REPRODUCTIVE BIOLOGY OF A MOUTHBROODING CICHLID IN A NEOTROPICAL MOUNTAIN RIVER

FEDERICO RANGEL SERPA

UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
ESCUELA DE BIOLOGÍA
BUCARAMANGA
2005

REPRODUCTIVE BIOLOGY OF A MOUTHBROODING CICHLID IN A NEOTROPICAL MOUNTAIN RIVER

FEDERICO RANGEL SERPA

Trabajo de grado presentado como requisito para optar al título de Biólogo

Director
GERMÁN GALVIS
BIOL. DR. ZOOLOGÍA
UNAL

Codirectora
MARTHA PATRICIA RAMÍREZ PINILLA
BIOL. DR. CIENCIAS NATURALES
UIS

UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
ESCUELA DE BIOLOGÍA
BUCARAMANGA
2005

CONTENT

TABLE LIST

FIGURE LIST

ABSTRACT

TITLE REPRODUCTIVE BIOLOGY OF A MOUTHBROODING CICHLID IN A NEOTROPICAL MOUNTAIN RIVER*

AUTHOR FEDERICO RANGEL SERPA**

KEYWORDS Annual reproductive activity, visceral fat mass, fecundity, *Geophagus steindachneri,* gonadal mass, liver mass

DESCRIPTION

Geophagus steindachneri (Teleostei: Cichlidae) is characterized by a remarkable sexual dimorphism in the adults and by the presence of mouthbrooding in females. This species is widespread along the rivers of the north of South America, including the floodplains of the Magdalena River and some mountain rivers from its basin. One of these is the Fonce River which has two low water seasons yearly, from December to March and from June to August. The spawning season was determined using 3 methods: recording the occurrence of brooding females, analyzing the monthly significant differences in gonadal mass and measuring the monthly frequencies of reproductive condition of females. Sexually indeterminate juveniles and brooding females were found only during the low water seasons. A significant increase in ovary mass was also observed during the two low water seasons. The frequency females with ripe ovaries increased in January, whereas spent ovaries were only found during the low water seasons. Thus, there are two spawning seasons (from December to March and from June to October). Oocyte diameter frequencies showed that their development is synchronic in one batch. The testes mass increased significantly only during the first low water season of the year. However histological analyses show that all males were mature throughout the year. The reproductive biology of *G. steindachneri* in the Fonce River showed that spawning occurs during the low water seasons following a bimodal pattern; whereas males are reproductively active throughout the year representing a constant resource for females.

* Paper submitted to Journal of Fish Biology
**Faculty of Sciences, Biology School, Germán Galvis, Director; Martha Patricia Ramírez Pinilla Codirector.

RESUMEN

TITULO: BIOLOGÍA REPRODUCTIVA DE UN CÍCLIDO DE CRÍA BUCAL EN UN RÍO DE MONTAÑA NEOTROPICAL*

AUTOR FEDERICO RANGEL SERPA**

PALABRAS CLAVE: Actividad reproductiva anual, Grasa visceral, fecundidad, *Geophagus steindachneri,* peso gonadal, peso del hígado.

DESCRIPCIÓN

Geophagus steindachneri (Teleostei: Cichlidae) se caracteriza por su marcado dimorfismo sexual y porque las hembras realizan cría bucal. Esta especie se encuentra distribuida en los ríos del norte de Suramérica, incluyendo los planos de inundación del río Magdalena y algunos de los ríos de montaña que hacen parte de su cuenca, uno de los cuales es el río Fonce, el cual presenta dos temporadas de aguas bajas que comprenden a los meses de diciembre a marzo y de junio a agosto.
La temporada de desova fue determinada empleando tres metodologías: registro de la presencia de hembras con crías en la boca, análisis de los cambios temporales en el peso gonadal y cuantificación de la frecuencia de los estadios de madurez gonadal en las hembras.
Los juveniles sexualmente indeterminados y las hembras con crías en la boca, solo fueron encontrados durante las temporadas de aguas bajas. El peso de los ovarios se incrementó en forma significativa durante las dos temporadas de aguas bajas. La frecuencia de hembras con ovarios preovulatorios se incrementó durante el mes de enero; hembras con ovarios desovados solo fueron encontradas durantes las temporadas de aguas bajas. Por lo tanto representan dos temporadas de desova que corresponden a los meses de diciembre a marzo y desde junio a octubre. El análisis de las frecuencias de diámetro folicular indicó que el desarrollo es sincrónico en un grupo. El peso testicular presentó un incremento significativo durante la primera temporada de aguas bajas del año; sin embargo, los análisis histológicos indicaron que todos los machos capturados fueron maduros. El patrón reproductivo de *G. steindachneri* en el río Fonce indica que la desova se presenta durante las temporadas de aguas bajas siguiendo un patrón bimodal; por otro lado, los machos fueron reproductivamente activos a lo largo del año.

---

*Articulo enviado a la revista Journal of Fish Biology
** Facultad de Ciencias, Escuela de Biología, Director, Germán Galvis; Codirector, Martha Patricia Ramírez Pinilla.

INTRODUCTION

Studies concerning biological reproduction of neotropical cichlids have focused on species from lowlands. These studies concluded that these species have a continuous reproductive activity, with an extended reproductive season coinciding with the beginning of the rainfall season, showing multiple spawns during this period (Señaris *et al.* 1993, Cala 1996, González *et al.* 1996, Chellappa *et al.* 2003). Studies on species of the genus *Geophagus* (Teleostei: Cichlidae) have addressed different aspects of the reproductive biology of *Geophagus brasiliensis.* eg. gonadal histology (Barbieri *et al.* 1981), reproductive dynamic (Santos & Fortuna 2000) and life histories of riverine and lacustrine populations (Mazzóni & Iglesias-Rios 2002). These studies showed that this species has an extended spawning season with several spawns from September to April corresponding to the austral spring and summer.

Geophagus steindachneri (Eigenmann & Hildebrand) (Teleostei: Cichlidae) is widespread along the basins of the rivers of northem South America (Ries *et al.* 2003) including the floodplains of the Magdalena River and some mountain rivers from its basin (Dahl 1971, Galvis *et al.* 1997). A remarkable sexual dimorphism is found in adults males; they are conspicuously colored and have a red post-occipital cephalic hump. Another characteristic trait of this species is that females are mouthbrooding (Miles 1947).

This study concentrates on a population of *G. steindachneri* that inhabits the Fonce River, one of the mountain rivers from the basin of the Magdalena River. The river has two low water seasons yearly that go from December to March and from June to August. Sudden rises of the water level are known to occur during certain months in this type of rivers (Welcomme 1979). Therefore the conditions during the rise water period might create unfavorable spawning conditions. This study was traced to test this hypothesis. The aim of this study is to investigate if the annual reproductive activity of *G. steindachneri* is related to this shift in environmental conditions of its habitat along the hydrological cycle. This is the first report of the reproductive biology of this species in a neotropical mountain river.

1. MATERIALS AND METHODS

The study area was a section of the Fonce River located on the western slope of the Cordillera Oriental of the Colombian Andes. (Santander, Colombia, N 6º 25'- 6º 31',W 73º 7'-73º 9'. between 1100 and 1350 m of altitude). Historical and current meteorological and hydrological data were obtained from the Field Stations of IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia). The historical rainfall data show a bimodal pattern in the high section of the basin of the river's basin with peaks in mean rainfall occurring from April to May and from October to November. As expected, the historical river flow data show a similar pattern. The high waters match with this outline. The two low water seasons were from December to March and from June to August (Fig 1). Water temperature and pH were measured (pH-meter, Schott Handylab 1) three times a monthly for each variable in the sampling area, and these were used to obtain mean monthly values. Sampling was done between December 2003 and November 2004 using cast nets, seines, dip nets. The specimens were caught in different sites inside of the study area. Collected specimens were fixed with an injection of Bouin´s solution into their body cavities and immediately immersed in 10% formalin solution.

In the laboratory the total mass (M_T) of each fish was registered with an electronic balance ($\pm$ 0.001 g) and the standard length (L_S) were registered with a Vernier caliper ($\pm$ 0.02 mm). Specimens were dissected and sexed. Eviscerated mass (M_E), mass of liver (M_L), mass of visceral fat (Mvf), and mass of the onads (M_G) were also registered. After measurements all specimens were stored in 70% alcohol and added to the in the Ichtyological Collection of the Museo de Historia Natural, UIS (UIS-T-).

The gonads were dehydrated in ethanol series, cleared in xylene and then embedded in paraffin to obtain longitudinal sections of 7 - 15 µm that were stained with hematoxylin and eosin (H&E) and (PAS) - Alcian Blue 2.5% (Luna 1968). Histological sections were used to determine the spermatogenesis stage, classified following Smith & Walker (2004). Specimens with sperm in the testicular lobules were deemed mature. In females, oocyte developmental stages were identified following Coward and Bromage (1998). The maturation stages of females were classified according to Smith & Walker (2004) using histology and gross ovarian features. Oocyte diameters for ovaries in a range of maturation stages were measured using an ocular micrometer. Batch fecundity was quantified by counting the total number of mature ova in ripe ovaries.

1.1 Data analysis.

Body length, sex, reproductive stage, and brooding condition of females during each month were employed to characterize the population. The collected specimens were grouped as: sexually indeterminate juveniles, male and female juveniles, mature males, nonbrooding females and brooding females. The operational sex ratio was calculated using mature males and total females (nonbrooding females and brooding females). The brooding condition was assessed by the presence of embryos and larvae inside the mouth of the females. Differences in operational sex ratio and in the number of individuals in each of these categories through time were tested using Log-Likelihood Ratio tests (G-test) was applied (Zar 1999). Linear regressions were made, using the L_S or M_E, as independent variables, and gonadal and morphometrical variables as dependent variables. The data sets of these regressions that best fit were used to calculate the residuals of regressions, that are functionally equivalent to the structural index (Balshine *et al.* 2001), which eliminate the isometric effect of body size or body mass on the reproductive variables (Stockley 1997). The monthly significant differences in the residuals of M_T and M_E were tested using one way ANOVA; in the case of the residuals of M_L, M_{VF} and M_G a Kruskal-Wallis (K-W) test was applied (Zar 1999). All analyses were followed by their corresponding *a posteriori* tests. Because of low sample size of males in the months of December and February, male data for these months were eliminated for these months from the analysis. Juvenile females were not included in these analyses.

The spawning season was determined using 3 methods: 1) recording the occurrence of brooding females, 2) analyzing the monthly significant differences of ovarian mass and 3) measuring the monthly frequencies of maturation stages of females. A plot analysis employing the oocytes diameter frequency was used to determine the type of spawning (Vazzoler 1996). The effect of L_S on fecundity was tested with a Spearman correlation (Zar 1999).

2. RESULTS

A total of 401 specimens were sampled (127 males and 252 females). Which corresponds to an operational sex ratio was 1:1.98, and a significant difference was observed between the number of individuals from both sexes through the whole year ($G_{0.05,1}$= 42.008 $p< 0.001$). Temporal changes were different in each category (Table I). Sexually indeterminate juveniles with L_S between 7.3 – 67.16 mm were absent at the beginning of both dry seasons (Fig 2c). Immature males were not captured through the year. Juvenile females with L_S between 43.00 – 77.88 mm were found in high water months (Fig 2b). The number of mature males increased in the second half of the year whereas the total number of mature females was constant along the whole year. The later group was arranged into sub-groups. 1) Nonbrooding females were significantly more frequent during the second half of the year, and 2) brooding females were significantly more frequent through the first half of the year, during the dry season (Fig 2a). The smallest female with ripe ovaries had a L_S of 74.86 mm, but there were smaller brooding females (L_S 68.5 mm) than the minimum size of maturity observed in non-brooding females. Therefore, maturity in females can be reached at smaller body sizes than those observed in the group of ripe females.

2.1. Variables associated with reproduction.

The variables M_T and M_E have a positive relationship with the L_S for both sexes. Similar results were found for variables M_L, Mvf and M_G which exhibit a positive relationship with M_E for both sexes (Table II). The residuals of these regressions were used to test monthly variation for these variables.

2.2. Monthly variation of M_T and M_E.

During the sampling period the values of M_T in males fluctuated from month to month, increasing significantly during the two low water seasons and dropping during the two high water seasons. The M_E of males remained constant through the year. This is not the same for females in which the M_T and M_E shows a remarkable and significant increase in January and drops in February (Table III)

2.3. Monthly variation of M_L and M_{vf}.

Both variables changed significantly through the year, showing a similar pattern for both sexes. M_L and Mvf were low during the first low water season of the year, but increased during the transition period and high water period of second half of the year these variables increased. (Table III) (Fig. 3a, b, d, e).

2.4. Reproductive activity.

Testes mass changed significantly during the year, increasing from November to January but then starting to decrease in March at the beginning of the first rainy season of the year. In contrast to the other months that did not show significant differences, mass of ovaries stayed constant throughout the year. When the data of brooding females were removed from the analysis, the mass of ovaries varied significantly through months, reaching the highest values in January and the lowest values in February. The residuals of ovarian mass remained low during the transition period between the end of first low water season of the year and first high waters season. It increased again in June at the beginning of the second dry season of the year. (Table III) (Fig. 3c, f).

Based on histological observations, testes of *G. steindachneri* are of the unrestricted spermatogonial testis-Type (Parenti & Grier 2004). Lobular lumens of specimens from all months had sperm. Therefore, all males were mature and spermatogenesis occurred actively throughout the year.

In immature ovaries the most frequent oocytes are Stage 2 (early perinuclear stage). Ripe ovaries have a high percentage of oocytes in Stage 6 (maturation). In spent ovaries the frequency of postovulatory follicles increased (Fig 4). Postovulatory follicles were found only in the brooding females; in these ovaries the most advanced oocytes were at the vitellogenesis stage and in some cases with a few atretic follicles. Mature females were caught throughout the year. A similar pattern was observed for ripe females, however a seasonal pattern was found for spent females that occurred more frequently during the low water seasons. In contrast, during the high water season the frequencies of immature females increased (Fig. 5).

2.5. Batch fecundity.

The analysis of oocyte diameter frequencies showed that, oocytes in Stage 6 (maturation) display a larger size and are spawned at the same time. Hence, oocyte development is synchronous in one batch (Fig 6). The quantification of batch fecundity ranged from 160 (77.8 mm LS) to 456 (122 mm LS) with an average of 220 oocytes. A positive relationship was found between standard length and batch fecundity (N=29 r_s^2 = 0,477 p = 0,028).

3. DISCUSSION

Sexual selection increases under male-biased operational sex ratio (Jirotkul 2000). Santos & Fortuna (2000) found a sex-ratio of 1:1 throughout the year from *G. brasiliensis*. These results differ from the observations of Morley (2003) who found a male-biased sex ratio for the cichlid *Eretmodus cyanostictus*. In this population of *G. steindachneri* the operational sex ratio was female biased. This could be a consequence of a spatio-temporal distribution of males and females; however, any of the factors that influences the operational sex ratio like sexual differences in reproductive rate, a spatio-temporal distribution of males and females (Clutton-Brock & Parker 1992, Balshine-Earn 1996) were not tested in this work and request more attention in future works.

There was a temporal pattern in the occurrence of juveniles, nonbrooding females, brooding females and males. The occurrence of brooding females had a temporal bimodal pattern, which corresponds to the two low water seasons. Interestingly they were more frequent in the first low water season. It may be a consequence of the increment in water temperature and the drastic reduction of the river flow. Similar results were found for two mouthbrooding tilapias in ponds that showed an increase in fry production that is attributed to increases in water temperature joined to a larger photoperiod (Ridha 2004). Therefore, the dry season, with its low river flow and higher water temperature, seems to be better suited for brooding of *G. steindachneri* in Fonce River.

Juvenile recruitment seems to have a similar temporal distribution. It occurs in the months after brooding females were more frequent, and is absent at the beginning of first low water season. These results are similar to those found by Winemiller (1989) for six species of cichlids in Venezuelan Llanos; he observed an increment in the juvenile/adult ratio during the dry season. Reproductive seasonality of recruitment is controlled by favourable condition for juveniles (Kramer 1978). According to the Figure 2b the size of sexually indeterminate juveniles increases gradually. This pattern could benefit juveniles of smaller size which find food and shelter during the low water seasons. The substrate in this river is composed mainly rocks, which offer little protection during high waters. Thus attaining a larger body size quickly during low waters might help to juveniles survive the following high water season.

3.1. Total body mass and eviscerated mass.

The variation of the M_T from both sexes along the year showed that the nutritional condition increased during the low water months. The M_E differences for females showed the same pattern. The increase of M_T is related with the mass of viscera, especially the gonads. For *G. brasiliensis* the Kn of reaches highest values in September that is two months before the first peak of I_G, and the lowest values were in February for both sexes (Santos & Fortuna 2000). Similar studies were done for other cichlids from the floodplains of the Amazon River. One of these is with *Astronotus ocellatus* in which Kn increased during the flooding season but was not associated with reproduction (Gonzalez *et al* 1996). *Cichla monoculus* is the other species in which Kn reached high values during flooding period, but in this case they were related with reproduction (Cala *et al* 1996). The Kn values from an introduced population of *Cichla monoculus* in the Northeastern of Brazil remained constant through the year with little reduction during the gonadal maturation (Chellappa *et al.* 2003). Hence, the relationship between M_T and M_E varies among different species. The increment of eviscerated body mass of *G. steindachneri* in the driest months may be ascribed to the low river flow, since these might be better suited for foraging. Contrary factors such as high river flow and high water turbidity can produce physiological stress such as limited movement and foraging during the rainy seasons. Therefore these factors could explain the low values of the eviscerated body mass for females.

3.2. Liver mass and visceral fat mass.

There was more stored energy for both sexes during the second half of the year, which corresponds to rising waters, that means that these reserves were accumulated during these months and spent during the first period of low waters. Thus, they are related to the months of intense reproductive activity, suggesting that energy reserves play an important role in the final oogenesis in females and courtship in males. These results agree with Faunce & Lorenz (2000) who reported for *Cichlasoma urophthalmus* in Southern Florida that the I_H was minimal through spawning season. The expenditure of stored energy during the spawn is common and has been reported for other fish populations (Villacorta-Correa & Saint-Paul 1999 & Huntingford *et al* 2001)

3.3. Reproductive activity.

Analysis of the frequencies of females at different maturation stages showed an increase in the proportions of ripe females in January. The presence of spent females was more frequent during the low water season. However, the analysis of ovarian mass for total females does not show differences throughout the year. The ovary mass increased in the two low water seasons when the data of brooding females were eliminated from this analysis. This suggests therefore that mouth-brooding plays a role in regulating the ovary mass as proposed by White et al (2002) for *Haplachromis burtoni*.

Several patterns of reproduction are found in *Geophagus*: Santos & Fortuna (2000) found that *G. brasiliensis* in a reservoir in south of Brazil had a high incidence of mature ovaries in November and February coinciding with highest peak of I_G during the rainy period of the austral spring and summer. Mazzoni & Iglesias-Rios (2002) found that another population of *G. brasiliensis* from a river in the south-east of Brazil had a high monthly occurrence of ripe individuals, concluding that spawn takes place throughout the whole year. They also found that a lagoon population from the same locality had a reproduction restricted from September to April, corresponding to the rainy periods of the austral spring and summer. Also, several patterns of reproduction are found in cichlids: Señaris & Alcála (1993) observed that *Caquetaia kraussii* in the flood plains of Venezuela recruits along the whole year. They also found two peaks in the I_G on rainy and dry season. They concluded that the reproductive activity is continuous throughout the year. In *Astronotus ocellatus* in the Amazon flood plains, high values of I_G were observed from December to April, that is the flooding season (González *et al* 1996). *Cichla monoculus* displayed the highest I_G values along September and January that match the rising water period (Cala *et al* 1996). In the Northeast of Brazil *Cichla monoculus* I_G showed that the spawning occurred throughout the whole year with a peak in October, when the dry season takes place (Chellappa *et al* 2003). Introduced populations of *Cichlasoma urophthalmusi* in Southern Florida, has high values of I_G between April and June, during the spring and summer (Faunce & Lorenz 2000). In this population of *G. steindachneri* the favorable conditions for the spawn are found during the low water season and then, the reproductive seasons occur from December to March and from June to October. Reproductive biology and reproductive seasonality of the different populations of this species can be related with particular environmental features or each habitat. The reproductive pattern should be analyzed for populations of this species inhabiting lowlands and in rivers with different flooding conditions.

The analysis of frequencies of oocyte diameters showed that oogenesis is a synchronous process. One group of oocytes develops simultaneously and is spawns together. Similar observations were found in *G brasiliensis* (Mazzóni. & Iglesias-Rios 2002). Histological analysis showed the presence of groups of oocytes in different stages of development in the same ovary. Similar observations were made in *G brasiliensis* by Barbieri *et al*. (1981) concluding that it has multiple spawns. It is feasible that females of *G. steindachneri* spawn more than once in the same spawning season. This statement has support in histological observations that showed that spent ovaries have advanced vitellogenic oocytes, and it suggesting that oogenesis is a continuous process even during the parental care period. However, females were not ready to spawn again immediately after the end of parental care. This agrees with the observations of Morley & Balshine (2003) in the mouthbrooding cichlid *Eretmodus cyanostictus*.

The batch fecundity of *G. steindachneri* was low (220 oocytes); this result is similar with reports for other mouthbrooding species of the genus: *G. surinamensis* (250) and *G. jurupari* (300) eggs (Keit 2000). The low batch fecundity of these species can be attributed to the type of parental care. Buccal cavity volume and batch fecundity are positively related in fish with this type of parental care (Balshine-Earn & Earn 1998, Wisenden 1999, Smith 2000).

The continuous reproductive pattern of males in this population probably was related with low energetic requirements for sperm production or to the fact that males do not invest energy in parental care. Behavior, given a special attention to territoriality is a field that needs more study to know how the males are distributed. It is unknown if most small males have access to females or need opportunistic tactics to reproduce like was found by Sato *et al.* (2004) for *Lamprolous callipterus* in lake Tanganika.

The reproductive biology of this population of *G. steindachneri* exhibits several characteristics that are similar to the reports of other species of cichilids. These traits are an extended spawning season, the potential for repeated reproductions, mouthbrooding, prolonged breeding season (Señaris & Alcál 1993 Cala *et al.* 1996; González *et al.* 1996, Mazzóni. & Iglesias-Rios 2002, Chellappa *et al.* 2003), low fecundity and large eggs (Keith 2000, Winemiller 1989). The results indicate that the studied population has an equilibrium strategy (Winemiller 1989, 1992). However, the absence of brooding females and spent ovaries during the high waters months indicate that the spawn season is limited. This fact is related with environmental factors like rainfall season and high river flow. There are several possible explanations for the reproductive seasonality of this population. Kramer (1978) proposes among other hypotheses that reproductive seasonality in neotropical fishes may be controlled by adult or juvenile food availability, but this may not be the only factor affecting this species in this situation. It is possible that the environmental conditions produce a physiological response (Patiño & Sullivan 2002), which can modulate or stop the reproductive activity of cichlid populations (Duponchelle *et al* 1999). Therefore, it is possible that under more stable hydrological conditions, they spawn during the whole year (Jepsen *et al.* 1999) since favorable conditions increase the reproductive potential (Duponchelle *et al* 2000). The reproductive biology of *G. steindachneri* in the Fonce River showed that the spawning occurs during the low water seasons following a bimodal pattern; whereas males have a continuous reproduction, representing a constant resource for females.

4. ACKNOWLEDGEMENTS

To M. Torres, M. Valderrama-Vernaza, P. Rueda-Cediel, for all their support and help in all the different aspects of this work. M. Alkins-Koo, K. Winemiller and K. Coward & M. Turcotte, contributed with important comments and bibliography. N. Pinto-Sánchez. J. Santander, O. Rojas, J. Torres, M. Rojas, M. Quijano-Abril and A. Motta assisted with the fieldwork. R. A. Gavilán and Escuela de Biología (UIS) kindly facilitated limnological equipments. Special thanks to the members of the LBRV-UIS. The Bucaramanga office of INCODER for issuing the permission to capture the specimens that formed the basis of this study (15 December 2003). This study was supported by LBRV-UIS, L. Mejía-Ayala and G. Serpa de Rangel.

5. REFERENCES

Balshine-Earn. S. (1996). Reproductive rates, operational sex ratios and mate choice in St. Peter's fish. *Behavioral Ecology and Sociobiology*. 39, 107- 116

Balshine-Earn. S. & Earn.D. J. D. (1998). On the evolutionary pathway of parental care in mouth-brooding cichlid Fish. *Proceedings of the Royal Society of London B*. 265, 2217-2222.

Balshine S., Leach, B. J., Neat, F., Werner, N. Y & Montgomerie. R. (2001). Sperm size of African cichlids in relation to sperm competition. *Behavioral Ecology.* 12 (6), 726–731.

Barbieri M. C., Barbieri G., Marins M. De A. (1981) Sobre a anatomia e histologia de testículo de *Geophagus Brasilliensis* (Quoy & Gaimard, 1824) na represa do Lobo, Estado de Sao Paulo. *Revista Brasileira De Biología.* 41(1), 169-173.

Barbieri M. C., Barbieri G., Marins M. De A. (1981) Sobre a anatomia e histologia de ovário de *Geophagus Brasilliensis* (Quoy & Gaimard, 1824) na represa do Lobo, estado de Sao Paulo. *Revista Brasileira De Biología*. 41(1), 163-168.

Cala, P., González, E. & Varona, M. P. (1996). Aspectos biológicos y taxonómicos del Tucunare, *Cichla monoculus* (Pices: Cichlidae). *Dalia* 1, 23-37

Chellappa S., CÂmara M. R., Chellappa N. T., Beveridge M. C. M. & Huntingford F. A. (2003). Reproductive ecology of a neotropical Cichlid fish, *Cichla monoculus* (Osteichthyes: Cichlidae). *Brazilian Journal of Biology*. 63(1), 17-26

Coward. K. & Bromage. N. R. 1998 Histological classification of oocytes growth and the dynamics of ovarian recrudescence in *Tilapia zillii*. *Journal of Fish Biology*. doi:10.1111/j.1095-8649.1998.tb00981.x.

Clutton-Brock. T. H. & Parker. G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology*. 64 (4), 437-456.

Dahl, G. 1971. Los peces del norte de Colombia. INDERENA. Colombia. pp 391

Duponchelle. F., Cecchi. P., Corbin. D., NIñez. J. & Legendre. M. (1999). Spawning season variations of females Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Cóte d'Ivore. *Environmental Biology of Fishes*. doi: 10.1023/A:1007588010824.

Duponchelle. F., Cecchi. P., Corbin. D., NIñez. J. & Legendre. M. 2000. Variations in fecundity and egg size of females Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Cóte d'Ivore. *Environmental Biology of Fishes.* doi: 10.1023/A:1007575624937.

Faunce, C. H. & Lorenz, J. J. (2000). Reproductive biology of the introduced Mayan Cichlid *Cichlasoma urophthalmus* within an estuarine mangrove habitat of southern Florida. *Environmental Biology of Fishes.* doi: 10.1023/A:1007670526228.

Galvis, G. Mojica, J. I. & Camargo, M. 1997 Peces del Catatumbo. Asociación Cravo Norte. Colombia. pp 110.

González, E., Varona, M. P. And Cala, P. (1996). Datos biológicos del Oscar, *Astronotus ocellatus* (Pices: Cichlidae) En los alrededores De Leticia, Amazonia. *Dalia.* 1, 51-62

Huntingford, F. A., Cellappa, S., Taylor, A. C. & Strang, R. H. C. (2001). Energy reserves and reproductive investment an male three-spined Sticklebacks, *Gasterosteus aculeatus. Ecology of Freshwater Fish.* doi:10.1034/j.1600-0633.2001.100206.x.

Jepsen. D. B., Winemiller. K. O., Taphorh. D. C. & Rodriguez Olarte .D. (1999). Age structure and grow of peacock cichlids from rives and reservoirs of Venazuela. *Journal of Fish Biology*. doi:10.1111/j.1095-8649.1999.tb00689.x

Jirotkul. M. (2000). Operational sex ratio influences the opportunity for sexual selection in guppies.
Journal of Fish Biology. doi:10.1111/j.1095-8649.2000.tb00769.x.

Kramer, D. L. (1978). Reproductive Seasonality in the Fishes of a Tropical Stream. *Ecology* 59 (5), 976-985.

Keith, P., Le Bail. P. Y. & Planquette. P. (2000). Atlas des poissone d'eau douce de Guyane . Tome 2, Fasicule I. Batrachoidiformes, Mugiliformes , Beloniformes , Cyprinidontiformes, Synbrenchiformes , Perciformes, Pleuroniformes, Tetrodontiformes. *Patrimones nauturales* (M. N. H. N. /S. P. N), 43 (I) pp 286.

Luna L. G. (1968) Manual of Histologic Staining Methods of the armed Forces Institute of Patology. 3er ed. Mc Graw. Hill Book Company, pp 258. New York.

Miles, C. 1947. Los peces del Río Magdalena. Ministerio de Economía Nacional (Colombia). pp 214

Mazzóni. R., And Iglesias-Rios, R. (2002). Environmentally related life histories variations in *Geophagus bresilinsis. Journal of Fish Biology.* doi:10.1111/j.1095-8649.2002.tb02501.x.

Morley, J. I. & Balshine. S. (2003). Reproductive Biology of *Eretmodus cyanostictus*, a cichlid fish from Lake Tanganyika. *Environmental Biology of Fishes*. doi: 10.1023/A:1023610905675.

Parenti, R. L. & Grier, H. J., (2004). Evolution end Phylogeny of Gonad Morphology in Bony Fishes. *Integrative and Comparative Biology*. 44, 333-348.

Patiño. R. & Sullvan. C. (2002). Ovarian follicle growth , and ovulation in teleost fish. *Fish Physiology and Biochemistry*. doi: 10.1023/A:1023311613987.

Ries, R. E., Kullander, S. O. and Ferraris, C. J. (2003). The Check list of the Freshwater Fishes of South an Central America. Edipucrs, pp 742. Porto Alegre, Brazil.

Ridha, M. T., (2004). Observations on the reproductive performance of three mouth-brooding tilapia species in low–salinity underground water. *Aquaculture Research*. doi:10.1111/j.1365-2109.2004.01110.x.

Santos, G. O. & Fortuna, N. F. (2000). Dinâmica reproductiva de *Geophagus brasiliensis* (Quoy & Gaimsard, 1824), no açude águas belas, viamao, rio grande do sul. (Teleostei – Cichlidae) *Pasq. Agrop. Gaúcha*. 6 (1), 131 – 144.

Sato. T., Hirose. M., Tabrsky. M. & Kimura. S. (2004). Size- depedent male altrenative reproductive tactics in the shell-brooding cichlid fish *Lamprologus calllipterus* in Lake Tanganyica. *Etology.* 110, 49-62.

Señaris, J. C. & Alcála C. L. (1993). Ecología alimentaría y reproductiva de la mojarra de rio, *Caquetaia kraussi* (Steindacher 1878) (Pisdes; Cichildae), en los llanos inundadles de Venezuela. pp 93. Caracas.

Smith. B. B. & Walker. K. F. 2004. Spawning dynamics of common carp in the river murray, South Australia, show by macroscopic and histological staging of gonads. *Journal of Fish Biology*. doi:10.1111/j.0022-1112.2004.00293.x.

Smith, L. W. (2000). The reproductive biology of an open-water spawning Lake Malawi cichlid, *Copadichomis chrydonotus*. *African Zoology*. 35, 51-164.

Stockley, P. M., Gage J. G., Parker G. A., Møller A. P. (1997). Sperm competition in fishes: The evolution of testis size and ejaculate characteristics. *American Naturalist*. 149, 933–954.

Vazzoler A. M. A. De M (1996). Biologia da reprodução de peixes teleósteos: teoria e práctica. Nupelia Maringá. pp 169.

Villacorta-Correa, M. A. & Saint-Paul, U. (1999). Structural index and Sexual Maturity of Tambaqui *Colossoma macfopomum* (Cuvier, 1818) (Chariformes: Characidae) In Central Amazon, Brazil. *Revista Brasileira De Biología.* 58(4), 637-652.

Welcomme, R. L. (1979). Fisheries ecology of floodplain rivers. Longman, 317 pp. London.

Wisenden. B. D. (1999). Alloparental care in fishes**.** *Reviews in Fish Biology and Fisheries.* DOI: 10.1023/A:1008865801329.

Winemiller K. O. (1989). Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia.* 81, 225-241.

Winemiller K. O. (1992). Life history strategies and the effectiveness of sexual selection. *Oikos* 63 (2), 318-327.

White, S. A., Nguyen. T. & Fernald Russell. (2002). Social regulation of gonadotropin-releasing hormone. *The Journal of experimental biology*. 205, 2567-2581.

Zar J. H. (1999) Biostatistical analysis. Prentice Hall. pp 661. New Jersey, USA.

Table I: Monthly variation in the number of individuals collected in the categories assessed of the population of the Fonce River.

Category	*N*	*G*- test	*p*
Sexually indeterminate juveniles	142	$G_{(0.05,11)}$=276.5	<0.001
Juvenile Females	26	$G_{(0.05,11)}$=83.3	<0.001
Males	127	$G_{(0.05,11)}$=32.9	<0.001
Total Females	252	$G_{(0.05,11)}$=10.65	0.472
Non Brooding Females	184	$G_{(0.05,11)}$=25.14	0.008
Brooding Females	68	$G_{(0.05,11)}$=72.16	<0.001

Table II: Results of the linear regressions of the morphometrical variables of *G. steindachneri* population in the Fonce River.

	Independent Variable (ln)	Variable (ln)	R	*p*
Females	L_S	M_T	0.96	< 0.001
	L_S	M_E	0.952	< 0.001
	M_E	M_L	0.489	< 0.001
	M_E	Mv_f	0.239	< 0.001
	M_E	M_G	0.565	< 0.001
Non brooding females	M_E	M_G	0.611	<0.001
Males	L_S	M_T	0.99	< 0.001
	L_S	M_E	0.99	< 0.001
	M_E	M_L	0.859	< 0.001
	M_E	Mv_f	0.451	< 0.001
	M_E	M_G	0.881	< 0.001

(M_T) Total Mass, (L_S) Standard length, (M_E) Eviscerated Mass, (M_L) Liver Mass, (Mvf) Visceral Fat Mass and (M_G) Gonad Mass.

Table III: Monthly variation of the morpholometrical variables of *G. steindachneri* population in the Fonce River.

	Variable (ln)	ANOVA or K-W	*p*
Females	M_T	$F_{(11,149)} = 4.552$	<0.001
	M_E	$F_{(11, 149)} = 3.358$	=0.001
	M_L	$H_{(11, 149)} = 68.93$	<0.001
	Mv_f	$H_{(11,149)} = 52.31$	<0.001
	M_G	$H_{(11,149)} = 18.995$	=0.061
Non brooding females	M_G	$H_{(11,)} = 28.128$	=0.003
Males	M_T	$F_{(9,120)} = 2.686$	=0.007
	M_E	$F_{(9,120)} = 1.592$	=0.126
	M_L	$H_{(9,120)} = 51.4$	<0.001
	Mv_f	$H_{(9,120)} = 49.31$	<0.001
	M_G	$H_{(9,120)} = 24.7$	=0.003

(M_T) Total Mass, (M_E) Eviscerated Mass, (M_L) Liver Mass, (Mvf) Visceral Fat Mass and (M_G) Gonad Mass.

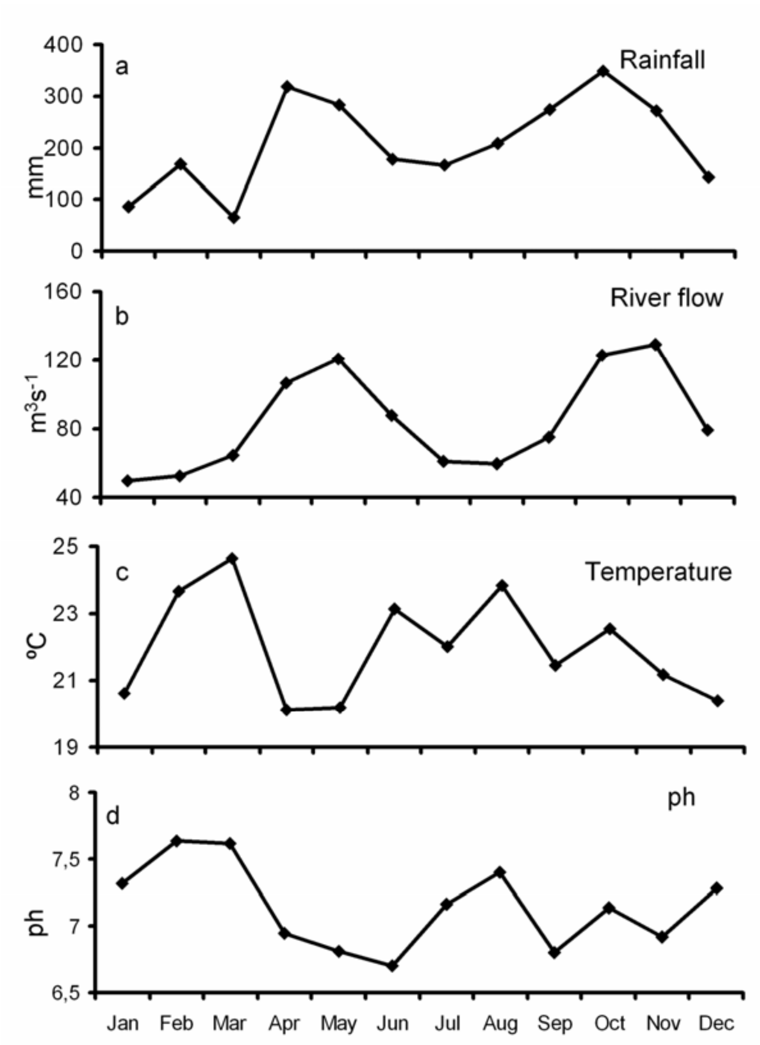
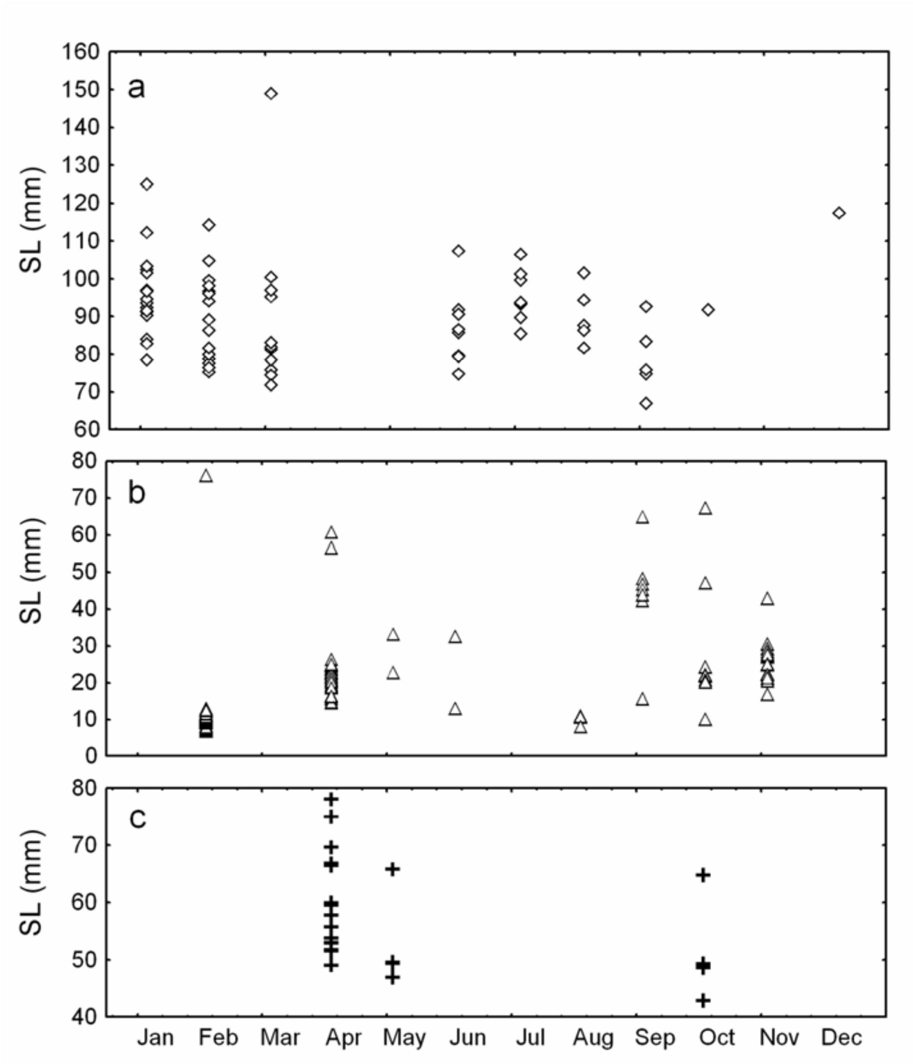

a
Rainfall
mm
400
300
200
100
0
b
River flow
m3s-1
160
120
80
40
c
Temperature
ºC
25
23
21
19
d
ph
ph
8
7,5
7
6,5
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 1



a
b
c
SL (mm)
SL (mm)
SL (mm)
160
150
140
130
120
110
100
90
80
70
60
80
70
60
50
40
30
20
10
0
80
70
60
50
40
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 2

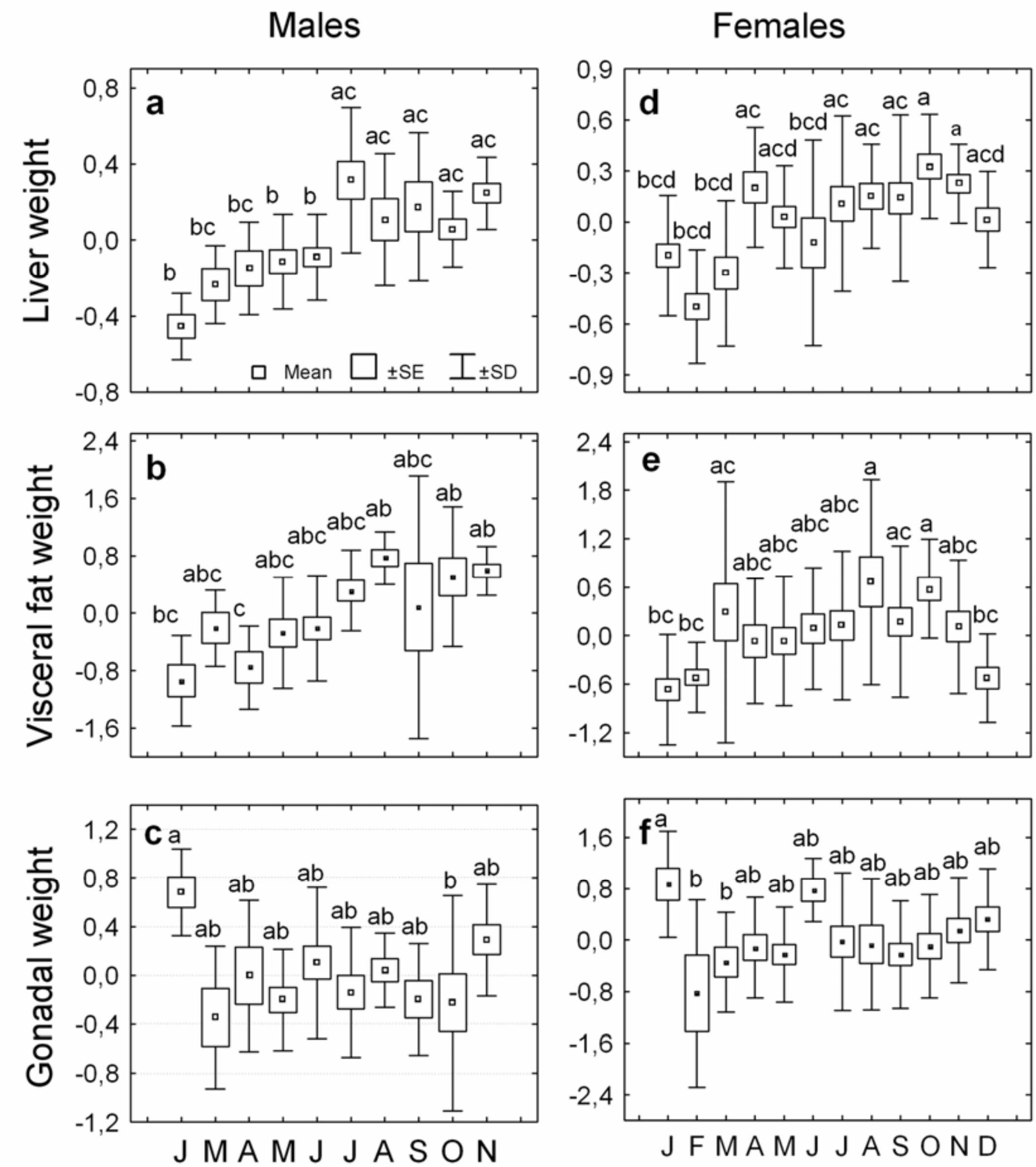

Males
Females
Liver weight
Visceral fat weight
Gonadal weight
a
b
c
d
e
f
Mean
±SE
±SD
J M A M J J A S O N
J F M A M J J A S O N D

Figure 3

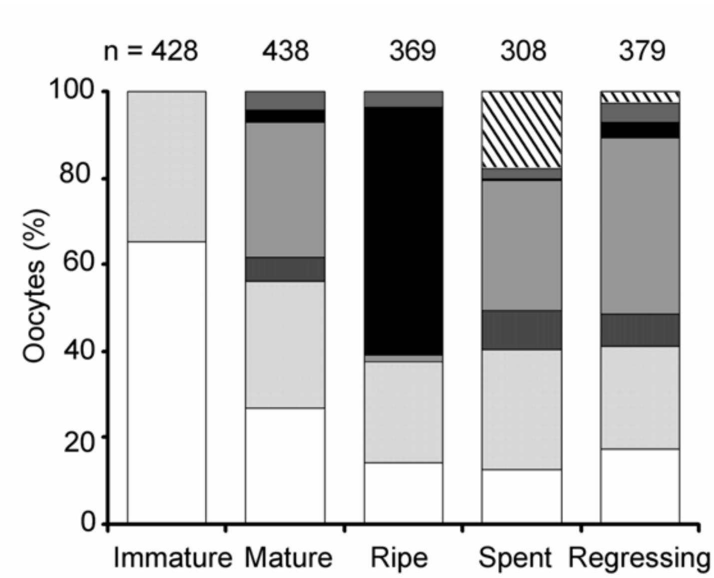

n = 428
438
369
308
379
Oocytes (%)
100
80
60
40
20
0
Immature
Mature
Ripe
Spent
Regressing

Figure 4

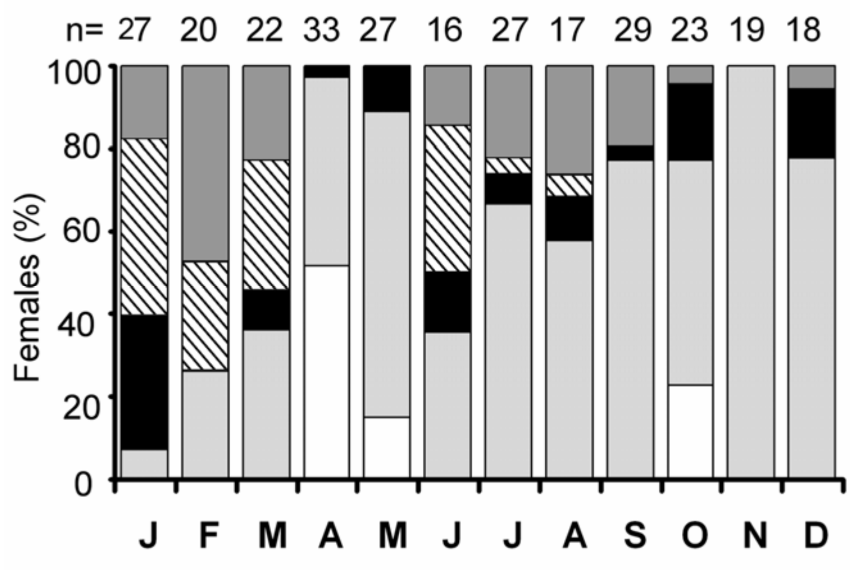

n= 27 20 22 33 27 16 27 17 29 23 19 18
100
80
60
40
20
0
Females (%)
J F M A M J J A S O N D

Figure 5

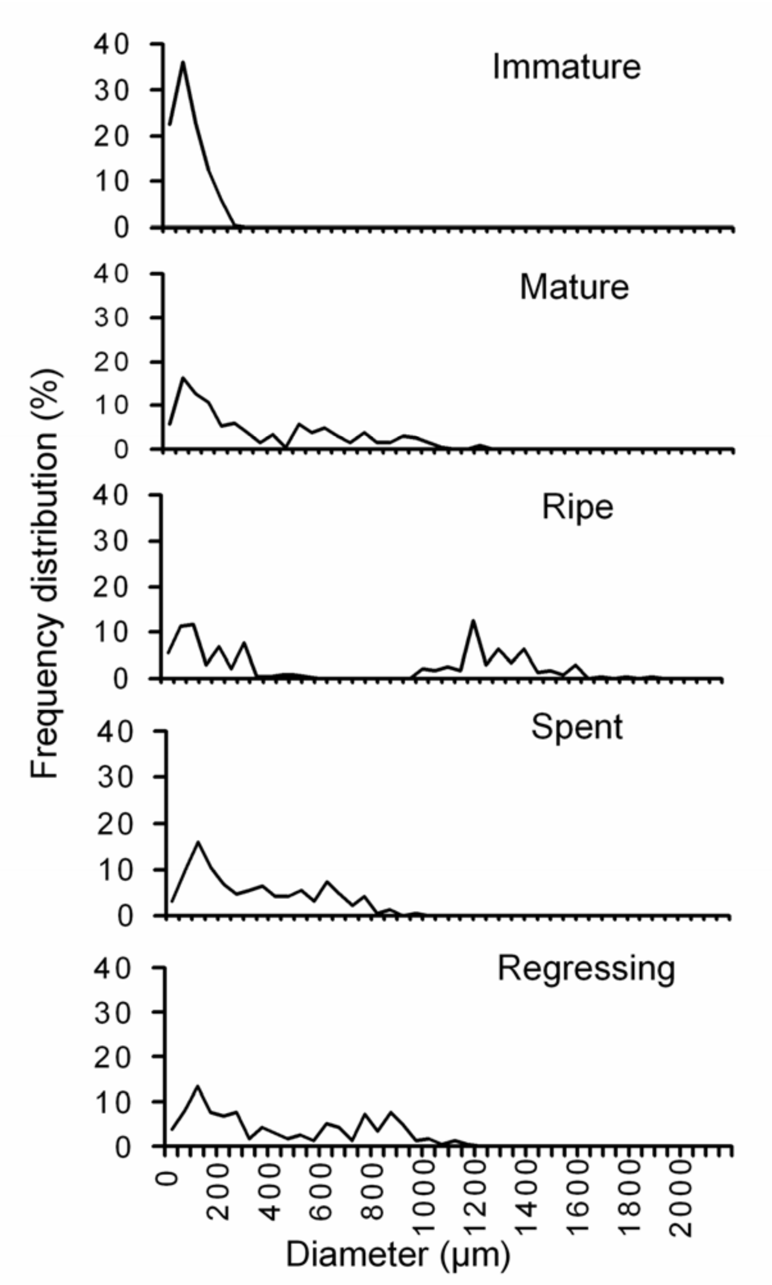

Immature
Mature
Ripe
Spent
Regressing
Frequency distribution (%)
40
30
20
10
0
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Diameter (µm)

Figure 6