectes plates*sa L.) between three periods since 1900. *ICES* J. Mar. Sci. 48, 253 – 280.
- TREWAVAS, E. (1983) Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia. British Museum Nat. Hist. 583 pp.
- TREWAVAS, E. & TEUGELS, G. G. (1991) Sarotherodon. In Checklist of the freshwater fishes of Africa (CLOFFA) (J. Daget, J.-P. Gosse, G.G. Teugels and Thys van den Audenaerde eds). pp. 425 – 437. ISBN, Brussels; MRAC, Tervuren; and ORSTOM, Paris. Vol. 4.
- TRIPPEL, E. A. (1998) Egg size and viability and seasonal offspring production of young Atlantic cod. *Trans. Am. Fish. Soc.* **127**, 339 – 359. *Doi:10,1577/1548-8659 (1998) 127-0339:ESAVAS-2.0.CO;2.*
- WITHAMES, P. R., GREER WALKER, M., DINIS, M. T. & WHITING, C. L. (1995) The Geographical variation in the potential annual fecundity of Dover sole, *Solea sloea*, from European Shelf

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