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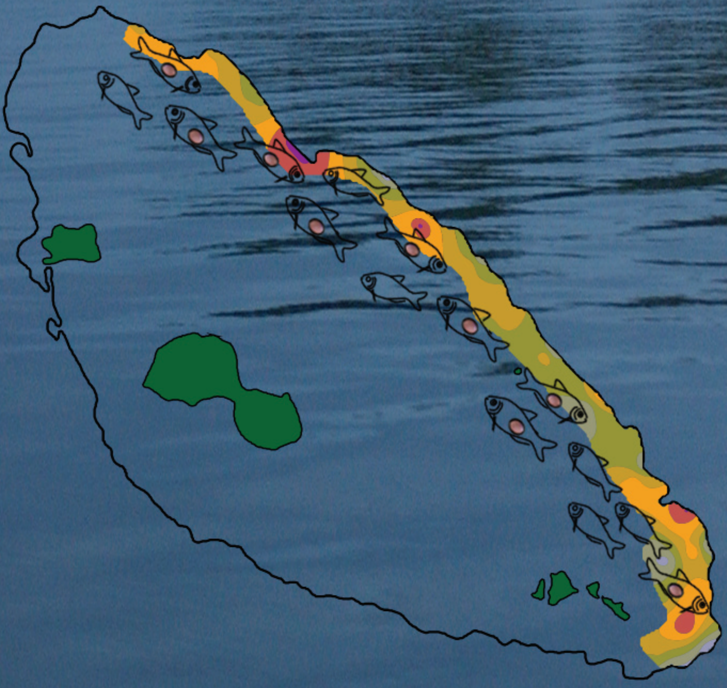
Departamento de Ecoloxía e Bioloxía Animal

Fishery ecology of the freshwater fishes in the Lake Nicaragua. Reproduction and management of *Brycon guatemalensis*

PhD. Thesis | Aldo Hernández Portocarrero



Vigo, España 2013

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Departamento de Ecoloxía e Bioloxía Animal

Memoria de Tesis Doctoral
para optar al grado de Doctor por la Universidad de Vigo

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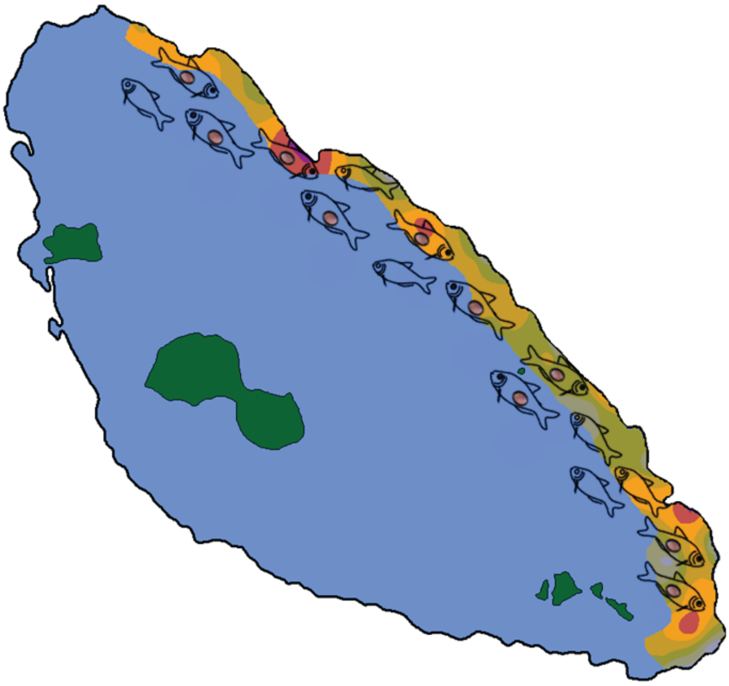

Presentada por:

Aldo Hernández Portocarrero

Vigo, España 2013

Dr. Juan Francisco Saborido Rey, Científico titular del Instituto de Investigaciones Marinas (Consejo Superior de Investigaciones Científicas).

Director de tesis,

Dr. Bernardino González Castro, Profesor Titular en la Universidad de Vigo.

Tutor,

Autorizan a la presentación de la memoria adjunta, titulada "**Fishery ecology of the freshwater fishes in the Lake Nicaragua. Reproduction and management of *Brycon guatemalensis***", realizada por Aldo Hernández Portocarrero para optar al grado de Doctor por la Universidad de Vigo.

Y para que así conste, se expide el presente certificado en Vigo, a 22 Abril de 2013.

Fdo. Juan Francisco Saborido Rey

Fdo. Bernardino González Castro

AGRADECIMIENTOS

La necesidad de conocer el estado de los recursos pesqueros del Lago de Nicaragua y sobre esta base impulsar el desarrollo del sector pesquero y las comunidades pesqueras asentadas a su alrededor, permitió que se concretara la ejecución de un estudio sobre los recursos pesqueros en la zona oriental del lago, como parte del proyecto financiado por la Agencia Española de Cooperación Internacional (AECI): "Apoyo a la actividad pesquera de las comunidades pesqueras del Lago Nicaragua (Cuenca del Río Mayales, Departamento de Chontales y Río San Juan)" AECI/ADPESCA. A todos los que hicieron posible la ejecución de este proyecto dirijo mi agradecimiento por impulsar el ordenamiento del sector pequero y el desarrollo de las comunidades pesqueras del lago; por apoyar las investigaciones de los recursos pesqueros en el lago, que además dieron origen a esta tesis doctoral; y por promover un mejor manejo de sus recursos basado en los resultados preliminares de las investigaciones realizadas, los que fueron plasmados en el documento "Abundancia relativa de los peces en la costa oriental del Lago de Nicaragua".

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Participantes en el estudio:

Como investigadores del Centro de Investigaciones Pesqueras y Acuícolas (CIPA): Luis Velásquez Chavaría, Ronaldo Gutiérrez García y Renaldy Barnuty Navarro;

Como ayudante de investigación y estudiante de la carrera de Ingeniería en Acuicultura de la Universidad Centroamericana UCA: Juan Bosco Mendoza Vallejos.

Como ayudante de investigación y técnico en redes: Luis Reyes González

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Dedico esta tesis: "*A la memoria de mis padres*".

INTITUCIONES/ORGANISMOS QUE APOYARON EL ESTUDIO

ADPESCA/INPESCA	Instituto Nicaragüense de la Pesca y Acuicultura
AECID	Agencia Española de Cooperación Internacional
IIM-CSIC	Instituto de Investigaciones Marinas
	Consejo Superior de Investigaciones Científicas

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Summary

The freshwater bodies are very dynamic systems, and have been the first aquatic ecosystems susceptible to receive the direct impact of human activities, becoming very vulnerable ecosystems. The Lake Nicaragua has been recognised as a continental water body with an important source of fish living resources for the fishery sector. In addition, its dimension is very attractive for the development of aquaculture activities. However, the exploitation level of fishing resources in the lake has lead to an overexploitation of some species already included in UICN red list, while others are in risk of being overexploited if management measures are not taken. Studies on species diversity in the lake defined two demersal fish habitats: the "shallow benthic" habitat, which has a higher index of species diversity and the "deep benthic" habitat with lower diversity index.

The landings data series do not allow ascertaining the catches composition. Hence, any evaluation of the fish exploitation pattern in the Lake Nicaragua derived from landings record is imprecise. Besides, the large gap on knowledge of many other important biological parameters of the fish species - the dynamic of reproductive behaviour of the population, the reproductive cycle, spawning ground, egg production and the maternal features affecting reproductive output and fitness- prevents the implementation of management actions directed towards the conservation of the lake stock reproductive potential, such as regulations on closing season and/or areas, and minimum landing sizes. This study, besides providing information about actual state of distribution and abundance of *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis*, and *Brycon guatemalensis*, provides information of the reproductive strategy of *B. guatemalensis* and proposes some management alternatives based on its biological features.

The present study was conducted along the eastern part of the Lake Nicaragua and showed that even all the species studied were widely distributed in this area, species abundance varied geographically (zones: northwest, central and southeast) and vertically (depth: from shallow to deeper areas). The patterns of abundance of cichlid (*A. citrinellus*, *H. nicaraguensis* and *P. managuensis*) are affected by spatial (zones) and environmental factors as the vertical profiles (depth), whereas in *B. guatemalensis* was also affected by seasons of the year, i.e., dry and rainy season. Cichlids were more abundant in shallow waters and in the

southeast zone, whereas *B. guatemalensis* larger abundances were found in the southeast and northwest side. Similarly, the size distribution pattern was influenced by both latitude and vertical profiles. Overall, larger fishes are found in the southeast and to a lesser extent in the central zone of the lake, whereas in the northwest are smaller. Furthermore, larger fish are found in relative deeper waters.

The reproductive studies on *B. guatemalensis* using histological procedures showed that the oocytes final maturation ended with the migration of the germinal vesicle to the animal pole, without oocyte hydration, and oocytes being surrounded by mucus indicative of eggs adhesiveness. The species presented a protracted spawning season that lasted 8 months. Both small and large females started the spawning activity in July, but spawning asynchrony occurred between female sizes as spawning season progressed.

Based on histological procedures, the female length at 50% maturity of *B. guatemalensis* was estimated in 27.3 cm, which largely differed from the ones previously reported based on the gonad macroscopic observations. The present study indicated that *B. guatemalensis* has determinate fecundity and presented group-synchronous ovarian organization. The potential annual fecundity of the species showed that this allometrically increased with female size, and that larger females produced larger eggs. Nonetheless, egg size decreased as spawning season progressed.

Gillnet selectivity studies were performed on four species (*A. citrinellus*, *H. nicaraguensis*, *P. managuensis*, and *B. guatemalensis*) and selectivity was quite different among species, partly reflecting growth patterns. The absence of larger and smaller fishes was notorious in the catches. The absence of larger fish likely indicated the expected maximum size of each species within the lake ecosystem, while the minimum size captured may be attributed to the fish shape and/or different behaviour of the life stages of each species. The most vulnerable fraction of the population of cichlids was males, and females in the case of *B. guatemalensis*, particularly during reproductive periods. The sex ratio of each species obtained in the present study very likely is similar to those in the catches in a routine fishing operations performed by the fishers in the lake.

The establishment of a minimum landing size (MLS) is one of the most common management measures, particularly in data limited stocks exploited by the small-scale fisheries, and often this measure is reinforced with regulations on fishing gears mesh size. Generally, legal mesh size is determined combining gear selectivity and length-at-50% maturity of the target species. The main objective of this management rule is the protection of the immature or juvenile components of the stock, a measure often considered enough to ensure the sustainability of the fishery. However, reproductive studies have evinced that larger mature females are more productive than smaller mature ones, thus, the catches of larger fish could also lead to a significant reduction of stock productivity. In this study, we analyzed the impact of gillnet selectivity on *B. guatemalensis* in relation to ontogenic maturation, reproductive phase, and reproductive potential. Results showed that juveniles and recruit spawners are the most vulnerable to the 75 mm mesh-size, whereas the majority of the spawning stock biomass (SSB), and particularly those with higher reproductive potential, are highly vulnerable to the 100 mm mesh size, due to the interaction between the female length-mesh relationship and the seasonal behaviour pattern of those females. Based on these results, a MLS of 30 cm is proposed as management measures to protect the immature or juvenile components of the stock, and to increase egg production of the SSB and reduce the fishing mortality of young females we recommended the use of 100 mm mesh size of net for fishing operation in the Lake Nicaragua.

CHAPTER 1: General Introduction

1.1. Lakes as source of natural resources

The freshwater bodies are very dynamic systems, and since ancient history have been the first aquatic ecosystems susceptible to receive the direct impact of human activities, becoming very vulnerable ecosystems. Their uses are very diverse, from drinking water, transport, irrigation, energy production, as a vehicle to eliminate waste material, recreation, aquaculture, to the exploitation of the wild living resources inhabiting these ecosystems. Wrong agriculture practices in the surrounding areas, including deforestation, industry and domestic waste disposal are the most important human activities inducing drastic changes in many freshwater environments. Water pollution by industrial and domestic sewage, eutrophication, silting, acidification and heated waters are some of the consequences of those activities. These activities commonly reduce the abundance and diversity of plants and animals. Hence, local communities traditionally exploiting living resources, mainly fishes, as mayor source of food, are often affected. The magnitude of this impact depends on the level of contamination of rivers, wetland and open waters. Surprisingly, freshwater habitats will respond positively to sensible management procedures aimed at restoration, although for exploited peat-lands recovery may be extremely slow (Maitland & Morgan, 1997). Buffer zones surrounding the main water bodies declared, protected areas under different categories (e.g. nature reserves, biosphere reserves), management plans and monitoring programs are some of the mechanism for the protection and management of the fresh water environment and their living resources.

Freshwater habitats have traditionally been divided into two major types as wetlands (including peatlands) and open water. They are very variables in character, ranging from running (rivers) to standing waters (lakes), through alkaline marshlands to acid peat bogs, mountain trickles to major rivers and small puddles to deep lakes (Maitland & Morgan, 1997). Lakes are closed systems consisting of a defined body of water and ecologically stable relative to rivers (Welcomme *et al*., 2010). Standing water or lakes have been classified according to the type of origin, physical (especially thermal), chemical and biological characteristics, being these characteristic extremely variable.

Lakes have ecological, economic and social importance. Ecologically, lakes moderate temperatures influencing the climate of the surrounding areas. As water reservoirs help to regulate stream flows, recharge ground water aquifers and moderate droughts. Lakes provide habitat to aquatic and semiaquatic plants and animals, which in turn provide food for many terrestrial animals. In catchment basin where precipitation is greater than evaporation, lakes have an outlet from which water eventually flow to the sea. In lakes of tropical areas light levels and temperature do not vary much, and depth is one of the most important parameter influencing the ecosystem, because on it depend the proportion of the lake´s volume that receives solar radiation (Maitland & Morgan, 1997). In relation to light penetration the lakes water column is divided in photic or euphotic and aphotic zone or region (Brönmark & Hansson, 2005), being the first the most important since it is exposed to sufficient sunlight for photosynthesis to occur and most living life occur too. The transparency of the water depends on the depth of the photic zone, which may be altered by the amount of sediment entering in the system. Ecological changes in water bodies due to introduction of exotic freshwater fish species have been observed in lakes, particularly damaging, causing the extinction of native fish species mainly through predation among other mechanism (Cowx, 1998; 1999).

Inland fisheries production has increased from 9.8 million tonnes in 2006 to 11.5 million tonnes in 2011 (FAO, 2012), this last representing 12.7 % of total fishery production of the world. However, consistently it is pointed out the constraints of poor quality statistics and information available for inland water fisheries. In spite of the reported increasing production it is known that the degree of fisheries resource utilization differs greatly from lake to lake and according to two main types of fisheries: demersal/inshore and pelagic/offshore. Currently, the demersal/inshore resources are heavily exploited or overexploited and this fact contribute to the overall perception that inland fisheries are not sustainable because catches are allegedly falling, species are disappearing and many other symptoms of chronic overfishing are reported (Welcomme *et al*., 2010). Inland fisheries has a great impact in local economic since it provide income to hundreds of millions household. This fisheries have diversified in proper fisheries for commercial purposes and recreational for tourist development. These fisheries are generally characterized by small-scale/household-based activities and have immense importance as sources of food and employment within undeveloped rural communities.

The Lake Nicaragua or Cocibolca is a vast freshwater of tectonic origin (Hayes, 1899) and an important biological diversity. It is the largest lake in Central America with a total surface of 8 000 km^2 at 31.40 meters above sea level (mean altitude), the 9th largest in the Americas and the 19th largest lake in the world. The Lake Nicaragua is slightly smaller than Lake Titicaca located between Bolivia and Peru. The lake is oval shaped which the length of major axis is 160 km, maximum width of 70 km, maximum depth is approximately 45 meters with an average of approximately 13 m (Montenegro-Guillén, 2003).

The Lake Nicaragua has been recognised as a continental water body with an important source of fish living resources for the fishery sector (Davies & Pierce, 1972), but its dimension become very attractive for aquaculture development also, since a tilapia cultivation project was installed in Lake Nicaragua around year 2000 (NICANOR, 2000) and some attempt have been made to develop similar project in another areas of the lake. However, it contrasts with the fact that some species are over-exploited and some others are in risk, if management measures are not taken (Thorson, 1982; Adams *et al.*, 2006).

1.2. The Lake Nicaragua ecosystem and environmental condition

The central mountain chain permits the definition of an eastern region with a tropical rain forest with rainfall between 4,000 and 6,000 mm per year; a western zone or tropical savannah region located in the drainage area of Lake Nicaragua, with rainfall ranging from 700 to 2,500 mm but with a very marked dry season; and an intermediate region with rainfall of more than 2,500 mm and without a marked dry season (PENUMA-OEA, 1997). The waters of the Lake Nicaragua-San Juan River drainage basin, flow through at least eight distinct terrestrial ecosystems (Figure 1): 1. dry tropical forest to the east, north, and west of Lake Nicaragua; 2. cloud forest in the high areas of the Central Volcanic Cordillera of Costa Rica; 3. moist tropical forest to the south and southwest of Lake Nicaragua and in the eastern foothills; 4. very moist tropical forest in the San Juan Valley and on the coastal plains; 5. gallery forest along river banks; 6. wetlands to the south of Lake Nicaragua and at the confluences of the Colorado and Tortuguero rivers with the San Juan; 7. second-growth forest, meadows, and agricultural land in extensive areas of the basin; and 8. coastal forest and mangrove swamps on the Caribbean coast (Montenegro-Guillén, 2003). The absence of physical-chemical and chlorophyll-a stratification indicates it is a polymictic lake, i.e., there is mixed water from top to bottom, and the Carlson´s trophic state index calculation indicates it is eutrophic, with a tendency to lower its water quality (PROCUENCA-SAN JUAN, 2004). The eutrophic condition is referred to lakes nutrient-rich, usually shallow, turbid that may have an oxygen deficiency in deeper water at some times of the year (Maitland & Morgan, 1997). Changes in water quality are the major drivers of lake ecology and shifts in water transparency, dissolved oxygen regimes and resident organisms occur with nutrient enrichment (Welcomme *et al*., 2010).

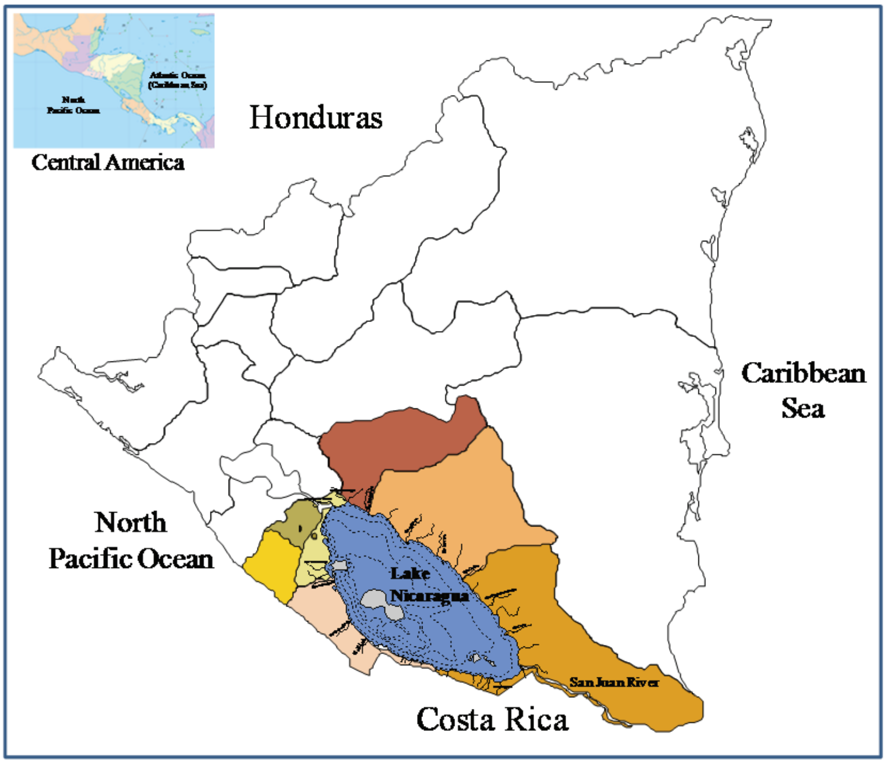
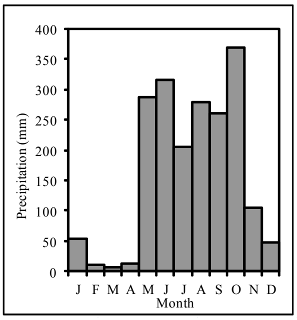


Figure 1. Map of the Lake Nicaragua basin and regions. Tributary rives and San Juan River drainage basin to the Caribbean Sea.

In tropical areas where Lake Nicaragua is located predominate two well defined seasons as wet or rainy season (winter season) from May to October and the summer season or dry season from November to April. During rainy season in 2005 the average precipitations in the area of the Lake Nicaragua, registered from three meteorological stations (Table 1), ranged from 286.3 mm in May to a maximum of 368.4 mm in October. On the other hand, the dry season is characterized by low and very low precipitations (Table 1). The Lake Nicaragua is affected by strong winds, especially during the months from January to May. These winds generally blow from east to west causing any thermal stratification to disappear. Bottom sediments become suspended and this, coupled with the usually high plankton production, causes a low transparency. These winds also make transportation difficult for the few vessels that operate on the lakes. Small fishing vessels, less than 5 m in length, can operate only in protected areas during this time of year (Davies & Pierce, 1972).

Table 1. Registered data of monthly precipitation in millimetres (mm) during the year 2005-2006, from three meteorological stations around the Lake Nicaragua: Data source Instituto Nicaragüense de Estudios Territoriales -INETER 2006.

	Year 2005 /Months											
Meteorological station	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Station: San Carlos / San Carlos - Code: 69 090 Latitud: 11° 07´42" N Longitud: 84° 46´36" W Level: 40 msnm; Type: HMP	45.8	30.3	15.5	11.1	261.6	284.3	232.5	394.5	284.2	203.4	153.5	72.6
Station: Juigalpa / Juigalpa - Code: 69 034 Latitud: 12° 06´00" N Longitud: 85° 22´ 00" W Level: 90 msnm; Type: HMP	2.2	0.1	2.5	19	214.1	313.7	185.2	248.1	183.6	402.5	49.7	49.7
Station: Rivas / Rivas - Code: 69 070 Latitud: 11° 26´06" N Longitud: 85° 50´ 00" W Level: 70 msnm; Type: HMP	3.4	0.2	0.8	8.9	383.3	349.7	197.8	193.4	312.9	499.2	114	23.2
Average precipitation (mm) on the Lake Nicaragua	17.1	10.2	6.3	13.0	286.3	315.9	205.2	278.7	260.2	368.4	105.7	48.5



The Lake Nicaragua collect water from a catchment area of 15,844 km^2, of these, 11,693 km^2 (74%) are on Nicaragua, and 4,151 km^2 (26 %) on Costa Rica. The total water volume is approximately 104,000 hm^3. Rainfall in the catchment varies from averages of 1200 mm per year in the northwest, at Malacatoya to 4000 mm per year in the southeast at Rio Frío in Costa Rica (Montenegro-Guillén, 2003). The outflow is allocated at San Carlos, through San Juan River. The Lake Nicaragua subsystem receives contributions from numerous rivers that tend to be short in length, especially in the western versant. The rivers located toward the north of Lake Nicaragua are intermittent, only run in the rainy season. Towards the south they become permanent, given the greater amount of rainfall. The most important rivers of the eastern versant are Malacatoya, Tecolostote, Mayales, Acoyapa, Oyate, Camastro, and Tule. Those of the eastern versant are minimally developed, and those of the southern versant, which originate in Costa Rica, are relatively developed; the most important being the Frío, Sapoá, and Zapote Rivers. The San Juan River (SJR) constitutes Lake Nicaragua's only outlet, it empties into the Caribbean Sea approximately 476.6 m^3/s at two points through the so-called Laguna de San Juan del Norte in Nicaragua and through the Colorado River in Costa Rica. These two are separated by approximately 20 km (PNUMA-OEA, 1997).

The lake's basin can be described as "saucer shaped" having a bottom comprised principally of mud and sand with an occasional small outcropping of rocks. The lake is further characterized by the presence of three large islands (Ometepe, Zapatera, and Mancarron), and numerous small islands. Ometepe Island is composed of two active volcanoes, Ometepe and Maderas. The water level of the lake fluctuates approximately 3 to 4 meters each year, and the lowest and highest levels occurring in April and October, respectively. Wetlands are located to the south of Lake Nicaragua (Montenegro-Guillén, 2003). Most of the aquatic plants observed were water hyacinth (*Eichhornia crassipes*) and water lettuce (*Pristis stratiotes*). These species are particularly abundant at the mouth of rivers and streams entering the lake and often form extensive floating plant islands. These islands are commonly colonized by a variety of other plant species, many of which are not truly aquatic, but they are able to grow due to the support of dense growths of hyacinth and water lettuce. 60 per cent of the eastern shoreline contains flooded bushes and aquatic plant growth, and that virtually all of the lake shore is "weedy" along the 60 km of shoreline between Colon and San Carlos. The open zone of the lake (central zone) i.e. deepest area, without island protections the bottom soil is mainly composed by sand and mud. The water of Lake Nicaragua has a low transparency, less than 0. 5 m. However, in or near the mouth of the rivers entering the lake, the water is much clearer, at least during the dry season. The turbid condition of the lake proper is attributed to soil colloids and other particulate matter kept in suspension by high winds, and to high plankton production (INFONAC, 1974; Davies & Pierce, 1972). The sandy areas near shore line and wetland areas are characterized by the presence of small fishes, whereas the open areas i.e. without island, rocky areas or plant, larger fishes are found (INFONAC, 1974).

The surface water of Lake Nicaragua ranged from 25° to 28°C, without thermal stratification in the water column, since the prevailing easterly winds cause slow westward drift at the surface and corresponding eastward circulation in the deeper waters (Swain, 1976). These prevailing easterly winds during the dry season commonly reach velocities of 20 knots (23 min/hr). Therefore, most of the western shore of the lake consists of wave-swept, debris-strewn, gray, sandy beaches. Exceptions to this are areas protected by large near-shore islands and peninsulas, and where rivers and streams parallel the shore before entering the lake. On the wind-protected eastern side of Lake Nicaragua much of the shoreline is covered with flooded dead bushes, and aquatic plants (Davies & Pierce, 1972).

In a global-scale, the wind named the Papagayo wind is a north to north-easterly wind which periodically blows through the gap in the mountain ranges of Central America in which Lake Nicaragua is located (Figure 2). The wind is stronger than the trade winds which normally blow here. It is notable for causing a pronounced increase in upwelling of cooler, nutrient-rich waters on the Pacific coast which in turn supports an abundance of sea life. The wind and upwelling are together referred to as a Papagayo event (NASA-Papagayo wind).

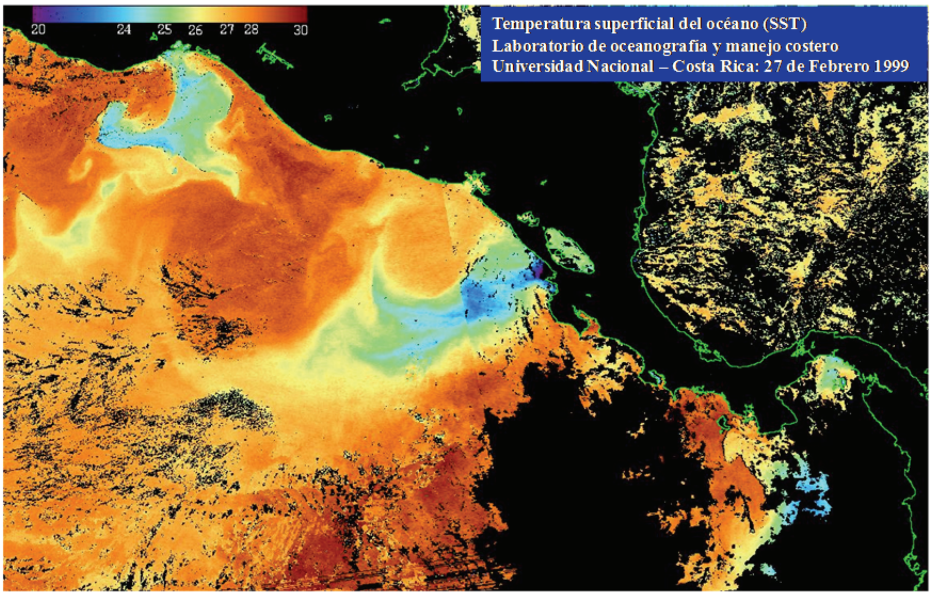


Figure 2. Satellite image of the Sea Surface Temperature (SST) in the Gulf of Papagayo, Nicaragua region where is observed also the temperature of the Lake Nicaragua: February 1999.

1.3. Fish ecology in the Lake Nicaragua

1.3.1. Origin and ecology of fish species

The studies on distribution and taxonomy of the Central America freshwater fish have permitted to recognize the existences of four fish provinces (Figure 3): Usumacinta Province; Isthmian Province; Chiapas-Nicaraguan Province and San Juan Province (Bussing, 1976). The *Usumacinta* province includes the entire Atlantic versant of Honduras and northern Nicaragua to between the Rio Coco and Prinzapolka drainages, where 130 species representing 34 genera and 10 families of freshwater fishes occur. *Isthmian* province lies between Peninsula Valiente (forming part of Laguna de Chiriqui) and Río Coclé Norte.

Unlike the Atlantic slope boundary of the Isthmian Province, which represents a biological filter-barrier created by a merging of discrete faunas over a rather monotonous physical environment, the isthmian assemblage reaches an exceptionally sharp terminus on the Pacific slope at Punta Mala (Punta Judas), Costa Rica. Just north of this point several coastal ranges extend to the sea creating an impressive physical barrier that eliminates the coastal swamp environment as a dispersal route for freshwater species. 97 species representing 51 genera and 12 families of freshwater fishes occur in the Isthmian Province. The *Chiapas-Nicaraguan Province* extends from north of the Punta Mala promontory to mid Pacific Costa Rica; this narrow Pacific coastal plain receives much less rainfall than southern Costa Rica or the Atlantic lowlands. Depauperate as it is, endemism is marked and several species are autochthonous. Forty-five species representing 18 genera and 9 families of freshwater fishes occur in the region. It must be pointed out however, that at least 14 of the 45 known species are primarily Atlantic forms that have gained access to the Pacific slope through several dispersal routes in the southern part of the province. Finally, the *San Juan province* includes the Atlantic slope drainage basin from the Rio Prinzapolka, Nicaragua to the Golfo de los Mosquitos in western Panama (Figure 3). The Nicaraguan freshwater fishes were assigned to this province. 54 species representing 25 genera and families of freshwater fishes occur in the San Juan Province. Species of marine affinity (most of which are presumably euryhaline), are recorded in freshwaters in the province, number at least 84 species. The greatest diversity is found in the San Juan drainage itself where 46 freshwater species occur. Thirty-two of these species are found in the Lakes Nicaragua proper (Table 2). Nine species of marine affinity are reported to enter in the lake (Table 2). Additionally fourteen non-lake species typical from San Juan River have been collected in affluent to the lake or tributaries of the Rio San Juan. Some of these, especially those found in lakes affluent, probably occur from time to time in the lake.

Fish reproduction and breeding areas of more studied species are diverse e.g. for cichlids, the most representative family in the lake, rocky areas conform suitable environments for both reproduction and breeding (McKaye, 1977; Olfield, McCrary & McKaye, 2006), whereas sand depressions are suitable habitats for spawning on cichlids like *Hypsophrys* (Conkel, 1993). For other migratory species as *B guatemalensis*, which exhibit potamodromous migration, recruitment have been identified along the San Juan River drainage (PROCUENCA-SAN JUAN, 2004), whereas spawning areas are mentioned to occur upstream i.e. towards the lakes (Horn, 1997) and in to tributary rivers (McLarney *et al*., 2010).

Most species with marine affinities (Table 2) migrate back and forth between Lake Nicaragua and the Caribbean Sea through San Juan River. Among those species, the biology and movements of the bull shark, *Carcharhinus leucas*, and to some extent the sawfishes, *Pristis ssp* were described. Bulk shark reproduce throughout of the year along the Caribbean coast, especially near the river mouth (Jensen, 1976). They move between fresh and brackish water at random (Thorson, 1976a), especially young fish that often reach the lake. Conversely, *Pristis* migrates to the lake at maturation, i.e., about 3 m. Gestation lasts about five month and the young are born in the Lake Nicaragua or along the San Juan River, migrating to the sea (Thorson, 1976b). Another big fish is tarpon, *Megalops atlanticus*, which is found in the lake and in tributary rivers in juvenile and adult stages. It reproduces throughout the year with main peaks in December-February and June-September, and spawn in oceanic waters. The snook, *Centropomus parallelus*, population is found in the lake from September to December and is found always mature, close to spawn (Gadea, 2003). Snook is thought also to complete its life cycle in estuarine environment (Cervigón, 1991). The relative larger sizes are recorded in the San Juan River drainage to the sea.

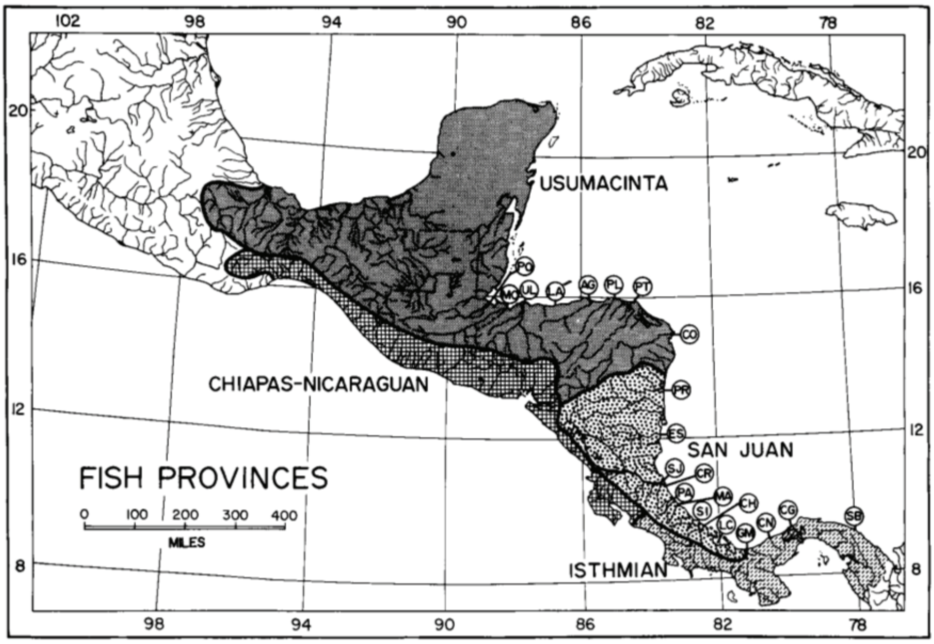


Figure 3. Distribution of the Middle American ichthyofauna by major fish provinces. The circle (SJ) in SAN JUAN province correspond to the fish species associated to the Lake Nicaragua (Bussing, 1976).

1.3.2. Species diversity

Based on the application of Shannon-Weiner diversity index and the specie evenness ratio, two demersal fish habitats were defined in the central area of Lake Nicaragua: the *shallow benthic* and the *deep benthic*, which extended from 3.66 to 9.14 meters and 12.8 to 16.46 meters, respectively (Koenig, Beatty & Martínez, 1976). But also a transition zone between the two distinct habitats and even a possible third discrete habitat were identified (*op. cit*). The "shallow benthic" habitat, which has a higher index of species diversity, is dominated by *Dorosoma chavesi*. In decreasing order of biomass are *Cichlasoma longimanus*, *Cichlasoma citrinellum*, *Lepisosteus tropicus*, *Cichlasoma centrarchus*, *Bramocharax bransfordi*, *Neetroplus nematopus* and *Brycon guatemalensis*. In the transition zone, *Cichlasoma nicaraguense* and *Roeboides guatemalensis*, at 10.98 m, are present at greatest proportions, and the "deep benthic" habitat is dominated by *Rhamdia spp*. The same study also indicates that shoreline, midwater and rocky zones of the lake probably represent distinct habitats from that of the open water.

Some of the listed species (Table 2) are actually included in IUCN red list (International Union for Conservation of Nature), because have been overexploited in the lake, such is the case of large-tooth sawfish *Pristis pectinatus* and *Pristis perotteti* which are in the category of "critically endangered -CR", and Bull shark *Carcharhinus leucas* included in the category of "near threatened -NT" (Adams *et al*., 2006). The principal threat to all sawfishes and bull shark was the fisheries, both targeted and by-catch. Some of the conservation actions imposed was a temporary moratorium on targeted fishing for sawfishes in Lake Nicaragua in the early 1980s (Thorson, 1982), after the population collapsed following intensive fishing in the 1970s. The aim was to allow the population to recover, but no such recovery has occurred (McDavitt, 2002). In the last decade another fish species has showed some sign of over-exploitation as Gaspar, *Atractosteus tropicus*, therefore in 1998 was enacted a management measure in which it was established a "closed season" for this species. However, Hernández-Portocarrero & Saborido-Rey (2007) indicated the low abundance of Gaspar and recommended two year as temporary moratorium for its fishery. Recently, in 2008 were included in the national regulations the "closed seasons" for four new fish species (Table 3) because those have being considered necessary to be protected (Normas Jurídicas de Nicaragua, 2008).

Table 2. The following is a list of teleost fish species reported in the Lake Nicaragua (Regan, 1906-08; Miller, 1966; Bussing, 1976).

Order	Family	Species	Common name
Characiformes	Characidae	*Astyanax fasciatus* (Cuvier 1819)	Sardina
		Astyanax nasutus (Meek 1907)	Sardina lagunera
		Bramocharax bransfordii (Gill 1877)	Sabalito
		Brycon guatemalensis (Regan 1908)	Machaca, sabalete, macabi
		Hyphessobrycon tortuguerae (Bohlke 1958)	Sardinita
		Carlana eigenmanni (Meek 1912)	Sardinita
		Roeboides guatemalensis (Gunther 1864)	
Siluriformes	Pimelodidae	*Rhamdia barbata* (Meek 1907)	Catfish, Chulin Barbudo
		Rhamdia managuensis (Gunther 1867)	Bagre
		Rhamdia nicaraguensis (Gunther 1864)	Bagre
		Rhamdia sp.	Bagre, Chulin
Lepisosteiformes	Lepisosteidae	*Atractosteus s tropicus* (Gill)	Gaspar, Gar
Ciprionodontiformes	Cyprinodontidae	*Rivulus isthmensis* (Garman 1895)	Rivulinos
	Poeciliidae	*Alfaro cultratus* (Regan 1908)	Olominas, Pepescas
		Belonesox belizanus (Kner 1860)	Pepesca
		Gambusia nicaraguensis (Gunther 1866)	
		Neoheterandria umbratilis (Meek 1912)	
		Phallichthys tico (Bussing 1963)	
		Poecilia gillii (Kner 1863)	Pepesca
		Poecilia sp.	Pepesca
Perciformes	Cichlidae	*Archocentrus centrarchus* (Gill 1877)	Mojarrita
		Amphilophus labiatus (Gunther 1864)	Labiata
		Amphilophus longimanus (Gunther 1867)	Mojarra pechito rojo
		Amphilophus maculicauda (Regan 1905)	Vieja
		Herotilapia multispinosa (Gunther)	Mojarrita
		Neetroplus nematopus (Gunther)	Picaculo
		Cichlasoma nigrofasciatum (Gunther 1867)	Mojarra
		Amphilophus rostratum (Gill 1877)	Masamiche
		Amphilophus citrinellus (Gunther 1864)	Mojarra
		Hypsophrys nicaraguensis (Gunther 1864)	Moga
		Parachromis managuensis (Gunther 1867)	Guapote tigre
Sybranchiformes	Synbranchidae	*Synbranchus marmoratus* (Bloch)	Anguila
Species with Marine affinities			
Carcharhinidae	Carcharhinidae	*Carcharhinus leucas* (Muller & Henle 1839)	Tiburon toro
Pristiformes	Pristidae	*Pristis pectinata* (Latham 1794)	Sawfish, Pez sierra
		Pristis perotteti (Muller & Henle 1841)	Largetooth sawfish
Elopiformes	Megalopidae	*Megalops atlanticus* (Valenciennes 1847)	Tarpon, Sabalo Real
Clupeiformes	Clupeidae	*Dorosoma chavesi* (Meek 1907)	Sabalete, Sandillero
Atheriniformes	Atherinidae	*Melaniris sardina* (Meek 1907)	Sardina
Perciformes	Centropomidae	*Centropomus parallelus* (Poey 1860)	Snook, Robalo
	Pomadasyidae	*Pomadasys croco* (Steindachner 1869)	Roncador
	Gobiidae	*Gobiomorus dormitor* (Lacèpede 1800)	Guavina

Table 3. List of fish species from the Lake Nicaragua under protection for the local regulations in 2008. (*): In September month is only permitted the sport fishing (catch-and-release) in the San Juan River (RSJ). Taken (translated for this study) from Normas Jurídicas de Nicaragua (2008).

Category	Scientific name	Common name	Closed season and location
Permanent	*Megalopus spp.*	Sábalo real (Tarpon)	Whole year (except September)*
	Carcharhinus leucas	Tiburón toro (Bull Shark)	Lake Nicaragua and Río San Juan
	Pristis pectinatus	Pez sierra (Saw fish)	Lake Nicaragua
	Pristis perotteti	Pez sierra (Saw fish)	Lake Nicaragua
Temporary	*Lepisosteus tropicus*	Gaspar	1May / 30 Octubre
	Lepisosteus spatula	Gaspar	1May / 30 Octubre
	Centropomus parallelus	Robalo (snook)	15 November / 31 December
	Centropomus pectinatus	Robalo (snook)	16 November / 31 December

1.4. The fishery in the lake

1.4.1. Catches and trends

Overall the fish species exploitation pattern in the Lake Nicaragua have dramatically varied with time, starting in the 1960s with the exploitation of largest fishes, consumed domestically and exported overseas (Thorson, 1982) as large-tooth sawfish (*Pristis pectinatus* and *Pristis perotteti*) and bull shark (*Carcharhinus leucas*). This fishery industry collapsed in the 1980s, and since then the sawfish and shark populations have not recovered from the devastating over-harvest (McDavitt, 2002). The sawfish and shark fishery was replaced by an incipient fishery of relative smaller species as tarpon (*Megalops spp*), snook (*Centropomus spp*), gar (*Lepisosteus spp or Atractosteus spp*), guapote (*Parachromis spp*), and many mojarra varieties (*Amphilophus ssp*) locally demanded. Davies & Pierce (1972) visualised the expansion of these untapped species if market development was stimulated.

On the historical data series of almost the last 30 years of registered fish landings from the Lake Nicaragua, have been observed that the recorded fish landings till 1987 were lower than 300 t (Figure 4) probably because only the main local market where fish was commercialized was monitored. The monitoring and statistics improved since 1993 and figures are more reliable since then. Reported fish landings peaked in 1995, followed by a marked decrease for eight years, and since then landings remained at high levels, between 500 and 800 t, except in 2007. However, since 1994 to 2006, for the first time ever, it was estimated the portion of fish landings unregistered every year (Figure 4). In general, the unregistered landing for that period (6158 tonnes) is equivalent to the registered (6610 tonnes) (ADPESCA, 2006). The landing statistics mostly come from the fishing processing plant for exporting fish products, while the unregistered landings were estimated by random inspection, of the local markets where the local institution does not routinely register it. Still, the catches used for self-consumption are not accounted its magnitude is ignored. Around the lake exist three established fish reception centre as San Carlos, the Nancital (island) and Granada (city) where fish are landed and from that places send to the fish processing plant in the capital city where statistical landing are collected, but fish are also landed and commercialized directly in the local market or restaurant by fisherman or in different places (docks) where an intermediary person with cold storage facilities eventually show up and negotiate directly with the fisherman their selling fish products. Since only fish first class fish species are commercialized in the fish reception centre and this in turn is the one registered from the fish processing plants, many species escapes from the national statistics record. All of this highlights the necessity on further improving the monitoring to account properly the unreported fish catches.

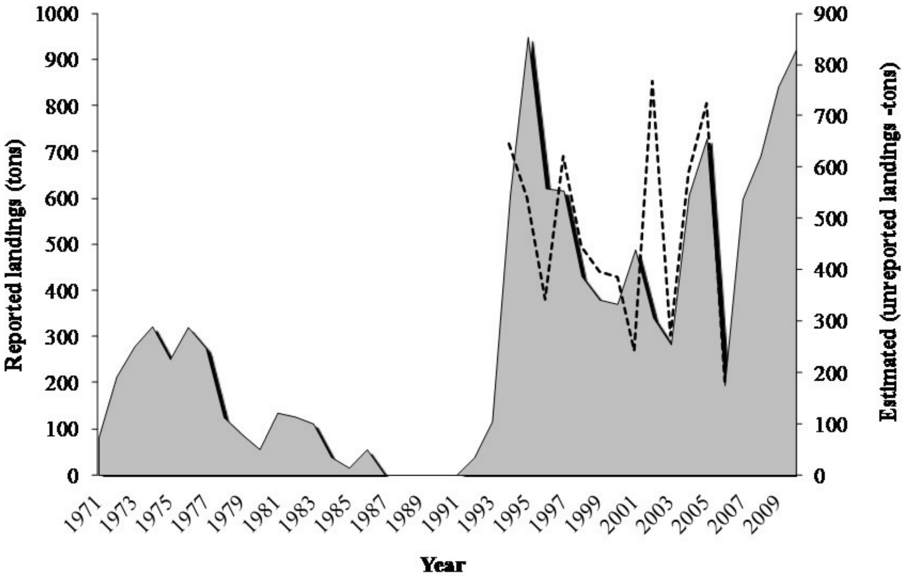


Figure 4. Data series of fish landings from the Lake Nicaragua: Gray: Reported landings; Dashed red line: Estimated (unreported) landings. Source: ADPESCA (2006) and INPESCA (2011).

The landings data series do not allow ascertaining accurately the catch species composition. First, because the observed gaps in catch reports as mentioned above and because many species are reported under the same name category e.g. in the mojarra category are included *Amphilophus citrinellus*, *A. labiatus*, *A. longimanus*, *Astatheros rostratus*, *Hypsophrys nicaraguensis* and others. Hence, any evaluation of the fish exploitation pattern in the Lake Nicaragua derived from landings record is imprecise, yet some trends can be derived from landings (Figure 5), thus Robalo (snook), a marine migratory species, has decreased in importance and landings are now half of those in 2001. Tilapia is still the second most landed species and its importance is now similar to 2000, after a period of low landings. For the species registered only since 2004, the Mojarras showed an abrupt increase since 2006, while Guapote landings remained without important variations.

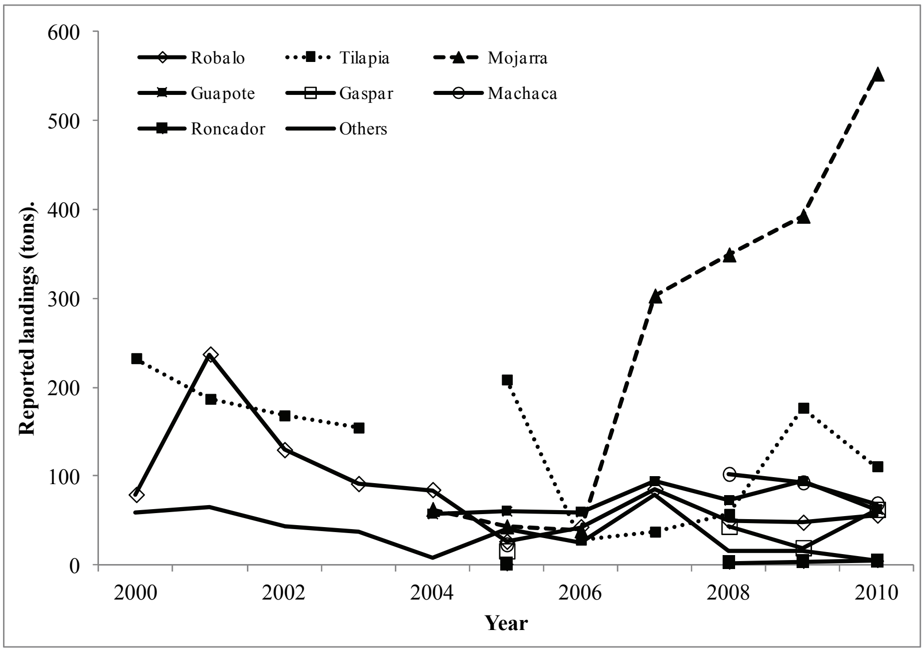


Figure 5. Fish landings by species category. Robalo: *Centropomus sp*; Tilapia: *Oreochromis sp*; Mojarra: *Amphilophus citrinellus*, *A. labiatus*, *A. longimanus*, *Astatheros rostratus*, *Hypsophrys nicaraguensis*; Gaspar: *Atractosteus tropicus*; Machaca: *Brycon guatemalensis*; Roncador: *Pomadasys croco*.

The fishery activity in the Lake Nicaragua is mainly developed by artisanal fishermen at small-scale. This activity has shifted from temporally to permanent (Davies & Pierce, 1972), i.e., formerly the majority of fishermen fished mostly during the dry season, November to March, becoming farmers during the months of April to October and fished occasionally only for their own consumption. At present, the artisanal fishermen operate full-time all year. On the other hand the three fishery census carried out in the lake indicates that the number of fishermen significantly increased from 500 in 1974 to 730 in 1995, but in 2002 the number had increased only slightly, to 762 (INFONAC, 1974; PRADEPESCA, 1995; ADPESCA, 2002).

The artisanal fishery in the Lake Nicaragua is characterized by the use of gillnets under different modalities: **a.** set gillnet (passive): this consists of a single netting wall kept more or less vertical by a floatline and a weighted groundline (FAO, 2013), and the net is set for several hours on the bottom of the lake and kept stationary by anchors on both ends. This gillnet type is considered a "*passive gears*" since fish have to swim into the net to get caught; **b.** bag seine (active): consist of a net operated by two fishermen which is placed offshore and hauled to inshore, the gillnet type is considered an "*active gears*" since the fishes are corralled in it; **c.** Pimponeo (active): the gillnet is set by two small boats and the fishes are induced to swim in to it hitting the water with a pole producing noise (Agareso, 2010). In some areas of the lake, this operation can be performed also by one fisherman only. Another fishing gear used in the lake fishery is hook and line (handline).

1.4.2. Fish stock biomass

During the 70s and 80s decades were carried out the major fisheries-independent surveys in the coastal and central zone of the Lake Nicaragua where different potentialities and biomass based on gillnet and trawl net surveys were reported (INFONAC, 1974), as the fishery production from the artisanal fisheries in the lake that were reported equivalent to 680 tons per year. Based on these studies the distribution and abundance of species, excluding shallower waters, were mapped estimating a biomass of 50,000 tons and maximum sustainable yield of 8,000 metric tons (Ketúnin *et al.*, 1983). This estimation increased to 49,000 metric tons when the biomass calculations from gillnet surveys in the coastal areas from the 1982-1983 studies were included (Orellana, 1986; Table 4). Beyond the referred biomass of the lake stocks, there has not been made any attempt to assess the state of the stocks either under exploitation or not.

Table 4. Biomass per species and zone of the Lake Nicaragua. The Central zone refers to the waters below 2 m deep, i.e., a surface area of about 2,957 km^2; the Coastal zone refers to the waters above 2 m deep (Orellana, 1986).

No	Species	Central zone	Coastal zone	Total	%
1	*Dorosoma chavesi* (Meek)	3939.9	1299.6	5239.5	10.5
2	*Gobiomorus dormitor* (Lacepede	762.7	18.0	780.7	1.6
3	*Roeboides guatemalensis* (Gunther)	200.7	18.6	219.3	0.4
4	*Cichlasoma nicaraguense* (Gunther)	9623.3	238.2	9861.5	19.8
5	*Cichlasoma longimanus* (Gunther)	7869.4	348.0	8217.4	16.5
6	*Cichlasoma citrinellum* (Gunther)	7163.9	764.4	7928.3	15.9
7	*Cichlasoma centrarchus* (Gill & Bransford)	754.8	65.4	820.2	1.6
8	*Cichlasoma rostratum* (Gill & Bransford)	904.8	769.8	1674.6	3.4
9	*Cichlasoma labiatum* (Gunther)	29.1	15.6	44.7	0.1
10	*Cichlasoma maculicauda* (Regan)		163.2	163.2	0.3
11	*Cichlasoma nigrofasciatum* (Gunther)		42.0	42.0	0.1
12	*Neetroplus nematopus* (Gunther)	2.7	81.0	83.7	0.2
13	*Herotilapia multispinosa* (Gunther)	0.9		0.9	0.0
14	*Mollienisia dovii*(Valenciennes)		86.4	86.4	0.2
15	*Melaniris sardina* (Meek)		39.0	39.0	0.1
16	*Alfaro cultratus* (Regan)		0.6	0.6	0.0
17	*Astyanax fasciatus* (Cuvier)		444.6	444.6	0.9
18	*Carlana eigenmanni* (Meek)		0.6	0.6	0.0
	Sub-total Omnivore species	31252.2	4395.0	35647.2	71.7
19	*Bramocharax bransfordii* (Gill)	26.9	106.8	133.7	0.3
20	*Rhamdia sp.*	2829		2829.0	5.7
21	*Cichlasoma dovii*(Gunther)	104.5	25.8	130.3	0.3
22	*Cichlasoma managuense* (Gunther)		22.2	22.2	0.0
23	*Centropomus undecimalis*(Bloch)	1079		1079.0	2.2
24	*Pomadasys grandis*(Roballo)	334.3		334.3	0.7
25	*Brycon guatemalensis* (Regan)	6124.4	353.4	6477.8	13.0
26	*Lepisosteus tropicus* (Gill)	3062.2		3062.2	6.2
	Sub-total carnivore species	13560.3	508.2	14068.5	28.3
	Total	44812.5	4903.2	49715.7	100

1.4.3. Fishery management

Inland fisheries are distinct from marine fisheries in their nature and in the range of drivers that influence them. Although commercially intensive fisheries exist, inland fisheries are generally characterized by small-scale/household-based activities (Welcomme *et al.*, 2010) The lake management can be divided into three major domains: 1. Management of the environment, like reserves or refuge areas, pollution control and prevention, environmental flows, freedom of passages, rehabilitation of degradated habitats; 2. Management of the fish assemblages such stocking natural waters to improve recruitment or to maintain productive species, introduction of new species to exploit underused parts of the food chain or habitats, removal of unwanted species; and 3. Management of the fishery strictly speaking by enforcement of various regulatory constraints to prevent overexploitation of the resources and maintain a suitable stock structure e.g. closed season and areas, type gear and landing size of the fish (Cowx, 1994; 1998; Welcomme *et al*., 2010). Fisheries management in the Lake Nicaragua face the same complexity as in many others inland waters, mainly due to the multi-specific nature of the exploitation. Many species, with different size and shapes are caught with the same net types, and virtually all species experience a fishing mortality well as target species or as inevitable by-catches (Sparre & Venema, 1998). At present there is not stock assessment for any of the exploited stocks in the Lake Nicaragua. Management measures, such as net mesh size, gillnet length, closed seasons and the limitation of fishery operation near to the river mouth have responded exclusively to the immediate necessity of reducing the catches of some key target species, though other species are more abundant in the catches. This management considers catches of less or non commercial species as by-catch, without being the case. As a consequence, these regulations, in the line of protecting some targeted species, expose other species to the risk of being over-fished. On the other hand, target species changes according to the artisanal fisherman interest, i.e., "what it is considered a target species for some fishermen group is not for others", increasing the complexity of fisheries management.

The enforcements regulatory measures in the Lake Nicaragua are in the line of: i) the recovery of overexploited fish species as Bull shark, Sawfish and Tarpon (Thorson, 1982; McDavitt, 2002; Adams *et al*., 2006); ii) the prevention of overexploitation of Gar (freshwater species), Snook and Roncador, which are both species of marine affinity (Camacho & Gadea, 2005); and iii) the sustainability of the commercially exploited fisheries resources, at present days, such as cichlids assemblage (Mojarras, Guapotes), characids (Machaca), gobies (Guavina) and Bagres (Gadea, 2003; Hernández-Portocarrero & Saborido-Rey, 2007). The regulations adopted for the lake fisheries range from the prohibition of trawl nets and long lines in lake basins, and gillnets near to the river mouth or inside the river properly. However, the biological references point for fisheries resources management have not been set yet in the lake, since most of those regulatory measures are based only on evaluation of catches distribution and abundances of the commercially important species, on gillnet selectivity analysis and on macroscopic determination of two biological parameter as length-at–maturity and gonad maturity stages (Davies & Pierce, 1972; INFONAC, 1974; Martínez, 1976; Ketúnin *et al*., 1983; Orellana, 1986; Gadea, 2003, Hernández-Portocarrero & Saborido-Rey, 2007).

At present there is a large gap on knowledge of many other important biological parameters of the fish species as the dynamic of reproductive behaviour of the population at intra-specific and inter-specific level, the reproductive cycle, spawning ground, egg production and the maternal features affecting reproductive output and fitness. This lack of information prevents the implementation of management actions directed towards the conservation of stock reproductive potential (Saborido-Rey & Trippel, 2013), such as regulations on closing season and/or areas, and minimum and maximum landing sizes. Those biological parameters should be of fundamental importance for the evaluation of the spawning stock and for better management of the species in the lake. In this study, besides providing information about actual state of distribution and abundance of *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis*, and *Brycon guatemalensis*, is provided information of the reproductive strategy of this last species and proposed some management alternatives based on its biological features.

1.5. Thesis objectives

The knowledge of the ecology of fish communities and their stocks is necessary for management purposes, but also this knowledge must be reliable, timely, cost effective and adequate for its purpose, and based upon appropriate, sound and defensible data (Hickley & Aprahamian, 2000). The aim of the present work is to develop an appropriate fishery management tool in the Lake Nicaragua based on biological and ecological knowledge of the exploited species. To achieve this in this study it is analysed: a) the distribution and relative abundance of the main species at spatio-temporal scale in function of environmental factors based in monthly fishery-independent surveys (Chapter 3); b) the reproductive strategy-related issues applying histological procedures, focusing on the reproductive biology and the stock reproductive potential using *Brycon guatemalensis* as study case (Chapter 4); and c) the impact of the fishing gears on the stock reproductive potential (SRP), determining the most sensitive and relevant part of the population in terms of productivity to delineate the management of the fish stocks in the Lake Nicaragua (Chapter 5).

CHAPTER 2: Material and Methods

2.1. The study site

The Lake Nicaragua or Cocibolca is the largest freshwater lake in the Central American isthmus, located south-western Nicaraguan territory, and is considered the most important freshwater ecosystem in the region (Figure 6). The Lake has a surface area of about 8,264 km^2 and it raises 31 meters (m) over the sea level, its mean depth is 13 meter and maximum depth of 40 meter. 51 rivers drain in the lake: 15 in the western, 17 in the eastern and 19 in the southern side. The Lake Nicaragua is connected with the Lake Xolotlán by the Tipitapa River and with the Caribbean Sea by the San Juan River (RSJ).

The study site is located in the eastern side of the lake. Along the shore line of approximately 183 km, six fishing communities are found, from south to north, San Carlos, Morrillo, San Miguelito, Morrito, El Nacital and Puerto Díaz. The study area covered a total of 1000 km^2, from the edge to 5.0 meter of depth and limited by the fishing ground named El Yolillal at the southeast of San Carlos and Río San Juan, and by Río Estrella at the northwest of Puerto Díaz (Figure 7). The study area and ranging depth overlap with the fishing ground where the small-scale fishers develop their major activity during the whole year.

Figure 6. Geographical locations of the Lake Nicaragua in the Nicaraguan territory.

2.2. Sampling surveys

Monthly stratified surveys were conducted along the studied area from February 2005 to January 2006. Nine strata were defined according to latitude and depth. First, the surveyed area was divided in three macro-zones: Southeast, Central and Northwest. These zones were defined as a combination of geographical location (north or south) and ecological aspects as the influences of major rivers flowing into the lake and the source of San Juan River, i.e., (PROCUENCA-SAN JUAN, 2004) located in the southeast area of the lake. Hence, the north-west zone corresponds to the internal part of the lake, whereas the southeast zone is the drain off the lake. Second, three depth strata were delimited: between shore and 1.5 m, 1.5 and 3.0 m and between 3 and 5.0 m depth.

A total of 47 stations were defined in 16 transects orthogonal to the shoreline with three stations in each transect, except in the one located closer to San Juan River, where only two stations were defined due to the curvature of the shoreline in that area (Figure 7). Thus between four to six stations were defined in each stratum.

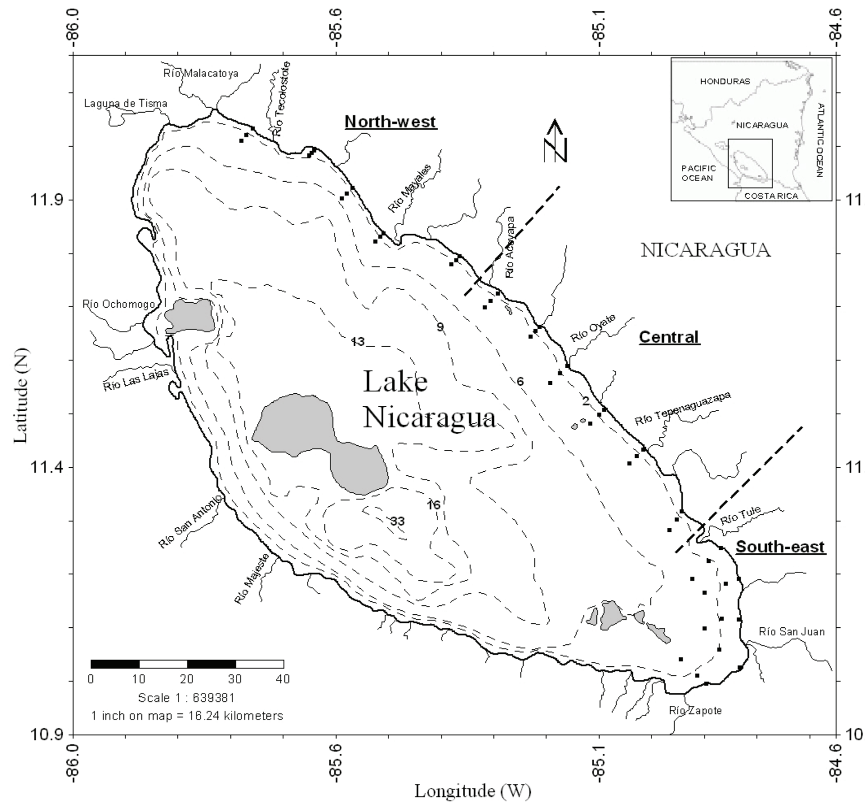


Figure 7. Geographical locations of the monthly fishery research campaign (●) in the eastern shore of the Nicaraguan Lake. February 2005 to January 2006. Dashed lines: Depth profiles in meters.

Table 5. Gillnet specifications: Characteristic and material of construction of the passive fishing gear used during the fishery-independent survey carried out in the Lake Nicaragua.

	Mesh size of the net of 50 m long each: Four nets			
Mesh size (mm)	75	100	125	150
Net twine (Monofilament type) diameter (mm)	0.33	0.33	0.40	0.50
Rope (multifilament type) diameter (mm): Tie-up net to net	12	12	15	15
Net heights (meter)	1.5; 3.0 and 5.0			
Buoys type	Y8			
Bottom line or lead line: Weight (g)	25			
Hanging coefficient	0.5			
Top line diameter (mm)	6.3			

2.2.1. Fishing gear characteristic

The gillnet was a monofilament type arranged in a gang of 200 m long, composed by four nets of 50 m each, of 75, 100, 125 and 150 mm stretch mesh size respectively. The four nets were tied end to end and leaving gaps between the nets (Table 5). The hanging ratio used for the construction of whole set of nets was 0.5. Three gillnets of 1.5, 3 and 5 m height were built to be used in the corresponding depth strata. Overall, the building nets obeyed to the importance to test the whole gillnet type used in the small-scale fishery in the lake, which vary from 75 to 150 mm, but the more frequently used 100 and 125 mm mesh size, and to the necessity of ensure that during the survey would be captured fish of similar variety and size captured in a normal fishing operation. Therefore:

a. The characteristic of the **material** of the nets construction (twine diameter and ropes) used for the survey, first of all, accomplished with some technical specifications required for the research purpose, but as pointed before, these only slightly differed from the nets used in the small-scale fisheries in the lake.

b. The four different **mesh size** (75, 100, 125 and 150 mm) used were assumed to catch and retain fishes from a size range of the population covering the ontogenic maturation (immature and mature).

c. The entire water column, of each sampled site, was covered by the nets heights used, and by that, to catch and retain fishes swimming at different depth, i.e., benthic, demersal and pelagic fishes.

d. The four nets were set in gangs in order to cover up more area, and to compare selectivity of different nets. The use of gangs is not recommended because the catch of one net may be reduced by competition with an adjacent, more efficient net (Larkins, 1963; 1964); a large fish may "lead" along a small-meshed net until they come to, and are captured by, a larger-meshed net (Anon, 1961). Instead of that Pope *et al.*, 1975 recommended to set different-meshed net at separate, randomly chosen locations. However, if nets must be set in gangs, leading can be minimized by leaving gaps between the nets. The last was the approach taken in to account in the present study.

2.2.2. Fishing operation

The net used in each survey was anchored to the bottom of the lake. This gillnet is a "*passive gear*" since fish have to swim into the net to get caught, implying that fish which move faster, have larger probability of encounter with the gear than slowly moving fish (Sparre & Venema, 1998). Gillnets were set systematically parallel to the shore line at three different depths (1.5, 3.0 and 5.0 m), that because it was assumed that fish move perpendicular to the shoreline, i.e., from shallow to deeper waters. Gillnets were anchored at exactly the defined depths of 1.5, 3 and 5 m, using the corresponding net with different heights. In this manner the net covered the entire water column, from surface to the bottom, as mentioned above.

The soaking time followed the pattern of fishing operation of the local fishers, and it was based on their empirical knowledge, who indicated that very early in the morning the fish increase swimming activity, probably for feeding or reproduction. Therefore the nets were shot before sunrise. Although initially the haul duration was set in 6 hours, in practice it ranged from 4.41 to 9.05 hours, because distance from one sampling site to the other, hauling time of each gang and whether conditions.

2.2.3. Biologic and environmental data recorded

After hauling the nets, the fish caught were carefully removed. Catch was recorded in numbers by species. The place within the net where the fish was retained was also recorded, as well the way in which the fish was stuck. The wedged or gilled, fish (Figure 8), which are the one held tightly by a mesh around the body-girth retained as far as the dorsal fin (Baranov, 1914; Karlsen & Bjarnason, 1986) were separated by mesh sizes of the net. Particularly for these girth retained fishes, besides collect routine bio-morph-metric information, was measured their body height between the operculum and first dorsal fins.

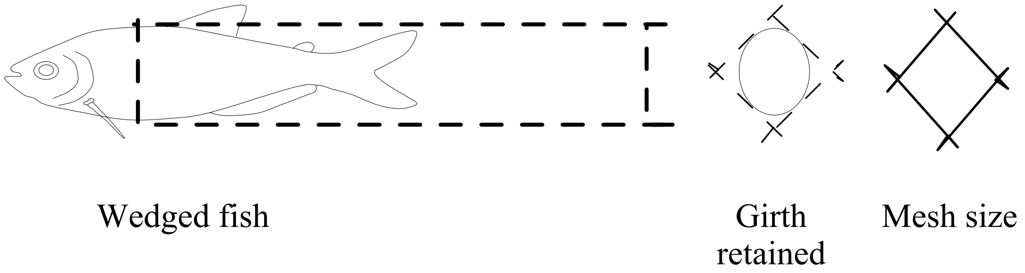


Figure 8. Schematic representation of a wedged fish in gillnets as indicated by Karlsen & Bjarnason (1986)

Table 6. Stages of fish sexual maturity used in present study (for field work) for macroscopic observations of fish gonads, (modified from the maturity scale of Holden & Raitt, 1974).

Stage	State	Description
III (Included stages: I, II and III)	Immature	Ovary and testis about 1/3rds to 2/3rds length of body cavity. Ovaries pinkish, translucent to yellow colour with granular appearance. Testis whitish to creamy. Eggs not visible to naked eye.
IV	Ripe	Ovary and testis from 2/3rds to full length of body cavity. Ovary orange-pink in colour with conspicuous superficial blood vessels. Large transparent, ripe eggs visible. Testis whitish-creamy, soft.
V	Spent	Ovary and testis shrunken to about 1/2 length of body cavity. Walls loose. Ovary may contain remnants of disintegrating opaque and ripe eggs, darkened or translucent. Testis bloodshot and flabby.

Table 7. Ovaries of *Brycon guatemalensis* collected from February 2005 to January 2006 by fish size range. The samples were taken in the eastern part of the Lake Nicaragua.

Total length (cm)	N
< 20	3
20-25	19
25-30	76
30-35	138
35-40	78
40-45	46
45-50	10
> 50	1
Total	371

Bio-morph metric data: From all specimens collected were registered information of the total length in centimetres, total body weight and gutted weight in grams and determined the sex (male, female). Additionally, the body height (cm) was measured in the wedged fish. In the field the sexual maturity stage was macroscopically determined through the observation of the gonad following three categories (Table 6).

Ovaries samples collection and fixation: In all surveys except in June 2005[1] ovaries of *Brycon guatemalensis* were collected (Table 7) and weighted in fresh condition. A total of 371 ovaries collected and fixed in a 4 % neutral phosphate buffered formaldehyde for the subsequent histological analysis (see section 2.3.1).

Environmental data: In each sampling station the bottom type, water temperature and turbidity were recorded. The bottom type was empirically determined by visual examination of the soil type in the anchor when lifted it out of the water. The temperature of the water column was registered using an ABT-1 thermometer, calibrated to register de temperature every meter, from the surface to the bottom. The water turbidity was registered in centimetres using a Secchi disk.

The annual precipitations in millimetres (mm) were obtained from the meteorological station located closer to the study area, from the Instituto Nicaragüense de Estudios Territoriales-INETER.

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[1] The bad weather condition and technical problems did not allow the gonad collection.

2.2.4. Catches-per-Unit-Effort (CPUE)

The CPUE analyses were based on the premise that CPUE estimated from fishery-independent survey is assumed to be proportional to true abundance, considering that survey is carried out under a strict random sampling framework (Harley, Myers & Dunn, 2001). Thus, the CPUE estimated is analysed in the context that spatiotemporal scales and environmental factors induce changes in the fish abundance.

The catches were obtained from the fishery-independent surveys described above. They were registered as total weight (kg) and numbers by species and sampling station (n = 561). Catch in each haul was estimated as the sum of the individual weight registered, as described in the previous section. In some analysis in this study catch is expressed in biomass, while sometimes we used catch in numbers, i.e., abundance.

The catch-per-unit-of-effort (CPUE) or catch rate assumes that, at small spatial scales, catch is proportional to the product of fishing effort and abundance:

$$C = qEN \qquad (1)$$

where E is the fishing effort expended, N the abundance, and q is the catchability, a constant. This leads to the fundamental relationship between catch rate and abundance.

$$C / E = q\,N \qquad (2)$$

Catchability, q, is usually considered as constant, but may change spatially and temporally due to where and when fishing occur (Hilborn & Walters, 1992). Catchability is thus defined as the relationship between the catch rates (CPUE) and the true population size, or abundance. So the unit of catchability is fish caught per fish available per effort unit and per time unit. Catchability is also called gear efficiency (Hilborn & Walters, 1992) or sometimes fishing power, and is strongly related to gear selectivity (defined below) because it is species and size dependent.

In the present study the abundance index (CPUE or catch rate) is expressed as the ratio between the catch (in number of specimens) and effort (in hours, multiplied by surface area of the net):

$$\mathrm{CPUE} = n/h*m^2 \qquad (3)$$

where "n" is the catch expressed in number of specimens and the effort is the soaking time measured in hours (h), multiplied by the fraction of the gillnet surface area in square meters (m^2). To estimate the fraction of the gillnet surface area, the largest net (the one used at 5 depth stratum) was used as reference resulting in surface areas of 0.3, 0.6 and 1.0 for the nets used at 1.5, 3.0 and 5.0 meter of depth respectively.

CPUE was modelled as function of spatiotemporal scale and environmental factors. The catchability coefficient "*q*" in the equation (2), thus, is considered constant between months, macro-zones (fishing ground divided in three zones as southeast, central and northwest), seasons (dry and rainy), and depths.

One of the problems in CPUE analysis, is the occurrence of zero-catches during surveys, since arose the uncertainties if the non clear pattern of the spatiotemporal variations in the fish abundance, significant and non significant differences, and the no homogeneity of variances were related to these zero-catches. Lambert (1992) adverted that the presence of many zeros can invalidate the assumptions of the analysis and jeopardizes the integrity of the inferences if not properly modelled. Furthermore, zero-catches have been addressed as problems that arise in the case of less abundant species and for bycatch species and many reasons have been listed for these zero-catches (Maunder & Punt, 2004). These reasons can be used as criteria for defining if some zero-catches can be consider in the CPUE analysis or not. In the current study three hauls with zero-catches were not considered in the analyses due to gear failures, i.e., malfunctions of the gear, namely stations number 14, 315 and 482.

To overcome the problem of zero-catches still present in normal hauls, a small constant, 1 in our case, was added to CPUE before being log transformed, i.e., the ad hoc method (Robson, 1966). The Ln (CPUE $n/h * m^2 + 1$) was then used as response variable to analyse its spatio-temporal variation (macro-zones, depth and month), as well the environmental effects (season and turbidity) through General Linear Model (GLM) by mean of least square methods, using statistical software 6.0. This simple method was considered sufficient given the relative low frequency of zero catches events recorded during the whole survey, the 14.3 % off the total hauls (n=561). This ratio was smaller than 1/3 suggested being the threshold below which the ad hoc method should be applied from the practical viewpoint (Shono, 2008).

An overall analysis of the CPUE was made for whole catch in the 12 surveys conducted, with indication of catch rate by species. However, the detailed spatio-temporal analyses of CPUE, as index of abundance, was conducted only in the four main target species of the lake, *A. citrinellus* (Mojarra), *H. nicaraguensis* (Moga), *P. managuensis* (Guapote tigre) and *B. guatemalensis* (Machaca).

2.2.5. Length distribution

Length frequency distribution of the four target species was analysed and modelled using General Linear Model (GLM) and least square methods to investigate spatial (macro-zones and depth) and temporal (season) variations and their interactions. Previously, size frequency was compared by month and sexes using ANOVA. A linear regression (GLM) was done to assess the potential influence of water turbidity on individual length of the catch. For all performed analysis statistical software 6.0 were used.

2.3. Biological analysis

2.3.1. Ovarian histology

Histological studies were conducted on 371 ovaries collected from *Brycon guatemalensis*. After fixation a central portion of each ovary was extracted, dehydrated, embedded in paraffin, two slides sectioned at 3 µm and stained with Harris haematoxylin followed by eosin-phloxine b counterstain (Table 8). With this staining procedure eosinophilic structures acquire a red colour in bright field microscopy, while the rest of the substrates obtain a blue coloration due to haematoxylin staining.

Table 8. Haematoxylin-Eosin staining standard protocol used in ovaries of *Brycon guatemalensis*.

Step	Chemical	Time (min)
1	Xylene	10:00
2	Ethanol 100 %	4:00
3	Ethanol 80 %	3:00
4	Water	2:00
5	Papanicolau (Harris Haematoxylin)	4:00
6	Water	2:00
7	Acid alcohol	0:10
8	Water	3:00
9	Lithium carbonate	0:10
10	Water	1:00
11	Ethanol 70 %	1:00
12	Eosin-phloxine b	2:00
13	Ethanol 96 %	2:00
14	Ethanol 100 %	2:00
15	Xylene	5:00
16	Xylene	3:00

2.3.2. Oocyte development

The histological sections were analysed microscopically using a Leica DM RE (Digital Microscope series RE). The oocyte developmental stages were determined according histological terminology (Wallace & Selman, 1981; West, 1990; Tyler & Sumpter, 1996; Saborido-Rey & Junquera, 1998; and Murua & Saborido-Rey, 2003), as follows:

Primary growth stage (PG). This covers two phases: the chromatin nucleolar phase and the perinucleolar phase. The chromatin nucleolus is the first sign of the primary development of the teleost oocyte, which is very small with a central nucleus containing a large single basophilic nucleolus, surrounded by a thin layer of cytoplasm. As the oocyte grows, both the cytoplasm and the nucleus increase in size and multiple nucleoli appear in the periphery of the nucleoplasm, which is the perinucleolar stage.

Cortical alveoli stage (CA). We consider cortical alveoli (CA) oocytes to be secondary growth oocytes since their formation is gonadotropin dependent. The presence of secondary growth oocytes unavoidable means the fish has matured. The cortical alveoli in the periphery of the cytoplasm indicate the onset of ripening. With conventional haematoxylin–eosin staining, the alveoli appear as empty spheres. This stage is completed when yolk starts to accumulate.

Vitellogenesis. The vitellogenesis starts when yolk globules begin to be formed. In the present study vitellogenic oocytes were sub-divided in two stages: initial or early vitellogenesis (VIT1) and late or advanced vitellogenesis (VIT2). VIT1 is characterized by the appearance of yolk vesicles or spheres in the perinuclear cytoplasm lying between the cortical alveoli. As vitellogenesis progress the yolk spheres increase in size and lipid are displaced to the cytoplasm periphery. Oocytes in VIT2 have grown and yolk droplets are large and more visible. The yolk granules are distributed now more homogenously in the cytoplasm becoming the predominant structures and the lipids are completely displaced to the periphery of the cytoplasm. Although the nucleus remains in the centre of the oocyte, often it is not seen because the size of the oocyte has increased notably.

Germinal vesicle migrations (GVM) or migratory nucleus. It is the first visible event associated with final oocyte maturation (OM). The nucleus is eccentric located and often close to periphery.

Each oocyte developmental stage was characterized, in addition to its morphology, by their oocyte diameter range that was measured in histological sections from 66 ovaries. Oocyte diameter was computed as the mean of two lengths approximately orthogonal measured in the longest and shortest axis of the oocyte. Measurements were taken using the software Leica QWin Pro V 3.5.1.

Apart of these developmental stages, two other important ovarian structures, connected to oocyte development, were identified:

Atretic oocytes (AO). Atresia is a process in which ovarian follicles degenerate and are subsequently re-absorbed. It can occur in oocytes at any developmental stage. The observed characteristics of atresia are the oocytes walls break, the cytoplasmic disorganization leading to the occurrence unrecognizable structures in the cytoplasm.

Postovulatory follicle (POF). It consists of the follicular layers (the granulosa and the theca) that remain in the ovary of fish after the release of the ovum during spawning. It therefore indicates that the fish have spawned at least once.

2.3.3. Reproductive cycle

Ovaries were classified in reproductive phases following the terminology proposed by the Brown-Peterson *et al.* (2011). For simplification, in this study we have used the Actively spawning subphase as a reproductive phase. Thus, six phases were considered: Immature (I), Developing (D), Spawning capable (SC), Actively spawning (AS), Regressing (Rgs) and Regenerating (Rgn) based on the presence of the different oocytes development stages (PG, CA, VIT1, VIT2, GVM), the atretic oocytes and postovulatory follicles (Table 9).

For the analysis of the reproductive cycle of *Brycon guatemalensis* only the 320 mature females sampled were considered, i.e., those in Developing, Spawning capable, Actively spawning, Regressing and Regenerating. The immature females, those with oocytes in primary growth (PG) stages, considered “reproductively inactive females”, since are not capable for spawning in the current breeding season or in the near future (Hunter *et al*., 1992), were excluded.

2.3.4. Spawning fraction (Sf)

The Sf defined as the fraction of mature female spawning per day (Alheit, 1985) is assessed from the prevalence of spawning stages or phases determined from a random sample of gonads (Hunter & Golberg, 1980).

Thus the spawning fraction (Sf) was calculated as:

$$\mathrm{Sf} = \frac{\mathrm{SC} + \mathrm{AS}}{\mathrm{D} + \mathrm{SC} + \mathrm{AS} + \mathrm{Rgn}} \qquad (4)$$

Sf was estimated in each survey as a whole and by female length categories, i.e., smaller (females below 33 cm), middle (females between 33 and 43 cm) and larger (females above 43 cm). Regression analysis was performed to investigate trends in Spawning fraction along the year for all females and by length class. ANOVA, using statistical software 6.0, was used to analyse differences between female length classes.

Table 9. Terminology applied for reproductive classification of female fishes (Brown-Peterson *et al*., 2011).

Phase	Histological features
Immature: Never spawned	Only oogonia and primary growth (PG) oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
Developing: Ovaries beginning to develop, but not ready to spawn.	Primary growth (PG), cortical alveolar (CA), primary/initial/early vitellogenic (VIT1) and secondary/late vitellogenic (VIT2) oocytes present. No evidence of postovulatory follicles (POFs). Some atresia can be present. ***Early developing subphase***: PG and CA oocytes only.
Spawning Capable: Fish are developmentally and physiologically able to spawn in this cycle.	Vitellogenic, early and late, oocytes present or POFs present in batch spawners. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of oocytes maturation (OM) can be present. ***Actively spawning subphase***: Oocytes undergoing late germinal vesicle migration (GVM), germinal migration breakdown (GVBD), hydration, or ovulation.
Regressing: Cessation of spawning	Atresia (any stage) and POFs present. Some CA and/or vitellogenic (VIT1, VIT2) oocytes present.
Regenerating: Sexually mature, reproductively inactive.	Only oogonia and PG growth oocytes present and some residual cortical alveolar follicles can be present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs may be present.

2.3.5. Somatic indices

The **Gonado-somatic index** (GSI) and **Condition factor** (K) of *B. guatemalensis* were estimated on 240 and 305 specimens, respectively. The **Gonadosomatic index (GSI)** was estimated as:

$$GSI = \frac{GW}{W_g} * 100 \qquad (5)$$

where GW is the gonad weight and Wg the gutted body weight.

The **condition factor (K)** was estimated as:

$$K = \frac{W}{L^b} * 100 \qquad (6)$$

where W is the total body weight; L the total length and the coefficient *b* was fixed as 3.428, which is the value from the length-weight relationship of *B. guatemalensis*.

Differences in GSI and K between reproductive phases were analysed using ANOVA and Tukey HSD test. The relationship of both indexes within reproductive phases, together and separately, was analysed using regression analysis. For all performed analysis statistical software 6.0 were used.

2.3.6. Maturity

The female maturity ogives of *Brycon guatemalensis* was determined using: a. the gonad maturity macroscopic observation taking as reference the classification in Table 6 , and b. the maturity stage obtained from histological studies taking as reference the oocytes development stages described in section 2.3.2, in which the oocytes in primary growth (PG) stages in the ovaries is the main characteristic of immature specimens. The macroscopic maturity stage was determined in 1526 ovaries (Table 10), between April to December during which more than 10 % of females were spawning capable, and hence defining the spawning season (Table

11). This criterion was adopted to minimise the errors on staging macroscopically ovaries in developing and regenerating or recovery stages, which are difficult to stage and often confused and misclassified with immature fish (Wallace & Selman, 1981, Wyllie E., 1987). The assumption behind the criteria adopted in this study, is that while closer the females are to the spawning season, the gonads are more visually developed and, thus, is easier to macroscopically differentiate the ovaries of immature from mature females.

Histological (microscopic) maturity was determined in 371 females collected during the whole study period (from February 2005 to January 2006) (Table 10). Out of this, 51 ovaries, those who contain oocytes in primary growth stages, were immature fishes (size-independent), whereas those ovaries with oocytes in cortical alveoli (CA), initial vitellogenesis (VIT1), advanced vitellogensis (VIT2) and the one with germinal vesicle migratory (GVM), including the ovaries in regenerating (Rgn) phases, were pooled in the mature category (N=320).

Maturity ogives of *A. citrinellus H. nicaraguensis* and *P. managuensis* were estimated from the macroscopic maturity stage only (Hernández-Portocarrero & Saborido-Rey, 2007) in the same way as for *B. guatemalensis*. However, female maturity ogives of *A. citrinellus* and *H. nicaraguensis* did not fit properly to a logistic function due to a complete overlap in sizes between immature and mature fish. For these species male maturity ogive was used instead. The number of male and females by size class and maturity stage for each species is shown in Table 12.

In all cases the maturity was analysed as function of body length, thus a logistic equation was fitted to the maturity-at-length data. The applied logistic equation was:

$$\hat{P} = \frac{e^{a+bL}}{1+e^{a+bL}} \qquad (7)$$

and the logarithm transformation:

$$\ln \frac{\hat{P}}{1-\hat{P}} = a + bL \qquad (8)$$

Where “P” is the predicted proportion of mature individuals, “a” and “b” are the estimated coefficients of the logistic equation and “L” the female body length. The length at 50% maturity (L_{50}) is defined as the length at which 50 % of the females were mature and is estimated as –a/b.

For both, macroscopic and microscopic determination of maturity ogive at size, Statistica 6.0 for windows was used to calculate predicted values and coefficients using a logit non-linear model with a maximum likelihood as loss function. The differences between both methods were statistical evaluated by using generalized linear models with a binomial family function (McCullagh & Nelder, 1989) in R software version 2.13.0.

Table 10. Number of female *Brycon guatemalensis* by length class and maturity stage, based on macroscopic and microscopic observations.

	Macroscopic observation: Maturity ogives built including April to December			Histological analysis: Maturity ogives built including whole reproductive cycle (January to December)		
Length	Immature	Mature	N	Immature	Mature	N
8-10		1	1			
10-12						
12-14		3	3			
14-16		2	2			
16-18						
18-20	4	1	5	3		3
20-22	11	2	13	4		4
22-24	14	2	16	5	1	6
24-26	44	10	54	10	4	14
26-28	177	42	219	19	12	31
28-30	220	65	285	10	30	40
30-32	130	47	177		68	68
32-34	82	47	129		49	49
34-36	85	87	172		42	42
36-38	61	104	165		30	30
38-40	34	80	114		27	27
40-42	17	47	64		24	24
42-44	8	43	51		16	16
44-46	3	33	36		11	11
46-48		8	8		2	2
48-50	2	7	9		3	3
50-52	1	1	2		1	1
52-54						
54-56		1	1			
Total	893	633	1526	51	320	371

Table 11. Proportion of female *B. guatemalensis* macroscopically analyzed, by month and maturity stage. (*) Months considered to be the spawning season and included to stage maturity macroscopically.

	Macroscopic classification (%)			
Month	III	IV	V	Total number
Feb	95.4	4.1	0.5	196
Mar	94.5	5.5	0.0	91
Apr	78.9	21.1	0.0	152
May	58.6	40.8	0.6	157
Jun	62.9	37.1	0.0	194
Jul	56.1	42.0	2.0	205
Aug	64.7	31.7	3.7	218
Sep	68.4	25.9	5.7	193
Oct	57.7	29.3	13.0	123
Nov	43.4	30.3	26.3	99
Dec	30.8	12.4	56.8	185
Jan	36.6	3.8	59.5	131
			Total	1944
			Total used to estimate maturity ogive	1526

Table 12. Number of specimens (male or female) of *H. nicaraguensis*, *A. citrinellus* and *P. managuensis* by length class and maturity stage (based on macroscopic observations) analyzed for length-at-maturity estimation.

	A. citrinellus (males)		*H. nicaraguensis* (males)		*P. managuensis* (females)	
Length (cm)	III	IV+V	III	IV+V	III	V
10-12	5					
12-14	12	2	2	1		
14-16	41	59	15	8		
16-18	181	492	43	71		
18-20	290	1635	11	39		
20-22	95	1048		1		
22-24	30	718			17	3
24-26	5	318		2	21	7
26-28	1	69			2	3
28-30		11				2
30-32		1			1	
32-34						
36-38						1
40-42	1					
Total	661	4353	71	122	41	16

2.3.7. Fecundity

Fecundity was estimated using the gravimetric method aided with image analysis. The gravimetric method currently the most common method used, is based on the relationship between ovary weight and the oocyte density in the ovary and can be used to estimate batch fecundity, total fecundity and potential annual fecundity (Hunter & Golberg, 1980; Hunter, Macewicz & Kimbrell, 1989). The ovary was weighed at filed with a precision of 0.1 g and in the laboratory subsamples between 500 and 100 mg (average 824.6 milligrams) were taken from the central section of the ovary. Oocytes were then separated from connective tissue using a washing process (modified from Lowerre-Barbieri & Barbieri, 1993) and by size with sieves battery. This methodology presented some difficulties for oocytes separation, because these were surrounded in a mucus type (Figure 9). Nevertheless, it allowed the oocytes separation. After this, each separated portion was stored in eppendorfs with 3.6% buffered formaldehyde. Before they were counting and to improve safety conditions due to the toxicity of formaldehyde, oocytes were washed with water.

To establish the mesh size of the sieves it was considered the oocyte measurements taken as described in section 2.3.2. The mean diameter of each oocyte stage was calculated, and thus, it was defined the appropriate sieve for the oocytes size separation. Based on these oocytes measurements, it was selected sieve of 800, 300 and 150 µm as the appropriate sieves for separating three different groups of oocytes: i) VIT2 and GVM, ii) VIT1 and iii) CA stages, while primary growth (PG) stages, smaller than 150 µm were discarded.

The number and diameter of oocytes (Figure 10) contained in the ovary sub-sample were estimated by mean of a computer-aided image analysis system following Domínguez-Petit (2007) and Alonso-Fernández (2011) methodology using a QWin software (Leica Image Systems) on a PC (AMD Athlon XP 3000 +) connected to a video camera (Leica DFC490) attached to a motorized stereo macroscope (Leica Z6 APOA).

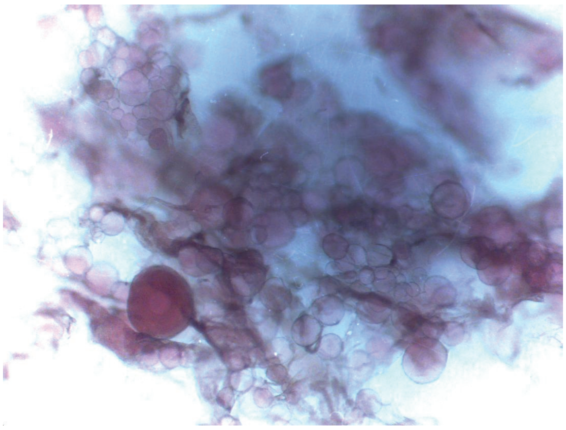


Figure 9. Oocytes image of *Brycon guatemalensis* surrounding by mucus before separation through a washing process method.

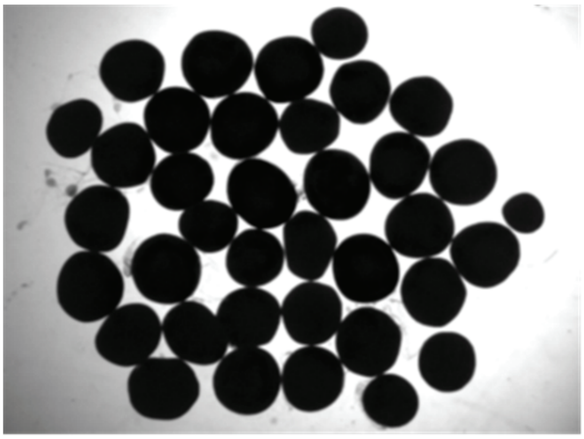


Figure 10. Oocytes counting image of *Brycon guatemalensis* for fecundity estimation, using a computer-aided image analysis system QWin software (Leica Imaging Systems).

The number of developing oocytes (NDO) per gram (g) of ovary weight was defined as the standing stocks of yolked oocytes in each ovary (Murua & Motos, 2006; Domínguez-Petit, 2007) and the relative number of developing oocytes (RNDO) was assessed dividing the NDO by the female gutted body weight.

Oocyte growth dynamic was studied according to the method of Haslob, Kraus & Saborido-Rey (2012), but in the present study the weighed mean oocyte diameter of each cohort was used instead the median. Diameter frequency distributions were analysed for each ovary. For this purpose, 53 ovaries (with total ovary weight available) in spawning capable (SC) and actively spawning (AS) phase, i.e., with oocytes in advanced vitellogenic (VIT2) and germinal vesicle migratory-GVM, were selected.

Potential annual fecundity (Fp) was estimated as the total number of oocytes larger or equal to 1000 µm, since above this threshold the leading cohort was defined, i.e., oocytes in more advanced developmental stages (VIT2 and GVM). Hence Fp was estimated in 48 females in SC and AS phase where no POF were observed.

Statistical regression analysis was performed to relate the oocytes diameter and fish length. Variation of NDO, RNDO, throughout the spawning season, was evaluated applying GLM in which the monthly pattern was the independent variable to assess the fecundity type of the specie. Power and linear regression were used to study the relationship between Fp and maternal features (length and weight) and oocytes diameter, respectively. For all performed analysis statistical software 6.0 were used.

Finally, the relation between the number of oocytes in GVM and in VIT2 was estimated in 47 females close to be spawn and containing both oocytes stages in their ovaries.

The Auto-diametric method developed by Thorsen & Kjesbu (2001) is used to estimates potential fecundity based on oocyte density – diameter relationships. It consist in the estimation of the number of oocytes using an image analysis system, by which is determined the average diameter of vitellogenic (yolk containing) oocytes in a sample, and then, the mean diameter is converted into oocyte density using a precise calibration curve. To establish the calibration curve pre-spawning ovaries are weighted and oocytes in an ovary sub-sampled counted and measured. The mean oocyte diameter, as independent variable, and the oocyte density, the dependent variable, are fitted to a power regression line. The application of the auto-diametric method for the potential fecundity estimation requires high and significant determination coefficient.

2.4. Gillnet selectivity

Gillnet selectivity studies were performed on four species (Table 13), but with special emphasis on the relation between selectivity and reproductive performance of *Brycon guatemalensis* females.

The selectivity parameters for each mesh size of the net tested 75, 100, 125 and 150 mm stretch mesh, during the fishery-independent survey, were estimated using the indirect method proposed by Holt (1963), who compared the catches C_1 and C_2 in two gill nets with different mesh sizes m_1 and m_2, assuming that: a) the selectivity curve for both mesh sizes are normal and have the same variance σ^2 or standard deviation; b) both selectivity curves have the same length and height; and c) the optimum length or modes of the selectivity curves are proportional to the mesh size. Then relationship between the natural logarithms of the number of fish catches and fish length was fitted to a linear regression (Hamley, 1975; Sparre & Venema, 1998):

$$\ln (C_m/C_{m+1}) = a + bL \qquad (9)$$

where C is the catch of each of the four nets, *m*, L is the mid-point of the length class and *a* and *b* are the intercept and the slope of the linear regression, respectively.

The selection factor (SF), the optimum length for being caught OL_m each net *m*, and the standard deviation are estimated from the next equations:

$$SF_m = \frac{-2a}{b(M_m + M_{m+1})} \qquad (10)$$

$$OL_m = SF * M_m \qquad (11)$$

$$s^2 = \frac{SF(M_{m+1} - M_m)}{b} \qquad (12)$$

where *a* and *b* are the parameters defined in Eq. 9, and M_m is the mesh size (in mm) for each net *m*.

The selection curves for each net, *m*, are then estimated as:

$$S_m = \exp\left(-\frac{(l - OL_m)^2}{2s^2}\right) \qquad (13)$$

From these and the catches, C, an abundance index for each mesh size net *m* and female size *l*, A_{ml}, is estimated:

$$A_{ml} = C_{ml}/S_{ml} \qquad (14)$$

From the estimated abundance values an estimated female mean length was calculated for each net.

Table 13. Species and specimens (male and female) considered in the gillnet selectivity analysis. Mesh size tested 75, 100, 125 and 150 mm stretch mesh.

		Specimens for selectivity studies		
Family	Species	♂	♀	Total
Cichlidae	*Amphilophus citrinellus*	4258	2487	6745
	Hypsophrys nicaraguensis	1556	97	1653
	Parachromis managuensis	393	331	724
Characidae	*Brycon guatemalensis*	1284	1643	2927
	Total			12049

2.4.1. Female abundance by size and reproductive phase

From the total number of captured females during the fishery-independent research survey, 371 ovaries (corresponding to the same number of female specimens) were randomly selected (see section 2.2.3) and categorized in reproductive phases (see section 2.3.3). Although Regressing and Regenerating have been defined as two distinct phases, for the purpose of this analysis they have been merged as one, and captioned as R phase. Hence, by knowing the proportion of the females of size *l* by a net of mesh size *m*, in the different reproductive phases, the abundance of females in each reproductive phase in the total female population sampled was estimated.

The abundance index of the females at size *l,* mesh size *m* of each reproductive phase *r*, NR_{lmr}, was then defined as:

$$NR_{lmr} = \frac{A_{ml} HR_{lmr}}{\sum HR_{lmr}} \qquad (15)$$

where HR_{lmr} is the number of females at size *l*, mesh size net *m*, and reproductive phase *r*.

2.4.2. The effect of gillnet on ontogenic maturation and eggs production

The impact of gillnet selectivity on the immature and mature females was assessed by comparing the maturity ogives estimated for each of the four species analysed and the derived length at 50% maturity with the optimum length obtained from equation 11. The male macroscopic maturity ogives *of H. nicaraguensis*, *A. citrinellus*, and females of *P. managuensis* and *B. guatemalensis* were previously estimated (Hernández-Portocarrero & Saborido-Rey, 2007). Additionally, in *B. guatemalensis* a microscopic ogive was estimated based on histological procedures (see section 2.3.6). Selectivity of each net was also estimated by the categorized reproductive phases (see section 2.3.3), and the results compared by environmental season, i.e., dry and rainy season.

The impact of gillnet selectivity on potential egg production was assessed estimating the number of eggs that potentially had produced the fish caught in each net, i.e., at different mesh sizes, by using the values of the power equation obtained from the relationship of the potential annual fecundity (Fp) and the length of *Brycon guatemalensis*:

$$EP_m = \sum_{l=1}^{n} HR_{lm} * 0.0626 l^{3.3094} \qquad (16)$$

Where EP_m is the potential eggs production at mesh size net; HR_{lmr} is the number of females at size *l* and mesh size net *m*.

CHAPTER 3: Population Ecology. Abundance and Distribution Patterns.

3.1. Introduction

Catch and effort information derived from commercial fisheries is a traditional manner on knowing the efficiency and performance of a fishery, and it typically reported as Catch per Unit Effort (CPUE), i.e., the amount of catch that is taken per unit of fishing gear (effort), expresses in a variety of units (FAO, 2013). CPUE can be used as a measure of the economic efficiency of a type of gear, but normally it is used as an index of abundance, i.e., a proportional change in CPUE is hoped to represent the same proportional change in abundance. Fishery CPUE is relative easy to obtain and often provide an good temporal coverage ,but it generally is poor when considering spatial coverage, as fishery always focus its activities where target fish show highest densities. However, it is known that there are many factors (including economics, geographical distributions) which may affect CPUE but do not represent changes in abundance. Additionally, catching methodologies are largely variable among fishers. All of it forces the standardization of CPUE data to remove the effect of factors that bias CPUE as an index of abundance. CPUE standardizes catch data based on the amount of the effort (total time or area sampled) exerted, for example, bag seine CPUE is reported as number of individuals captured per area sampled, whereas shrimp trawl, gill net, and oyster dredge are reported as number of individuals captured per hour sampled (Gonzalez, 2011).

CPUE data are the primary source of abundance information for many of the world's most valuable and vulnerable commercially and recreationally fished species (Maunder & Punt, 2004). Thus, indices of relative abundance estimated from catch-per-unit-of-effort (CPUE) data are one of the most commonly used data types in stock assessment (Maunder & Hoyle, 2006). However, CPUE information from commercial fisheries should be used cautiously, because it may not be an accurate index of abundance (National Research Council 2000). Harley *et al*. (2001) compiled and analyzed a large number of CPUE and survey abundance indices from International Council for the Exploration of the Sea (ICES) stock assessment reports, and found that commercial CPUE was hyperstable because there were nonlinearity between CPUE and abundance, since commercial fishing is not a random activity but an operation with clear targets. Besides that, Battaile & Quinn (2004) has indicated that the variation in fishing power (differences in vessel and gear types) create variation in CPUE unrelated to abundance; and Bishop, Venables & Wang (2004) mentioned that the improvement of fishing technology, accumulation of knowledge related to fish distribution and fishing operation will increase fishing power and create hyperstable CPUE.

Fishery independent survey with a standard vessel using standard fishing gear can avoid some of the biases inherent in fishery CPUE data. It seems to overcome many of the problems faced when information comes from commercial fisheries, since the resulting CPUE indices is assumed to be proportional to true abundance, considering that survey are carried out under a strict random sampling framework (Harley *et al.*, 2001). They are often preferred over fishery-dependent data for monitoring the status of harvested populations because (Rotherham *et al.,* 2006): (i) sampling is randomized rather than being concentrated where populations are (or are thought to be) most abundant; (ii) potentially, they provide more representative data on the entire size range of populations, rather than just retained components; (iii) there is no reliance on fishers reporting their catches and effort accurately; (iv) methodologies remain consistent over time; and (v) data can be collected on species not usually retained in commercial and recreational fisheries. Nevertheless, such surveys can be costly and require careful design, particularly if a stratified sampling design is adopted to improve precision. Hence, assumed that fishery-independent survey is proportional to true abundance, the variations on the abundance reflect fish vulnerability to fishing gear, fishing strategy, fish biology, including behaviour and response of individuals to environmental factors (Arreguín-Sánchez, 1996).

The behaviour pattern of the fish is a key factor included directly or indirectly in many of the dynamics of stock studies, but even before arriving to this, was the empirical observation and knowledge of the behaviour of the fish which allowed the fishing gear design and its modifications, improvement of fishing strategies and others. Furthermore, vulnerability is related to the probability of encounter of the fishing gear and the fish, thus, if fish is available, then vulnerability will depend of fishing gear efficiency, which implicitly assume identical behaviour of all fishes in the populations which is a merely ideal behaviour (Arreguín-Sánchez, 1996). Marine, estuarine and freshwater fish exhibit different behaviour and many authors have made reference to this matters, and particularly to freshwater fish, Matthews

(1998), has indicated that these fishes exhibit home range or homing affinities, daily or seasonal movement pattern or longer-distance migrations, which are considered to be truly "autecological, i.e., the interactions of an individual organism or a single species with the living and nonliving factors of its environment", with little apparent influence from other fish species and more related with searching for optimal environmental conditions.

The influence of spatiotemporal scale and environmental factors on the biology, life cycle, reproductive cycle, migration pattern and behaviour has been reported in the characidae family (Kramer, 1978a; Honji *et al*., 2009; Andrade & Braga, 2005; Lowe-McConnel, 1987). Particularly, the migratory habits upstream of *Brycon guatemalensis* for spawning or perhaps feeding has been described when studying the importance of the species for seeds dispersal in the Rio Puerto Viejo in Costa Rica (Horn, 1997). Cichlid movements have been described in relation with foraging and spawning activity (Conkel, 1993) even they do not undergo major reproductive migration (Lowe-McConnell, 1999). Some of these activities are conducted in flooded areas during the rainy season implying movements onto the floodplain out of the lagoon (Fernandes, Machado & Penha, 2010; Lourenço *et al*., 2012).

Most cichlids are stenotopic (Eccles, 1986), i.e., able to adapt only to a narrow range of environmental conditions, that because these fish are visually oriented fish and often associated with transparent water (Lowe-McConnell, 1999; Rodriguez & Lewis, 1997). The low visibility has being adverted in haplochromine cichlids in which the decrease of water clarity seems to affect foraging, social interactions, and to hamper mate recognition or even frustrate breeding (Fryer & Iles, 1972; Seehausen & Van Alphen, 1998). The behavioural response to water transparency may affect the fish catchability, since moderate levels of turbidity apparently decrease the likelihood that fish will perceive the net material (Kirkland, 1965) and reduce the reactive distances, altering foraging behaviour, and decreasing association with substrates (Noggle 1978; Gradall & Swenson 1982; Barrett, Grossman & Rosenfeld, 1992).

In the present work it is analyzed the pattern of variability of the relative abundance index (CPUE), expressed as Ln(CPUE No ind/h m^2+1), i.e., number of specimens captured per hour and surface area of the net, of three species belonging to the cichlidae family as *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* and one species of the characidae family *Brycon guatemalensis*. The CPUE pattern variability is assumed to be proportional to true abundance, since comes from a fishery-independent survey carried out under the sampling framework specified in the methodology section. The abundance index is examined as function of the temporal scale as the month of year, the spatial scales as the macro-zones (northwest, central and southeast zone) and depth strata (1, 3 and 5 m) and as function of the environmental factors as rainfall related seasons and water turbidity. In line with the objective of this thesis, special interest is placed on how is modulated the relative abundance index (CPUE) and the size distribution of *Brycon guatemalensis* by the spatiotemporal and environmental changes. Therefore, the discussion of this chapter is mainly focused on this species which in turn is considered as study case in the whole thesis.

3.2. Results

3.2.1. Environmental data

The bottom soil of the study area was composed mainly by soft material as sand, mud or a mixture of both, but some hard bottoms (rocks) were also identified. The sandy areas were localized most near the shoreline and in the central zone, while mixture of sand and mud were observed in both extremes of the area, i.e., southern and northern zones (Figure 11). In the southeast zone wider muddy areas were found near de shoreline. Sandy areas were associated with river mouths probably because of the effect of rapid currents generated by the rivers flows do not allow the deposition of clay particles in the bottom.

During the period of the study (February 2005-January 2006) rainfalls occurred in every month (Figure 12). The wet season according to Köppen climate classification (average precipitation above 60 mm) extended from May to November. However, average precipitation in November was slightly above 100 mm, considerably below the average between May and October, whose values ranged from 205 to 368.4 mm, the maximum reached in October which is normally the rainiest month of year (Figure 12). This period is considered as the regular winter period. The dry period months, occurring therefore from November to April, are characterized by the precipitation lower than 100 mm, especially from February to April, the driest months during the studied period.

Turbidity along the eastern coast of the lake of Nicaragua is generally related with the distance to the shoreline, from more turbid waters (values lower than 40 cm, secchi disc) to clearest waters (higher than 50 cm of visibility) registered off shoreline (Figure 13). During the dry season of the year, clearer waters were observed in most of the study area, being the most turbid waters located near to the river mouth, as for example close to Mayales River where the water visibility was less than 20 cm. On the contrary, during the rainy season water turbidity notably increased all along the lake edge become darker and the clearest water were observed only in the most distant studied zone (Figure 13).

Water temperatures in the eastern side of the lake shifted notably between seasons (Figure 14). The lower water temperatures were registered during dry season, and ranged between 26 and 28 degree centigrade (ºC), while in the rainy season it reaches a maximum of 30 ºC. Spatial variability in temperature was very low during the dry season. Variability increases during the wet season (Figure 14). In the two ends of the studied area, i.e., northern and southern zones, the water temperature was higher (30 ºC).

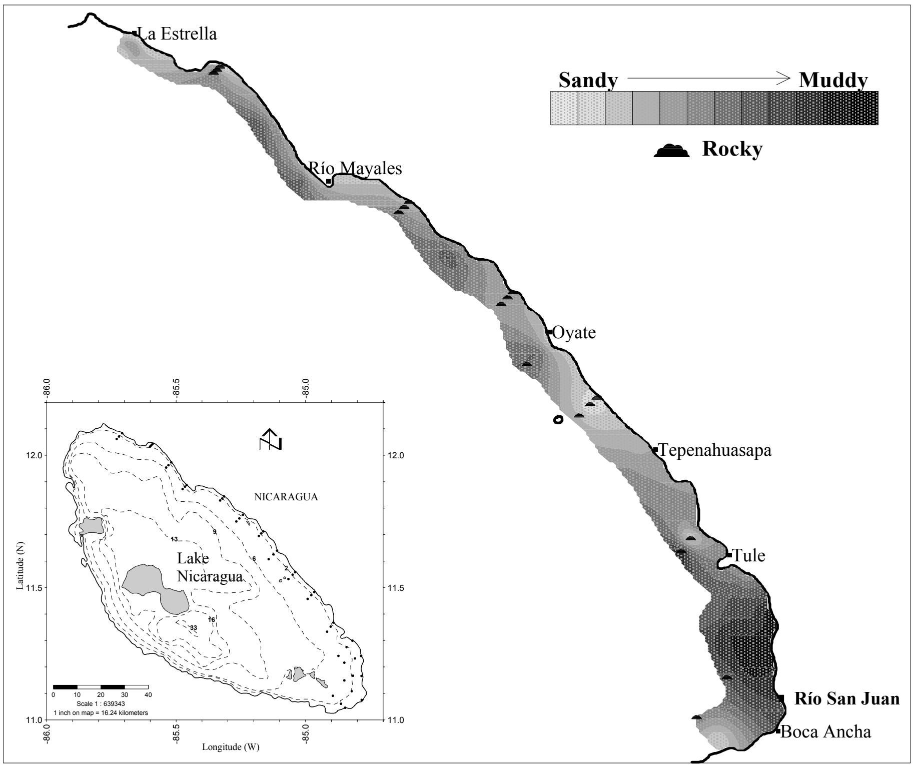


Figure 11. Bottom soil type identified in the eastern part of the Lake Nicaragua. February 2005 - January 2006.

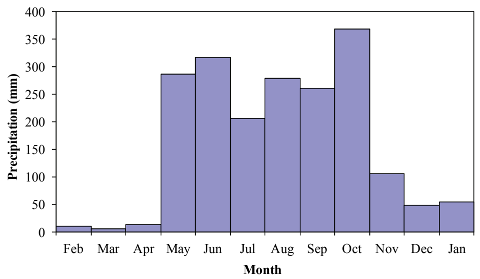


Figure 12. Monthly precipitation registered in the Lake Nicaragua during the study period, February 2005-January 2006. Data source: Instituto Nicaraguense de Estudios Territoriales- INETER 2006.

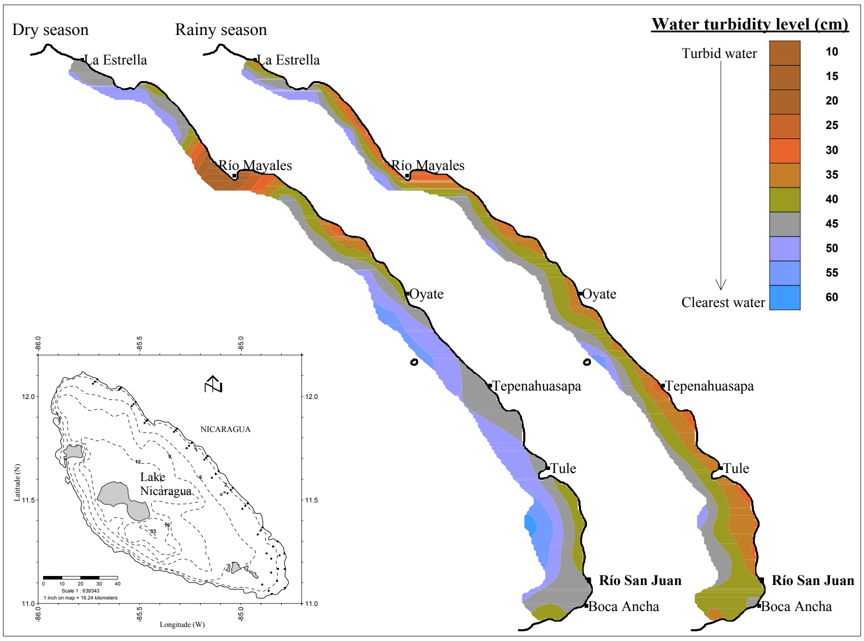


Figure 13. Water turbidity recorded in the eastern part of the Lake Nicaragua. February 2005 - January 2006.

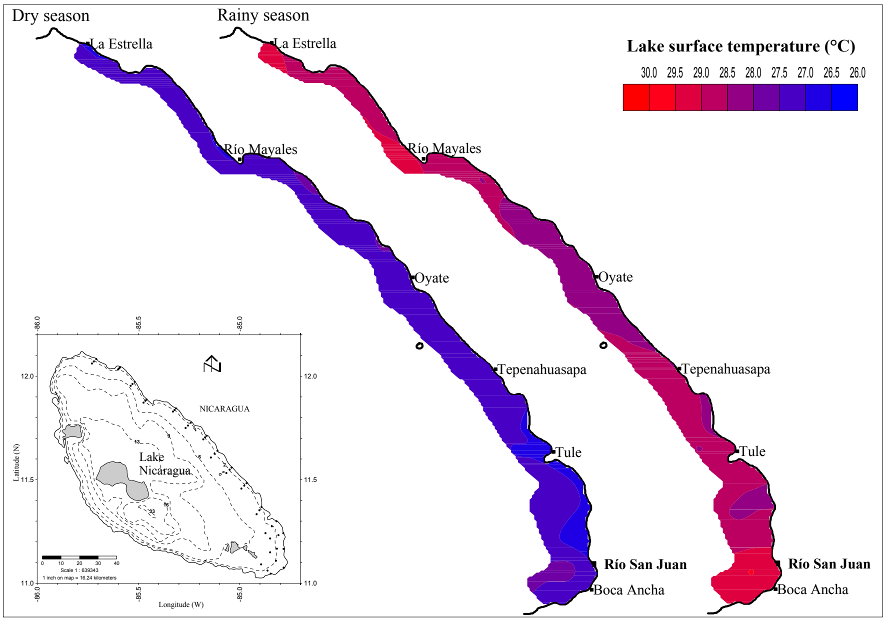


Figure 14. Surface temperature of the waters recorded in the eastern part the Lake Nicaragua. February 2005 - January 2006.

3.2.2. Survey indexes: Catches and effort

A total of 26 fish species were captured in the 561 stations made during this study (Table 14), and a total 4545.6 kg were obtained with an effort of 3546 hours. However, three species, *Amphilophus citrinellus*, *Brycon guatemalensis*, *Hypsophrys nicaraguensis* accounted for more than 72% of the catch in numbers and 76.5% in biomass. Moreover, seven species accounted for more than 95% in abundance (Table 14). The majority of the species caught have commercial value. Among those the species with higher commercial value was *Atractosteus tropicus* that were caught in low number, while sardine, *Dorosoma chavesi*, though it is caught in higher abundance it does not have any commercial value neither is consumed for local fisherman and is mostly discarded during the fishing operation. In term of occurrence, i.e., catch frequency, twelve species occurred most frequently in the 561 hauls made (Figure 15) and they accounted for 99% of the fish caught. Out of these species, seven occurred in at least 50% of the hauls, i.e., *A. citrinellus*, *B. guatemalensis*, *D. chavesi, A. rostratus*, *H. nicaraguensis, A. longimanus* and *P. managuensis* (Figure 15).Four species were selected for further analysis: *Amphilophus citrinellus*, *Brycon guatemalensis*, *Hypsophrys nicaraguensis* and *Parachromis managuensis*. *D. chavesi* and *A. rostratus* were not further considered due to its low fisheries importance. The taxonomy of the genus *Amphilophus* and *Astatheros* still remains under controversy (Rican, Zardoya & Doadrio, 2008). While identification of *A. citrinellus* was clear, in the case of *A. longimanus* many uncertainties arose in their identification during sampling because their taxonomic status was disputed. For this reason it was decided to exclude it from the current analysis.

Figure 16 shows the catch of the four selected species in relation with the effort unit (h) applied during the survey. The fishing time in each station, since setting till hauling the net, ranged from 4.41 to 9.05 hours (h) and the average fishing time was 6.32 h. On the other hand, the catches in number, pooled for the four species, varied from 1 to 127 ± SD 17.45 and in biomass (kg) from 0.11 to 26.48 ± SD 4.55 (Figure 16 A and C, respectively). Most of catches (92 %) were obtained at fishing efforts between 5.5 and 7.0 h, below an above that fishing time, the catches in number or biomass notably decrease. The cumulated catches by species in number and biomass (Figure 16 B and D, respectively) shows the rapid increases of the catches, starting from 5.0 to 7.0 hours of fishing time till the catches reach a maximum, and from that time the catches no longer increase. This pattern is the same for the four species.

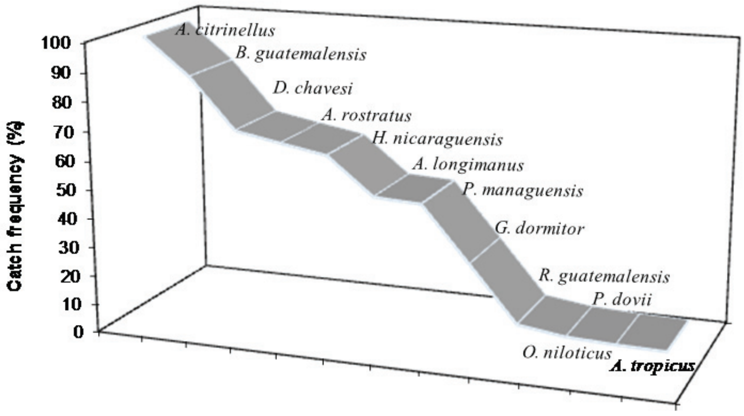


Figure 15. Catch frequency distribution of the most important species, ordered by abundance (see Table 14), along the east part of the Lake Nicaragua during the fishery survey from February 2005 to January 2006.

Table 14. Total catch in number and biomass, and catch per unit of fishing effort in gram per hour (g/h) by species captured during the fishery-independent survey carried out in the eastern part of the Lake Nicaragua February 2005-January 2006. * Most important commercial species for the local fishermen. February 2005-January 2006.

Species	Common name	Gross number	Gross weight (kg)	CPUE (g/h)
*Amphilophus citrinellus**	Mojarra	7983	1364.86	384.90
*Brycon guatemalensis**	Machaca	3507	1901.53	536.25
*Hypsophrys nicaraguensis**	Moga	2007	210.08	59.24
Dorosoma chavesi	Sardina	1521	100.49	28.34
*Astatheros rostratus**	Mojarra/Masamiche	1261	203.26	57.32
*Parachromis managuensis**	Guapote tigre	809	216.82	61.14
*Astatheros longimanus**	Mojarra	722	70.97	20.01
Gobiomorus dormitor	Guavina	297	68.13	19.21
*Rhandia guatemalensis**	Barbudo	100	29.35	8.28
*Oreochromis niloticus**	Tilapia	72	67.78	19.11
*Parachromis dovii**	Guapote pinto	63	33.35	9.40
*Atractosteus tropicus**	Gaspar	59	192.45	54.27
*Centropomus pectinatus**	Robalo	40	28.94	8.16
*Amphilophus longimanus**	Mojarra	36	6.42	1.81
*Pomadasys croco**	Roncador	35	21.29	6.00
*Oreochromis mossambica**	Tilapia	30	21.59	6.09
*Amphilophus labiatus**	Mojarra	16	3.35	0.94
Bramocharax bransfordii	Sardina	12	0.48	0.14
Roeboides ilseae	Sardina	10	0.18	0.05
----- Non identified-----	Mojarra pecho rojo	5	1.34	0.38
*Centropomus undecimalis**	Robalo	1	1.18	0.33
Cichlasoma maculicauda	Mojarra	1	0.09	0.03
Neetrophus nemotopus	Sardina	1	0.05	0.01
Pristis perotteti	Raya	1	1.60	0.45
Roeboides bouchellei	Sardina	1	0.01	0.00
----- Non identified-----	Sardina	1	----	----
Total		18591	4545.60	1281.89

The monthly catches of four species are presented in Table 15. The mean largest catch corresponds to *B. guatemalensis* (158.5 kg) followed by *A. citrinellus* (113.7 kg), and the lower mean catches were those of *H. nicaraguensis* (17.5 kg) and *P. managuensis* (18.1 kg). Their maximum catches occurred in February, June, May and March, respectively.

The CPUE ranged from 0.003 g/h of the small sardine *Roeboides bouchellei* to 536 g/h obtained for *B. guatemalensis*, and the total CPUE was 1281.89 g/h (Table 14). The monthly and annual CPUE for the four species with the highest CPUE are shown in Table 15. *B. guatemalensis* presented the higher CPUE, 536 g/h, this ranged from 319 to 735 g/h, in decreasing order *A. citrinellus* with a total of 385 g/h and range from 250 to 559 g/h, *P. managuensis* 61 g/h and ranged from 19 to 128 g/h and *H. nicaraguensis* with the lower CPUE 59 g/h with ranged from 17 to 115 g/h.

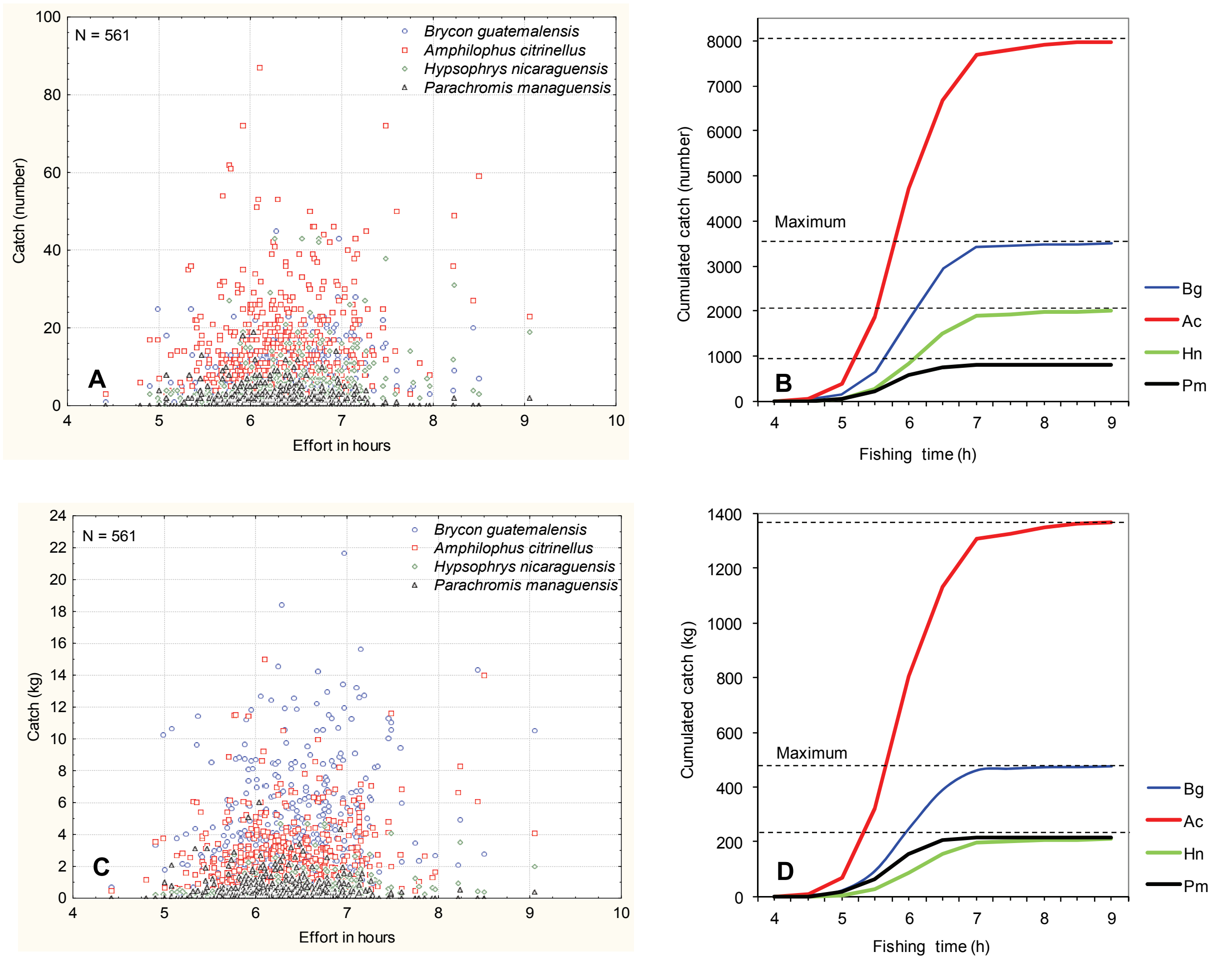


Figure 16. Catch and effort pattern during the fishery-independent survey. Bg: *Brycon guatemalensis*; Ac: *Amphilophus citrinellus*; Hn: *Hypsophrys nicaraguensis*; Pm: *Parachromis managuensis*: Dashed lines: Maximum catches. Lake of Nicaragua, 2005-2006.

Table 15. Monthly catches (kg and number), fishing effort (hours) registered and CPUE (g/h) estimated of four selected species captured during the surveys in the Lake Nicaragua 2005-2006.

Species	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Annual
Amphilophus citrinellus	114.0	134.2	122.2	77.8	155.3	99.8	116.1	89.7	149.5	125.9	85.2	95.2	1364.9
Hypsophrys nicaraguensis	12.0	21.1	29.0	35.6	23.4	15.2	22.9	11.1	18.5	6.2	5.1	10.1	210.1
Parachromis managuensis	33.8	39.4	25.8	16.4	14.8	5.7	8.7	10.9	25.2	8.9	10.1	17.2	216.8
Brycon guatemalensis	223.3	98.3	176.2	196.9	193.2	190.9	189.4	150.7	114.1	99.8	148.9	120.3	1901.8
Amphilophus citrinellus	624	831	734	468	855	564	676	549	860	729	532	561	7983
Hypsophrys nicaraguensis	112	199	291	354	231	145	211	106	176	54	43	85	2007
Parachromis managuensis	122	138	95	64	46	25	36	44	97	35	42	65	809
Brycon guatemalensis	389	178	282	326	320	348	379	334	205	188	303	255	3507
Fishing effort (h)	304	308	308	311	283	306	298	300	268	275	293	293	3546
Amphilophus citrinellus	375.2	435.8	396.6	250.3	549.3	325.9	389.1	299.4	558.7	458.5	291.2	324.7	384.9
Hypsophrys nicaraguensis	39.3	68.4	94.2	114.6	82.8	49.6	76.8	37.1	69.0	22.4	17.4	34.3	59.2
Parachromis managuensis	111.3	128.0	83.7	52.8	52.3	18.6	29.0	36.3	94.3	32.5	34.3	58.6	61.2
Brycon guatemalensis	734.8	319.2	571.7	633.5	683.3	623.1	634.9	503.0	426.4	363.5	508.5	410.4	536.4

3.2.3. Abundance index variability of target species

In this section it is analysed the relative abundance index estimated as the function of the number of specimens captured per hour and surface area of the net (Nº ind/h m^2), i.e., the standardized catch per unit effort, CPUE. The analysis is conducted in the four main target species of the lake, *A. citrinellus* (Mojarra), *H. nicaraguensis* (Moga), *P. managuensis* (Guapote tigre) and *B. guatemalensis* (Machaca).

As water turbidity may influence catch rates (see introduction), first the effect of turbidity on CPUE is evaluated. Then, the spatio-temporal variation of abundance is analyzed for each species.

3.2.3.1. CPUE and water turbidity

The effect of the water turbidity on the abundance index (CPUE) is analyzed in four species *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* and *Brycon guatemalensis*. The linear regression between secchi depth and the CPUE were significant for *A. citrinellus* and *P. managuensis* (Table 16). For these species increasing visibility reduced CPUE (Figure 17), especially in *A. citrinellus*. However, in the four species the scatterplots show a high data dispersion. And thus very low coefficient of determinations were obtained (Table 16), the highest, r^2=0.1, found in *P. managuensis*. When CPUE is compared among turbidity (secchi depth) classes (Figure 18) significant differences were observed in three species: *A. citrinellus*, *H. nicaraguensis* and *P. managuensis* (Table 16). The decreasing trend in mean CPUE is again observed in *A. citrinellus*; however, only CPUE in high turbid waters (10 cm secchi depth) was significantly different (Tukey HSD test $p<0.05$) and only from CPUE in clear waters (>50 cm secchi depth). In only 26 hauls, i.e., less than 5%, secchi depth was smaller than 10. Similar results were obtained in *P. managuensis* where only CPUE at high turbid waters (10 cm) differed (Tukey HSD test $p<0.01$). Although ANOVA showed significant differences between classes in *H. nicaraguensis*, the Post-hoc Tukey HSD test did not show differences between secchi depth classes ($p>0.15$).

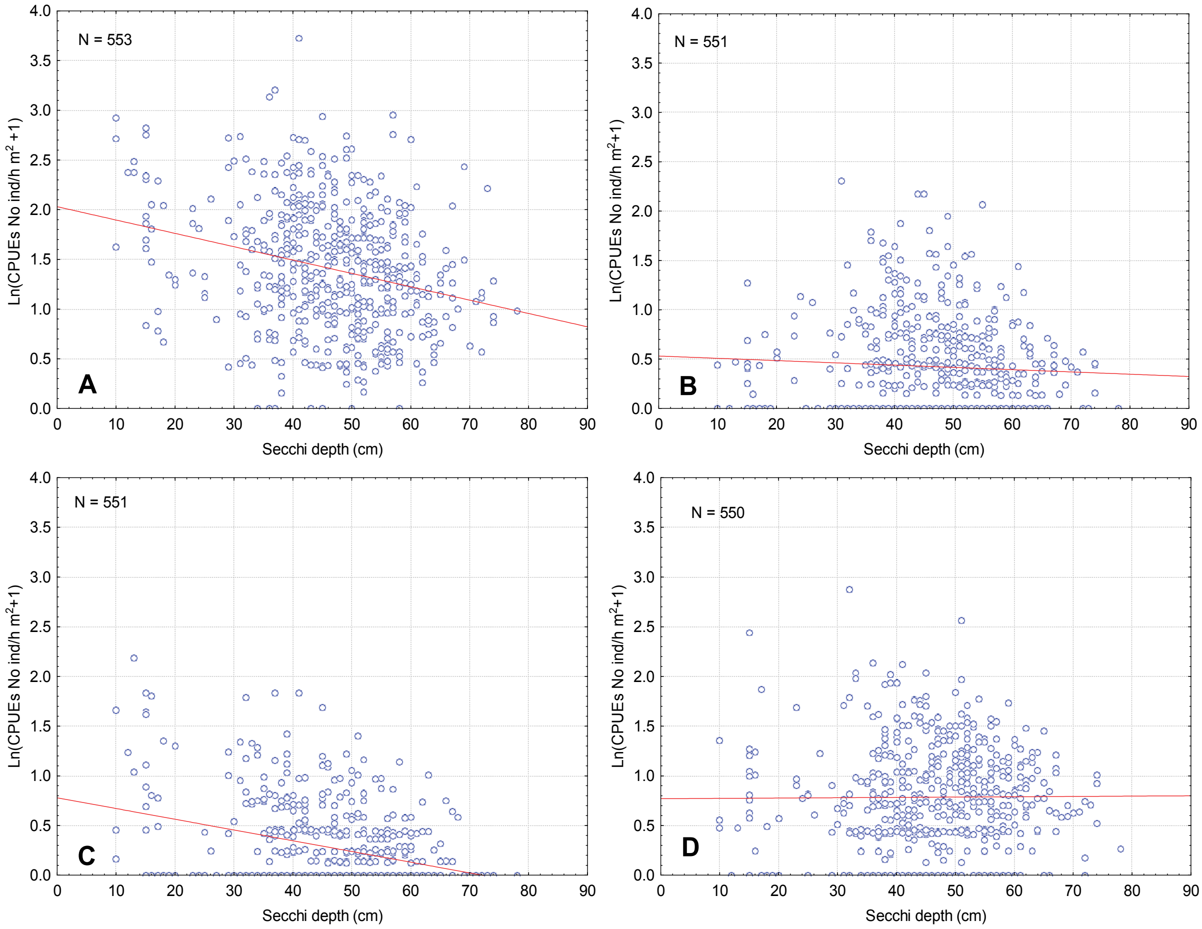


Figure 17. Scatterplot where is correlated the catch rates (number per hour per m^2) of four species and turbidity water level (secchi disk measurement) of the lake. (A) *Amphilophus citrinellus*; (B) *Hypsophrys nicaraguensis*; (C) *Parachromis managuensis*; and (D) *Brycon guatemalensis*.

Table 16. Determination coefficient and significant level of the linear regression, and ANOVA between water turbidity and the relative abundance [Ln(CPUEs No ind/h m^2+1)] of four species.

	Regression		ANOVA	
	r^2	p	F	p
Amphilophus citrinellus	0.064	< 0.05	7.205	< 0.001
Hypsophrys nicaraguensis	0.004	0.162	2.827	< 0.05
Parachromis managuensis	0.105	< 0.05	9.352	< 0.001
Brycon guatemalensis	0.000	0.859	1.172	0.319

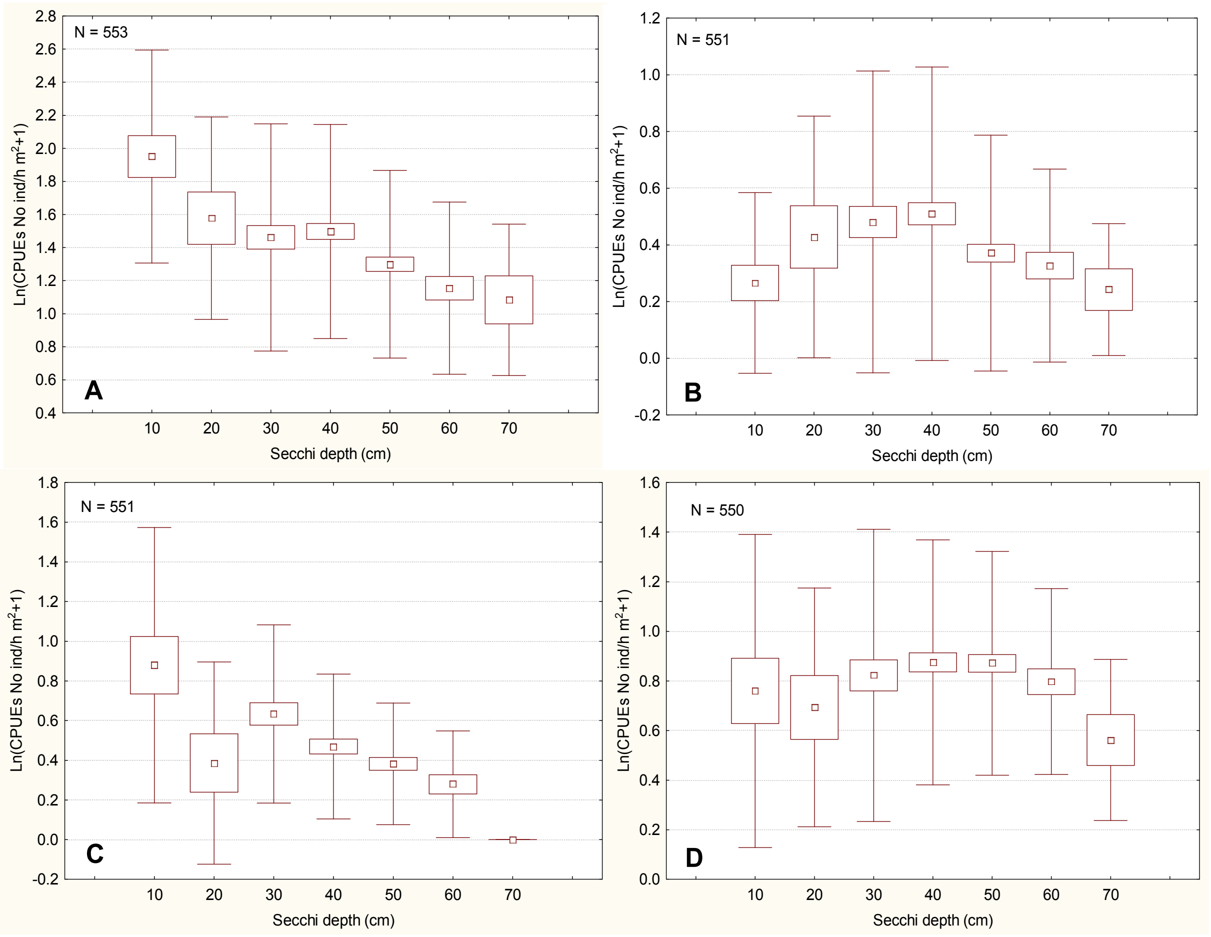


Figure 18. The CPUE by water turbidity classes (secchi disk measurement). (A) *Amphilophus citrinellus*; (B) *Hypsophrys nicaraguensis*; (C) *Parachromis managuensis*; and (D) *Brycon guatemalensis*. Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker)

3.2.3.2. Spatio-temporal variability

In this section it is described the spatial distribution along the study area considering the three zones defined, i.e., northwest, central and southeast (see figure 7 in Chapter 2), as well the three depth strata, i.e., above 1 m, between 1 and 3 m and between 3 and 5 m, coded as 1, 3 and 5 respectively. Temporal variations are analyzed along seasons and months, but considering the spatial movements observed during these periods of time and the interaction among these factors. The analyses are presented by each of the four key species considered.

Amphilophus citrinellus (Mojarra)

The mojarra is the most abundant species in the study area. The abundance index by haul ranged from 0.18 to 40.56 (mean 2.88 ± 3.75) individuals per hour and net square meter (No ind/h m^2). Abundance was significantly higher in the central and southeast zone, compared to the northwest (Table 17; Figure 19 and Figure 20), i.e., the lower abundance was recorded in the northwest and in the deeper waters of the study area. While abundance was similar between seasons for the whole area (GLM, $p=0.68$; Table 17), this species showed a clear seasonal distribution pattern. Thus, average CPUE was 3.95 ± 3.83 and 4.11 ± 3.68 individuals/h m^2 during dry and rainy season respectively. However, during the dry season the higher abundances (larger than 1.8) were mostly located in the southeast zone, closer to the Río San Juan mouth, with lower but not significantly different abundance in the central zone, and a significant lower abundance in the northwest (GLM, $p<0.0001$;Figure 19 and Figure 20). In the rainy season Mojarra moved northwards and a significant higher (GLM, $p<0.05$) abundance is located now in the central zone, compared to the other two zones that showed similar abundances (Figure 19 and Figure 20).

The monthly average CPUE pattern fluctuated between 2.87 and 5.59 /h m^2 individuals along the studied period (Figure 21). Overall, monthly range variability of the CPUE was low along the year, and the significant statistical difference (ANOVA: $F=3.318$; $p < 0.001$), was due to the high CPUE in October that differed from May, September, December and January.
Overall the major abundance index is located in the two strata nearer to the shore line of the study area, being the abundance in deeper waters significantly lower (Table 17 and Figure 22); this pattern did not show variations between seasons ($p=0.09$). However, depth distribution shifted among macro-zones, with a significant interaction ($p<0.001$, Table 17). Thus, the significantly lowest abundance at shallower waters was found in the northwest, while at depth stratum 3 the lowest abundance was recorded in the southeast (Figure 23). There were no differences among zones at deeper waters (Figure 23). This pattern become

more complex because the relative abundance of this species changed significantly between seasons, macro-zones and depth, i.e., the interaction between these factors is significant (GLM: F= 2.96; $p < 0.05$; Table 17). Post-hoc analyses revealed no significant differences at all within the deeper stratum, neither among zones nor between seasons (GLM: $p>0.1$; Figure 23). At 1 depth stratum, abundance was significantly smaller in the northwest in dry ($p<0.001$) and rainy ($p<0.05$) seasons, with a clear cline from south to north at least during the dry season (Figure 23). At 3 depth stratum the pattern differed by seasons, thus during the dry season it followed similar but less clear pattern as in shallow waters with a significantly lower abundance in the northwest zone ($p<0.05$), but the opposite trend was observed during rainy season with a clear cline south-north and significant lower abundance in the southeast ($p<0.001$; Figure 23). At 5 depth stratum no significant differences in the abundance were observed between macro-zones ($p=0.27$) neither with between season.

In summary, *Amphilophus citrinellus* prefers shallower waters mainly in the south and central zones of the study area but during rainy season search for intermediate and northern waters.

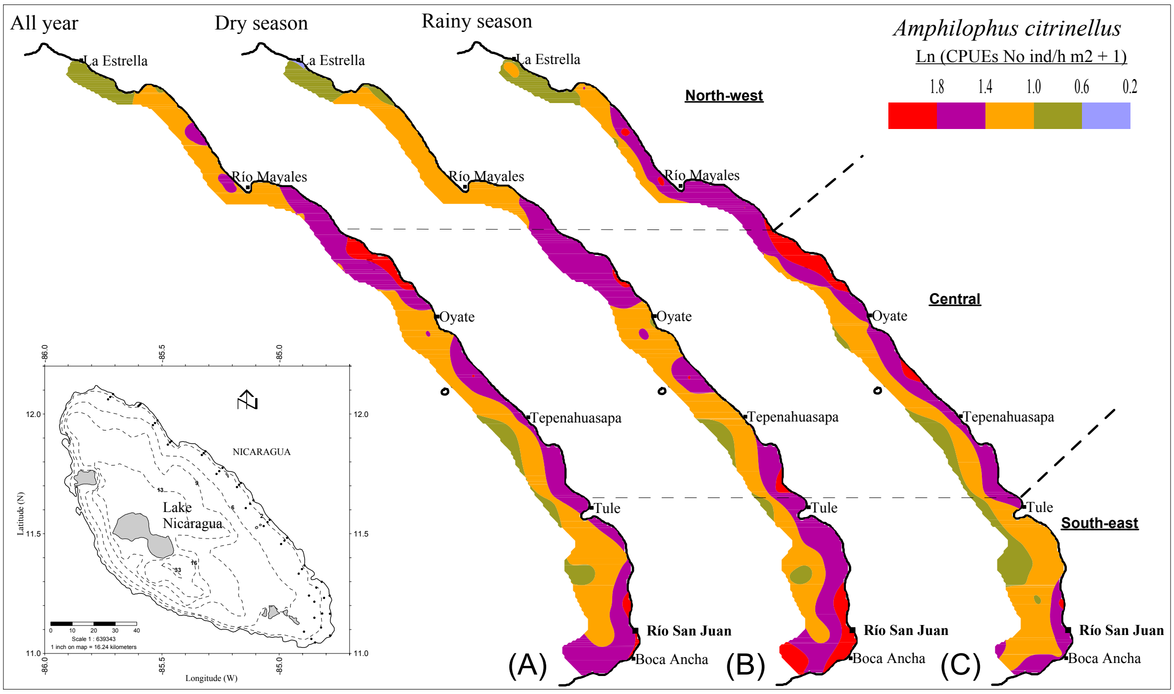


Figure 19. Distribution and abundance index [Ln(CPUEs No ind/h m^2+1)] of *Amphilophus citrinellus* in the eastern part of the Lake Nicaragua.

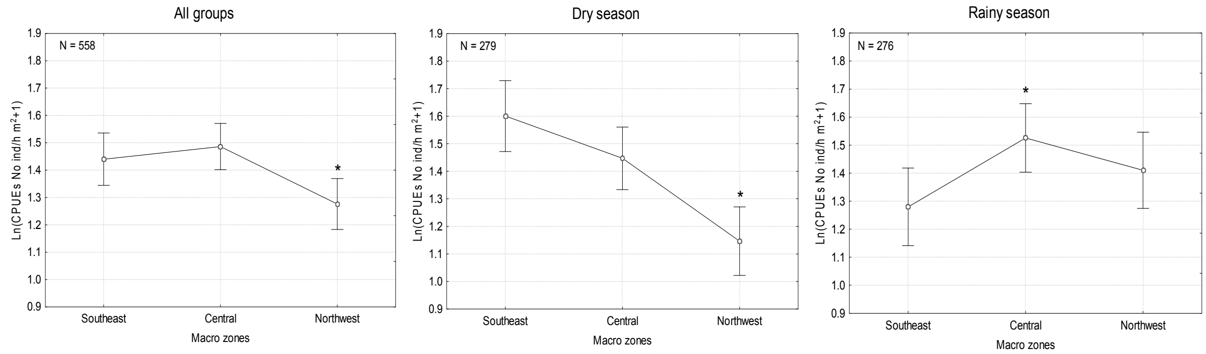


Figure 20. Catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Amphilophus citrinellus* in the eastern part of the Lake Nicaragua for the whole year and by seasons. * denotes significant differences. Vertical bars denote 0.95 confidence intervals.

Table 17. Results of the GLMs for *Amphilophus citrinellus* CPUEs (log-transformed) as function of season, macro-zones and depth.

	Amphilophus citrinellus [Ln (CPUEs No ind/h m^2 + 1)]					
Explanatory variables	n	SS	df	MS	F	p
Intercept		1106.792	1	1106.792	2844.779	0.000
Season	555	0.068	1	0.068	0.175	0.676
Error		215.929	555	0.389		
Intercept		1084.579	1	1084.579	2850.465	0.000
Macro-zone	**554**	**5.204**	**2**	**2.602**	**6.839**	**0.001**
Error		210.793	554	0.380		
Intercept		1098.236	1	1098.236	3094.353	0.000
Depth (m)	**554**	**19.373**	**2**	**9.687**	**27.293**	**0.000**
Error		196.623	554	0.355		
Intercept		1085.594	1	1085.594	2960.383	0.000
Season		0.016	1	0.016	0.044	0.834
Macro-zone		**5.186**	**2**	**2.593**	**7.071**	**0.001**
Season*Macro-zone	**551**	**8.671**	**2**	**4.335**	**11.823**	**0.000**
Error		202.056	551	0.367		
Intercept		1097.829	1	1097.829	3105.000	0.000
Season		0.053	1	0.053	0.149	0.700
Depth (m)		**19.389**	**2**	**9.695**	**27.419**	**0.000**
Season*Depth	551	1.744	2	0.872	2.466	0.086
Error		194.816	551	0.354		
Intercept		1073.515	1	1073.515	3332.159	0.000
Macro-zone		**5.195**	**2**	**2.597**	**8.062**	**0.000**
Depth (m)		**16.930**	**2**	**8.465**	**26.276**	**0.000**
Macro-zone*Depth	**548**	**15.110**	**4**	**3.777**	**11.725**	**0.000**
Error		176.548	548	0.322		
Intercept		1074.305	1	1074.305	3576.567	0.000
Season		0.039	1	0.039	0.130	0.718
Macro-zone		**5.238**	**2**	**2.619**	**8.718**	**0.000**
Depth (m)		**17.035**	**2**	**8.518**	**28.357**	**0.000**
Season*Macro-zone		**8.490**	**2**	**4.245**	**14.133**	**0.000**
Season*Depth		1.623	2	0.811	2.701	0.068
Macro-zone*Depth		**15.406**	**4**	**3.851**	**12.822**	**0.000**
Season*Macro-zone*Depth	**539**	**3.555**	**4**	**0.889**	**2.959**	**0.019**
Error		161.901	539	0.300		

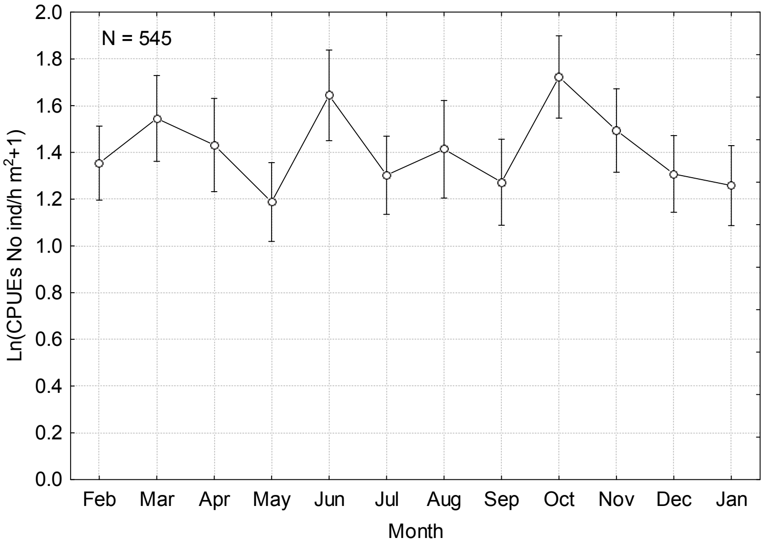


Figure 21. Monthly catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Amphilophus citrinellus* during a fishery-independent survey in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

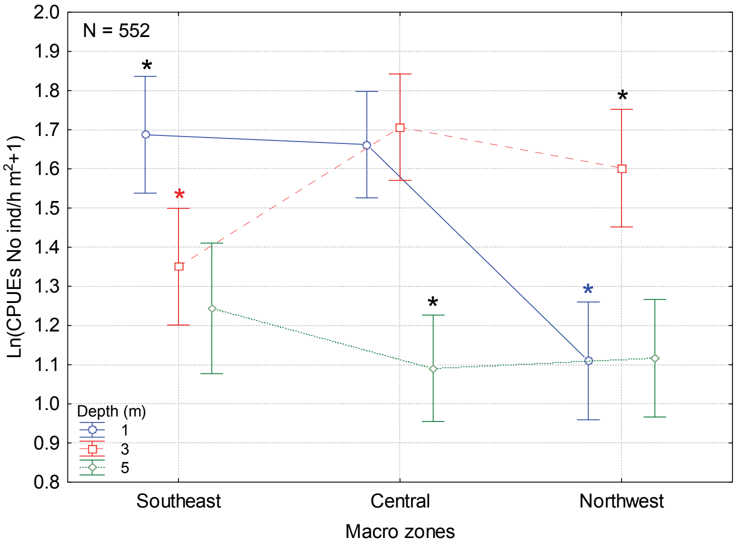


Figure 22. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Amphilophus citrinellus* between macro-zones and by depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

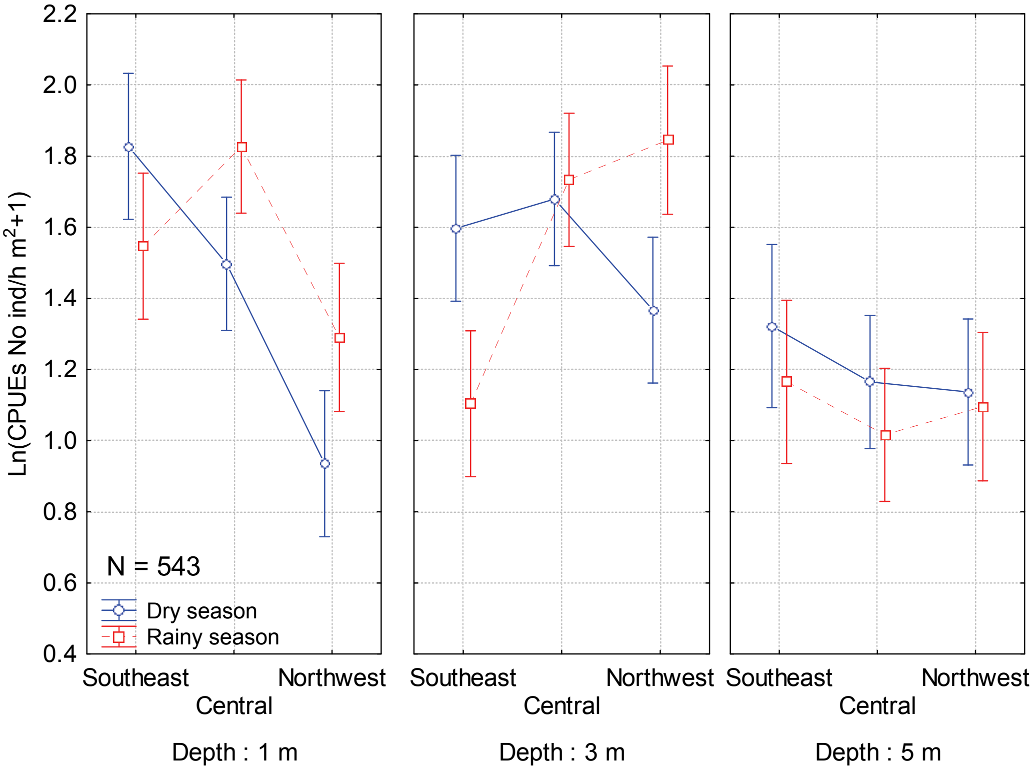


Figure 23. Spatio-temporal variation of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Amphilophus citrinellus*, by depth, macro-zones and season in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

Hypsophrys nicaraguensis (Moga)

This species is another member of the cichlidae family which is frequently captured in gillnets. It is found virtually in the whole study area, but with an uneven distribution. The catch rates by haul ranged from 0.14 to 10.91 individuals/h m^2 with an annual average rate of 1.26 ± 1.50. The highest CPUE was found in relative small spots located in southeast and northwest zones, with a secondary area in the middle of the lake (Figure 24 A), and significant variation is observed between Southeast and other two zones (GLM: $p<0.01$) (Figure 25: All groups). The abundance indexes experimented notable changes by season, macro-zones and by depth (Table 18). The dry season is characterized by lower abundances in the whole area (mean 1.08 ± SD 1.26), and the fish are concentrated in the deeper areas of the southeast zone and are absent of the shallower waters of the northwest and central zones (Figure 24 B). CPUE significantly decrease (GLM: $p<0.001$) toward northwest zone (Figure

25: Dry season). . On the other hand, in rainy season the average CPUE increased to 1.38 ± 1.64 (Figure 25: rainy season), and the CPUE was significantly lower in the central zone (GLM Post hoc $p<0.05$). During this season the individuals located northwards are closer to the shoreline, while those in the southeast are located in higher abundance in deeper waters. Largest catches rates are located in the middle of the north-west, central zone and in the extreme south-east zone, close to the Río San Juan mouth (Figure 24 C).

The monthly average abundance index along the year ranged from 0.16 to 1.67 (0.79 ± 0.47 individuals /h m^2). The abundant index of *H. nicaraguensis* increased from February till May when the maximum was recorded, with an average abundance index of 2.01 ± 1.91 individuals /h m^2. Since then until December CPUE steadily decreased to a lowest average abundance recorded, 0.45 ± 0.29 (Figure 26). Abundance significantly varied along the year (ANOVA: $F=9.533$; $p < 0.001$) and the post hoc analysis (Tuckey HSD test) shows that the months causing the differences in abundance were April, May and June.

The abundance index differ significantly between macro-zones and depth (GLM: $p<0.01$; Table 18). It increased from shallow (1 m) to deeper waters (5 m), and from North to South, except at 3 m (Figure 27). Significant differences between southeast and northwest were observed at 1 m (post hoc: $p<0.05$), and between the central and the other two zones at 3 m (post hoc $p<0.05$: Figure 27). Overall the abundance index varies significantly between seasons and depth strata, with significant interactions (Table 18). Thus, abundance increased with depth stratum during the dry season, but not so clear during the rainy season (Figure 28). Also abundance differed between seasons at 1 and 3 m ($p<0.01$), but not at 5 m ($p=0.99$). There was not significant interaction in CPUE between season, macro-zones and depth (GLM: $p=0.22$; Table 18). Abundance was consistently higher during rainy season in the three zones and depths, except at Southeast at 5 depth stratum, and abundance decreased from south to north at all depths during the dry season, but not during the rainy season (Figure 29.).

In summary, *Hypsophrys nicaraguensis* prefers indistinctly intermediate and deeper waters in the southeast zone during both dry an rainy season, while in the northwest it prefer intermediate water, particularly during rainy season.

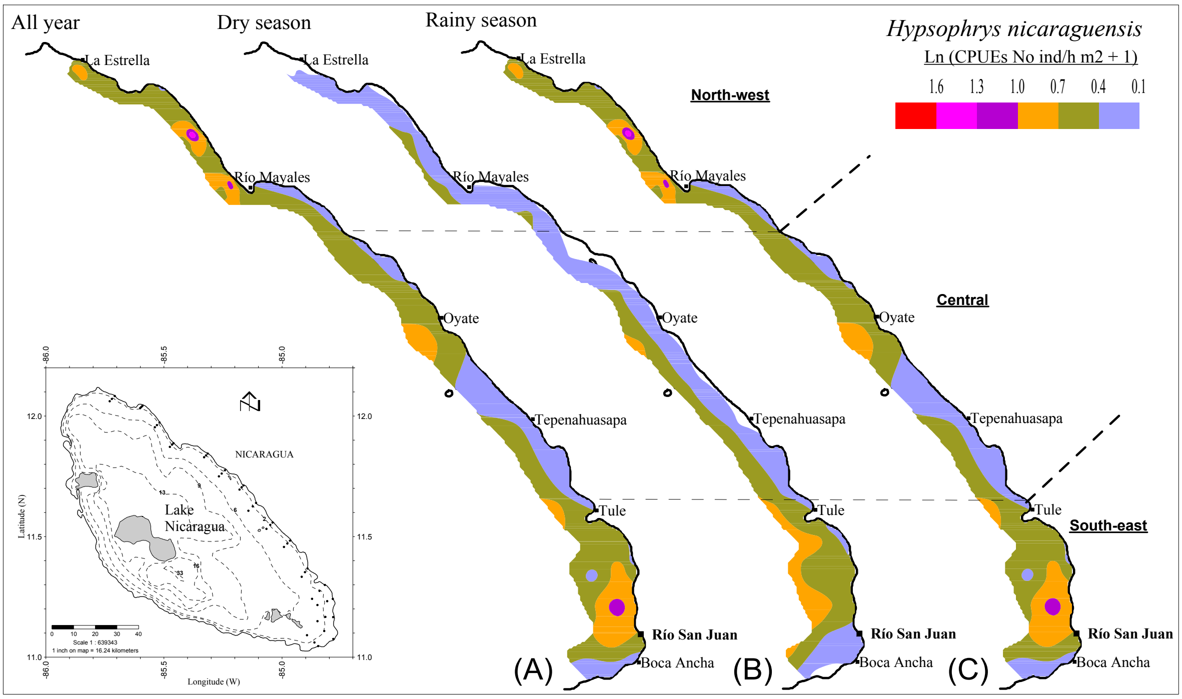


Figure 24. Distribution and abundance index [Ln(CPUEs No ind/h m^2+1)] of *Hypsophrys nicaraguensis* in the eastern part of the Lake Nicaragua.

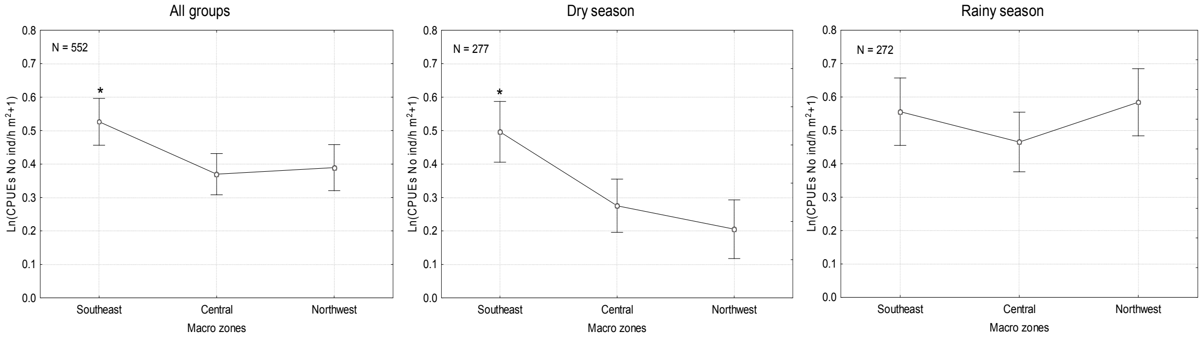


Figure 25. Catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Hypsophrys nicaraguensis* in the eastern part of the Lake Nicaragua for the whole year and by seasons. * denotes significant differences. Vertical bars denote 0.95 confidence intervals.

Table 18. Results of the GLMs for *Hypsophrys nicaraguensis* CPUEs (log-transformed) as function of season, macro-zones and depth.

	Hypsophrys nicaraguensis [Ln (CPUEs No ind/h m^2 + 1)]					
Explanatory variables	N	SS	df	MS	F	p
Intercept		99.73	1	99.73	486.66	0.00
Season	**553**	**6.15**	**1**	**6.15**	**30.00**	**0.00**
Error		113.33	553	0.20		
Intercept		100.63	1	100.63	475.24	0.00
Macro-zone	**552**	**2.59**	**2**	**1.29**	**6.11**	**0.00**
Error		116.89	552	0.21		
Intercept		100.18	1	100.18	509.99	0.00
Depth (m)	**552**	**11.04**	**2**	**5.52**	**28.10**	**0.00**
Error		108.43	552	0.20		
Intercept		101.50	1	101.50	513.07	0.00
Season		**6.00**	**1**	**6.00**	**30.33**	**0.00**
Macro-zone		**2.51**	**2**	**1.26**	**6.35**	**0.00**
Season*Macro-zone	**549**	**2.20**	**2**	**1.10**	**5.55**	**0.00**
Error		108.61	549	0.20		
Intercept		100.78	1	100.78	555.19	0.00
Season		**6.07**	**1**	**6.07**	**33.43**	**0.00**
Depth (m)		**11.15**	**2**	**5.58**	**30.72**	**0.00**
Season*Depth	**549**	**2.54**	**2**	**1.27**	**6.98**	**0.00**
Error		99.66	549	0.18		
Intercept		101.31	1	101.31	531.92	0.00
Macro-zone		**2.79**	**2**	**1.39**	**7.32**	**0.00**
Depth (m)		**11.28**	**2**	**5.64**	**29.61**	**0.00**
Macro-zone*Depth	546	1.56	4	0.39	2.04	0.09
Error		103.99	546	0.19		
Intercept		102.63	1	102.63	601.22	0.00
Season		**5.87**	**1**	**5.87**	**34.40**	**0.00**
Macro-zone		**2.67**	**2**	**1.33**	**7.81**	**0.00**
Depth (m)		**11.53**	**2**	**5.77**	**33.78**	**0.00**
Season*Macro-zone		**2.63**	**2**	**1.32**	**7.71**	**0.00**
Season*Depth		**3.07**	**2**	**1.54**	**9.00**	**0.00**
Macro-zone*Depth		**1.82**	**4**	**0.45**	**2.66**	**0.03**
Season*Macro-zone*Depth	537	0.98	4	0.24	1.43	0.22
Error		91.66	537	0.17		

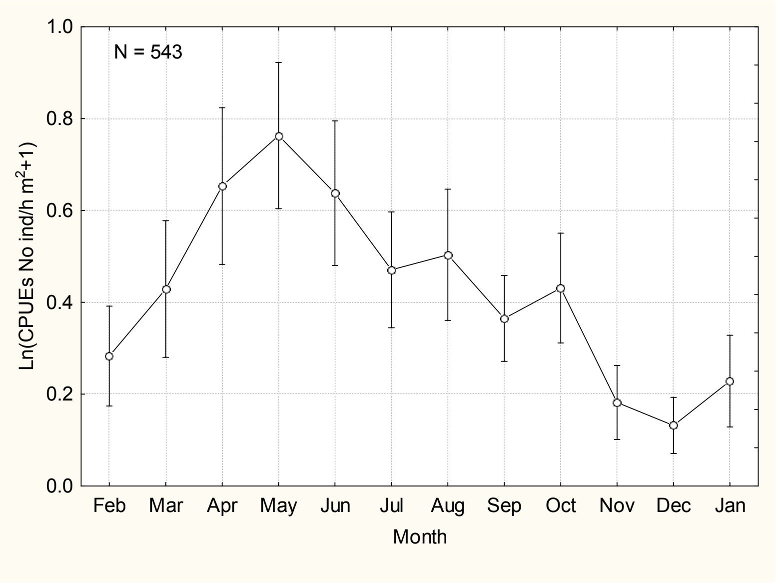


Figure 26. Monthly catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Hypsophrys nicaraguensis* during a fishery-independent survey in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

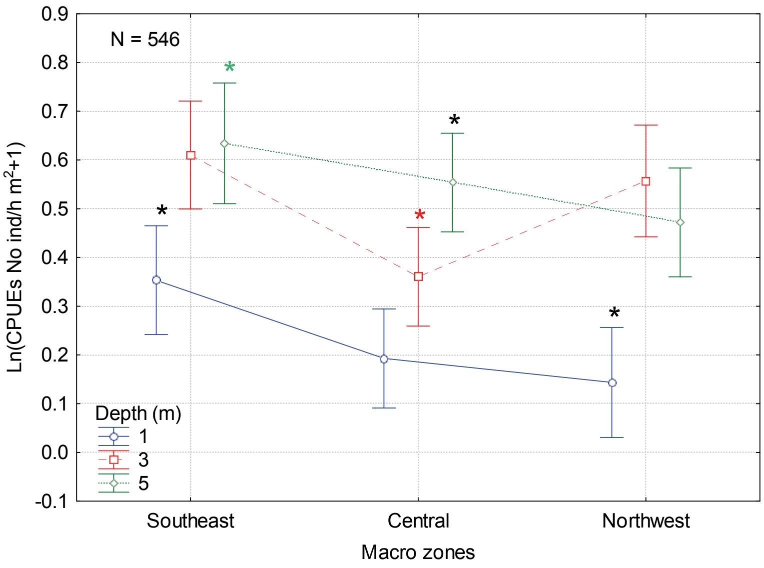


Figure 27. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Hypsophrys nicaraguensis* between macro-zones and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue, green and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

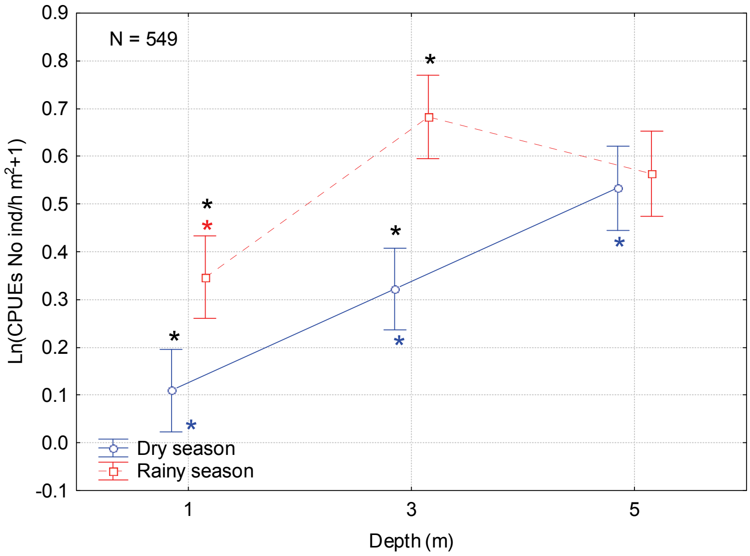


Figure 28. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Hypsoprhys nicaraguensis*, between season and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

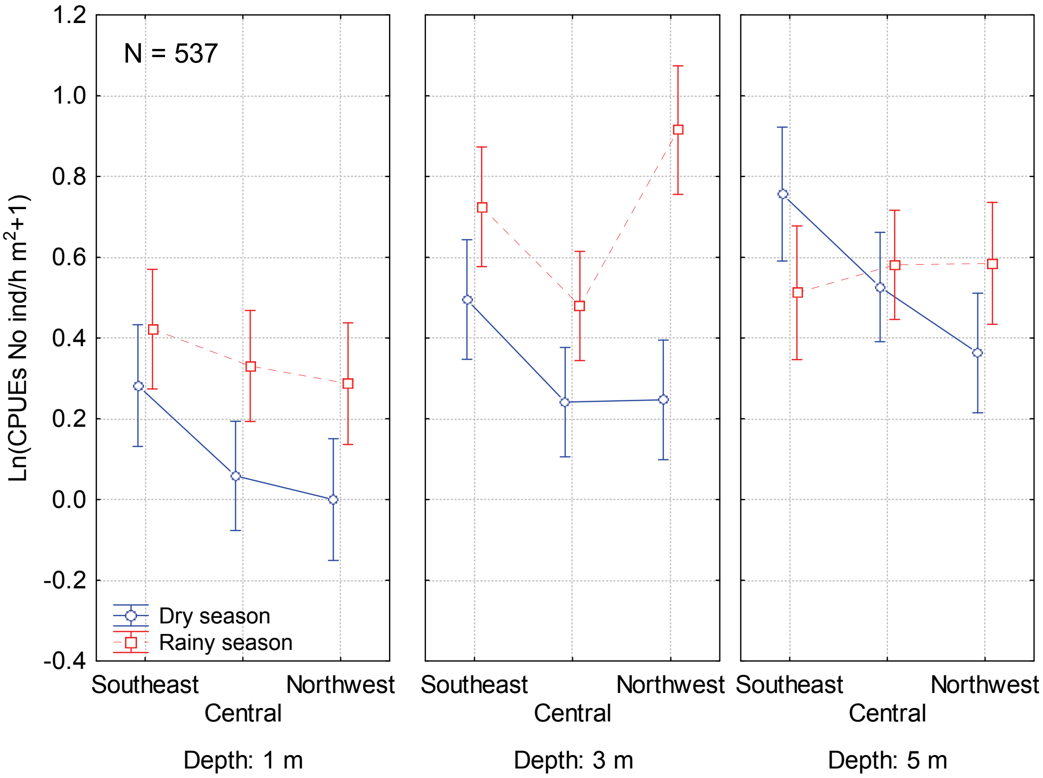


Figure 29. Spatio-temporal variation of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Hypsophrys nicaraguensis*, by depth, macro-zones and season in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

Parachromis managuensis (Guapote tigre)

The abundance index by haul ranged from 0.13 to 7.9 (average 0.97 ± 1.06) individuals/h m^2. As with previous species, this one was found in all sampled areas, and was not uniformly distributed. Largest abundances were found in the northwest zone, with a secondary patch in the central zones (Figure 30 A). Contrary to what it was observed in *H. nicaraguensis*, this species was significantly (GLM; $p<0.05$ Table 19) more abundant in dry season (0.52±0.25 individuals/h m^2) that in rainy season (0.42 ± 0.31) (Figure 30 B and C). However, these differences affected only the northwest zone (Figure 31). During the dry season, the guapote was widely distributed in the northwest, especially in deep waters in the vicinity of Rio Mayales, but also was abundant in the central-north area, up to Oyate (Figure 30 B). During the wet season they were more abundant slightly southwards occupying mainly the entire Rio Mayales mouth and the central-south area (Figure 30 C). The lowest abundances occurred in the central zones between Oyate and Tepenahuasapa rivers.

The monthly average abundance index ranged from 0.16 to 1.04 (0.47 ± 0.27) individuals/h m^2 (Figure 32). The monthly abundance vary significantly (ANOVA: F=5.881; $p < 0.001$) along the year. The highest abundance were observed between January and May, with a peak in March, while lowest values were found between June and December, with the significant exception of October, when a sudden increase in catch was obtained (Figure 32).

The abundance of this cichlid species varied significantly with depth (Table 19), and the higher catch rate are located in shallower waters, being the abundance at 5 depth stratum significantly lower (Post hoc $p<0.01$) mainly in the central and northwest zone (Figure 33). However, depth preferences shifted among zones, as interaction between depth and macro-zones was significant (Table 19). Thus, in the Southeast *P. managuensis* preferred shallowest waters, but selected intermediate waters (3 m) in the Northwest (Figure 33). The depth preference is maintained in both seasons (Figure 34), as shown by the lack of interaction between season and depth (Table 19). Overall, no significant effect in the abundance of *P. managuensis* was due to the interaction between spatio-temporal variables, i.e., season*macro-zone*depth was found (GLM: $p=0.14$; Table 19), but while in the southeast and central zones abundances did not much varied among seasons, in the northwest abundance was higher at 3 and 5 depth strata during dry season (Figure 35).

In summary, *Parachromis managuensis* prefers shallow waters and is more abundant in the northwest zone during rainy season, where concentrates near the river mouth. The second area of higher abundance is the southeast zone where it concentrates in shallower water and near to main river drainage of the lake, i.e., the San Juan River.

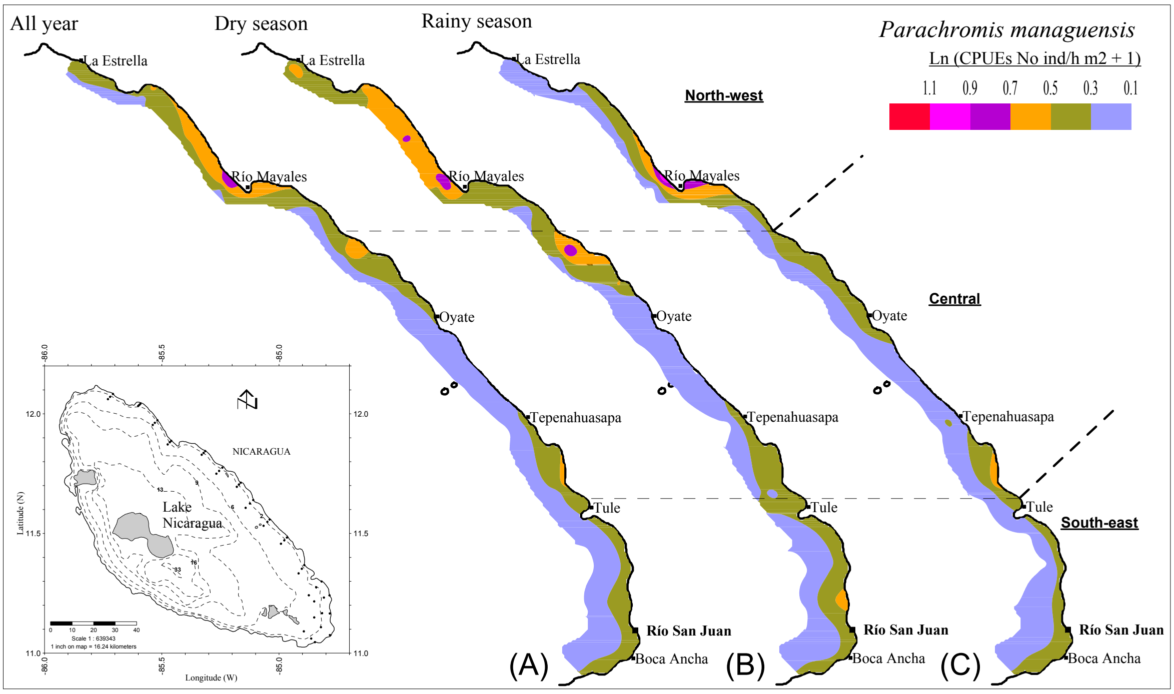


Figure 30. Distribution and abundance index [Ln(CPUEs No ind/h m^2+1)] of *Parachromis managuensis* in the eastern part of the Lake Nicaragua.

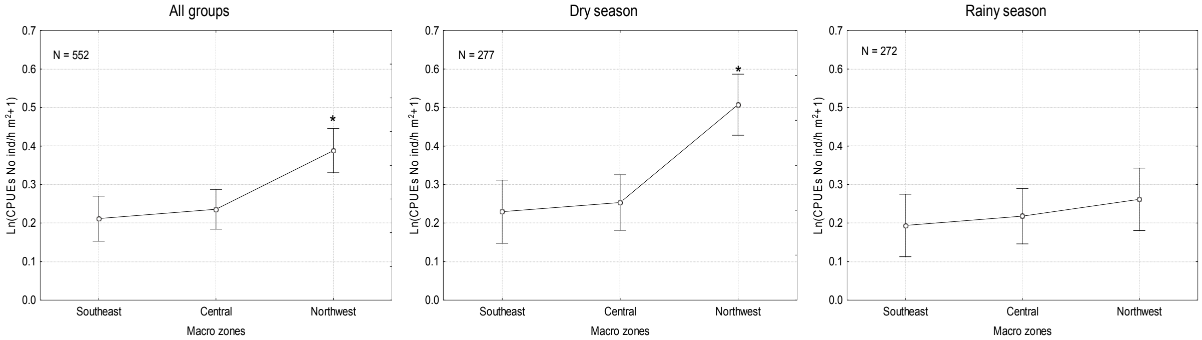


Figure 31. Catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Parachromis managuensis* in the eastern part of the Lake Nicaragua for the whole year and by seasons. * denotes significant differences. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

Table 19. Results of the GLMs for *Parachromis managuensis* CPUEs (log-transformed) as function of season, macro-zones and depth.

	Parachromis managuensis [Ln (CPUEs No ind/h m^2 + 1)]					
Explanatory variables	N	SS	df	MS	F	p
Intercept		42.13	1	42.13	279.91	0.000
Season	**553**	**1.47**	**1**	**1.47**	**9.80**	**0.002**
Error		83.24	553	0.15		
Intercept		42.52	1	42.52	287.96	0.000
Macro-zone	**552**	**3.21**	**2**	**1.61**	**10.88**	**0.000**
Error		81.50	552	0.15		
Intercept		41.62	1	41.62	291.16	0.000
Depth (m)	**552**	**5.81**	**2**	**2.90**	**20.31**	**0.000**
Error		78.91	552	0.14		
Intercept		42.14	1	42.14	293.73	0.000
Season		**1.53**	**1**	**1.53**	**10.65**	**0.001**
Macro-zone		**3.07**	**2**	**1.54**	**10.71**	**0.000**
Season*Macro-zone	549	1.31	2	0.66	4.58	0.011
Error		78.77	549	0.14		
Intercept		41.51	1	41.51	295.12	0.000
Season		**1.45**	**1**	**1.45**	**10.33**	**0.001**
Depth (m)		**5.81**	**2**	**2.90**	**20.64**	**0.000**
Season*Depth	549	0.24	2	0.12	0.84	0.431
Error		77.21	549	0.14		
Intercept		41.56	1	41.56	307.69	0.000
Macro-zone		**3.42**	**2**	**1.71**	**12.65**	**0.000**
Depth (m)		**5.88**	**2**	**2.94**	**21.75**	**0.000**
Macro-zone*Depth	**546**	**1.65**	**4**	**0.41**	**3.05**	**0.017**
Error		73.74	546	0.14		
Intercept		41.26	1	41.26	314.72	0.000
Season		**1.45**	**1**	**1.45**	**11.08**	**0.001**
Macro-zone		**3.31**	**2**	**1.65**	**12.62**	**0.000**
Depth (m)		**5.87**	**2**	**2.93**	**22.39**	**0.000**
Season*Macro-zone		**1.28**	**2**	**0.64**	**4.89**	**0.008**
Season*Depth		0.23	2	0.12	0.89	0.410
Macro-zone*Depth		1.65	4	0.41	3.14	0.014
Season*Macro-zone*Depth	537	0.41	4	0.10	0.78	0.537
Error		70.40	537	0.13		

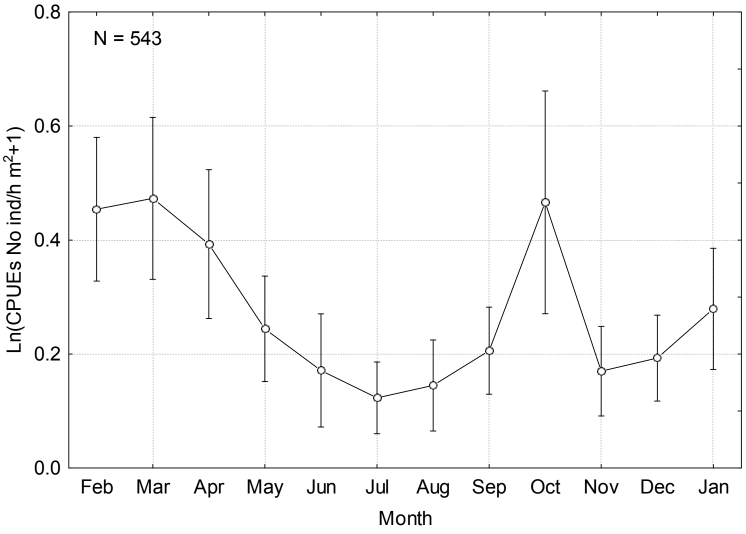


Figure 32. Monthly catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Parachromis managuensis* during a fishery-independent survey in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

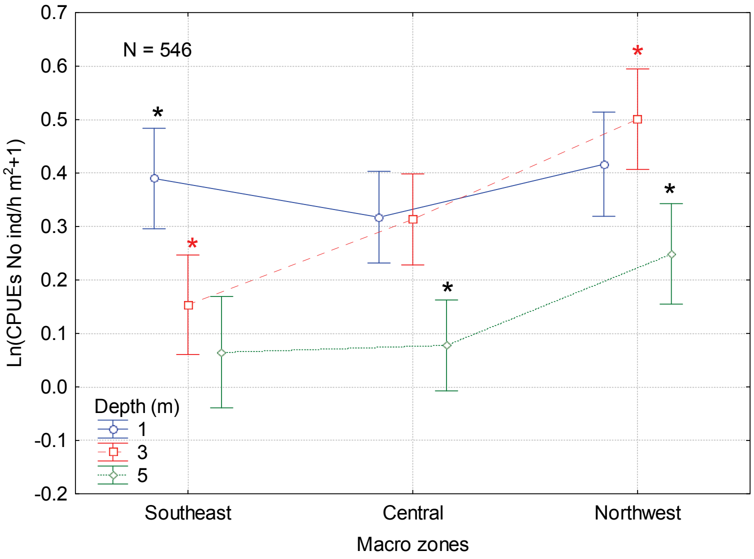


Figure 33. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Parachromis managuensis* between macro-zones and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

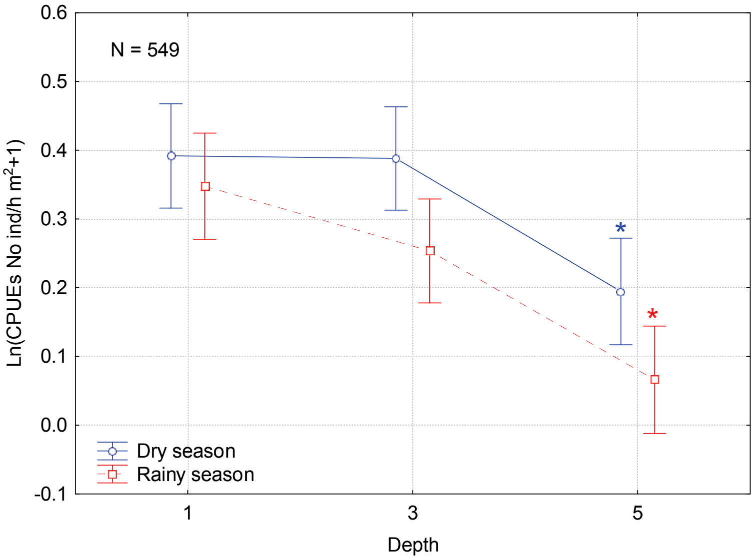


Figure 34. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m2+1)] of *Parachromis managuensis*, between season and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within seasons.

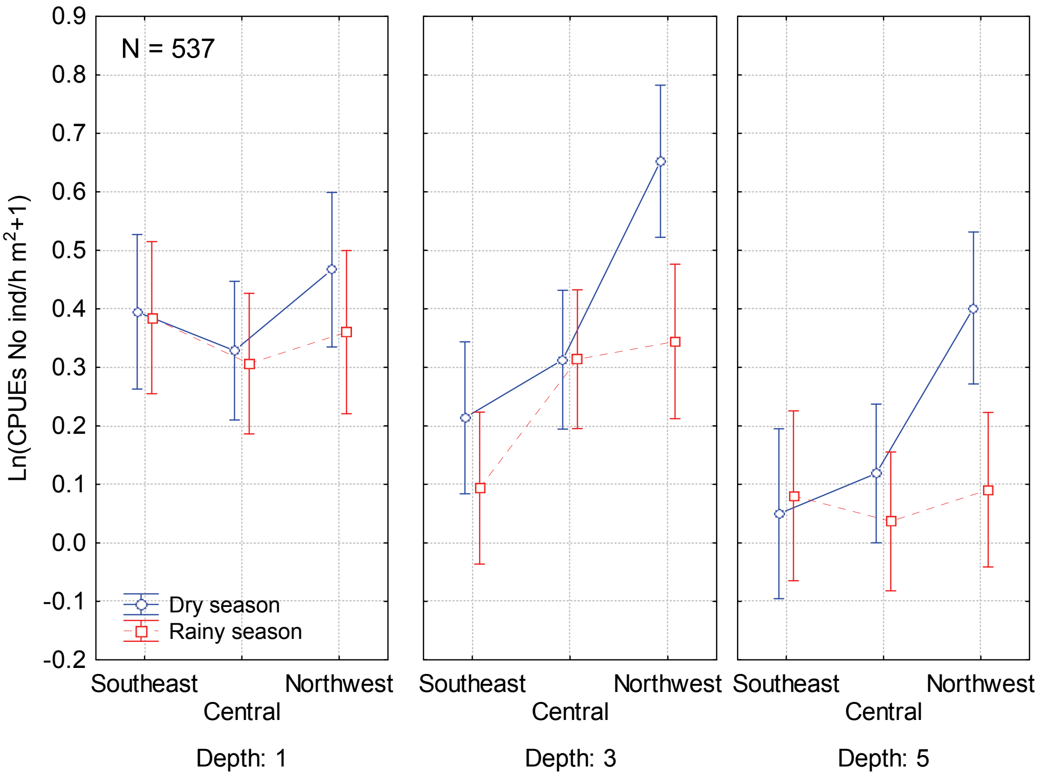


Figure 35. Spatio-temporal variation of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Parachromis managuensis*, by depth, macro-zones and season in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

Brycon guatemalensis (Machaca)

The overall CPUE by haul of this species, ranged from 0.1 to 16.7 (mean 1.8 ± 1.6) specimens per hour and square meter of the net, and the annual average was 0.8 ± 0.4. As expected this species was widely distributed in the area (Figure 36 A), but in average largest CPUE was found in the extreme areas, the southeast and northwest, with catches above 1.3 individual/h m^2. In the central part of the study area, the average CPUE decreased to a less than 1.0. However, no significant CPUE differences between areas were detected (Table 20 and Figure 37 All groups). The distribution pattern of the relative abundance index in the study area was significantly different between seasons (Table 20), as CPUE increased from 1.6 ± 1.1 to 2.0 ± 1.9 individuals/h m^2, respectively. During the dry season (Figure 36 B and Figure 37, Dry season) largest abundance (above 1 individuals/h m^2) was found in the southeast zone, otherwise was evenly distributed in the whole area at lower abundances (below 1 individuals/h m^2), and more frequently in deeper waters, but differences between zone are not statistical significant (GLM: $p=0.49$; Figure 37). During rainy season the overall abundance was not significant among zones (GLM: $p=0.41$; Figure 37 Rainy season), but some spots of higher abundance were observed close to rivers drainage, as Mayales in the northwest, Acoyapa in the central, Tule in the southeast, and in front of San Juan River and Boca Ancha rivers (Figure 36 C).

The monthly abundance index varied from 0.8 to 2.1 (mean 1.5 ± 0.4) individual/h m^2 (Figure 38) and was relatively low in March 0.8 ± 0.8 and November 1.0 ± 0.9 individual/h m^2. The rest of the year the CPUE was relatively higher, especially during the rainy season (May to October) when increased to a maximum in June of 2.3 ± 2.8 individual/h m^2. However, during the dry season the abundance largely fluctuated (Figure 38). The catch rates were statistically significant among months (ANOVA: $F=3.37$, $p<0.001$). The post hoc analysis indicated that differences in the catch rates occurred in the period June-September (Tuckey HSD test: $p<0.05$).

The abundance index of *Brycon* differed between depth strata, with a significant interaction with zones (Tukey HSD test: $p<0.05$). Thus, CPUE increased from southeast to northwest in shallower and deeper waters, but at 3 depth stratum an opposite pattern was observed (Figure 39). While no differences in abundance between zones was observed at 1 depth stratum (ANOVA: F=1.37, p=0.257), it was significantly higher in the southeast at 3 m and in the northwest at 5 m (Tukey HSD test: p<0.05). Overall, the abundances index varied with season and depth (p<0.001; Table 20), and the interaction between factors was significant but only at p<0.05; thus the depth preference of *B. guatemalensis* was similar between seasons being more abundant at deeper (3 and 5) than shallower waters (Figure 40). During rainy season the abundance increased significantly at 1 and 3 depth strata (GLM: p<0.001 and p<0.05 respectively; Figure 40).

When considered the three factors together, it can be observed that at 1m stratum the abundance was higher during rainy season in the three zones, with a clear trend to increase from south to east, especially during the dry season (Figure 41). The opposite trend was observed at 3 depth stratum were the abundance decreased from south to east, especially during the dry season, and abundance was higher during the rainy season only in the Northwest zone (Figure 41). At this depth stratum were registered the highest abundances in almost all zones and seasons. At 5 depths stratum there was no changes in abundance among zones during the dry season, but increased from south to north during the rainy season.

In summary, *Brycon guatemalensis* prefers intermediate and deeper waters and is more abundant in the southeast zone in both seasons, but especially during dry season. During rainy season it is more evenly distributed among depths and zones.

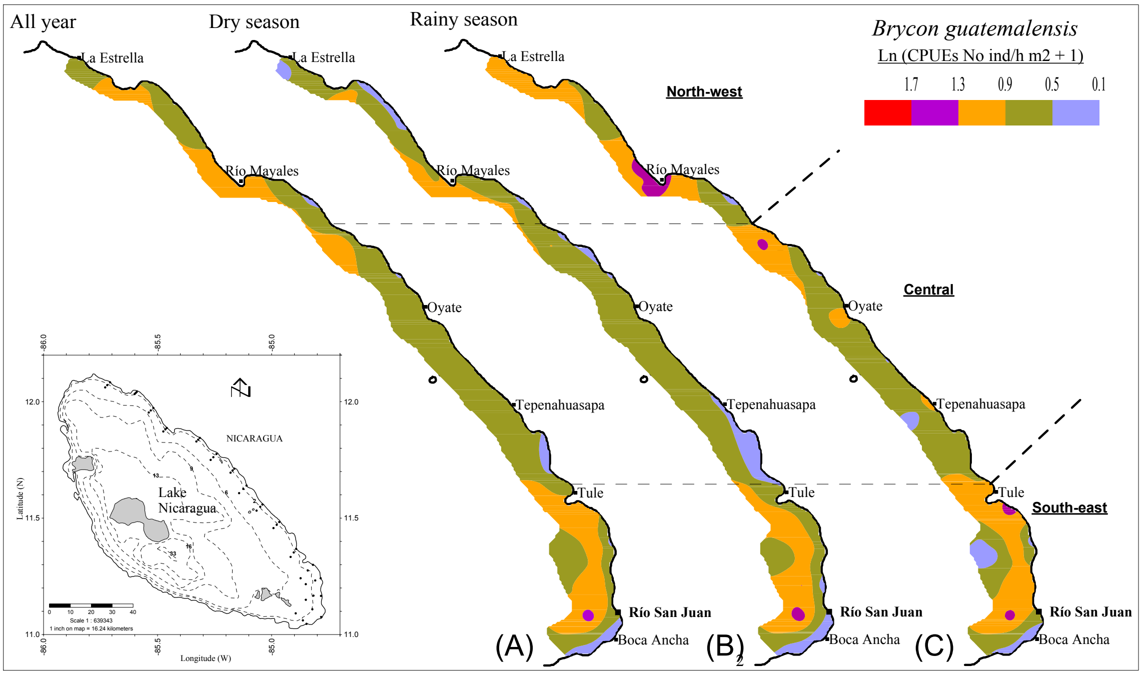


Figure 36. Distribution and abundance index [Ln(CPUEs No ind/h m +1)] of *Brycon guatemalensis* in the eastern part of the Lake Nicaragua.

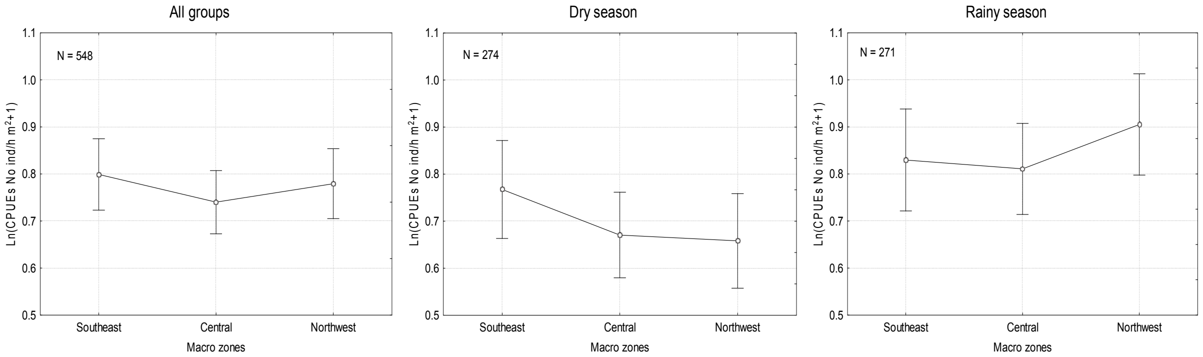


Figure 37. Catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Brycon guatemalensis* in the eastern part of the Lake Nicaragua for the whole year and by seasons. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

Table 20. Results of the GLMs for *Brycon guatemalensis* CPUEs (log-transformed) as function of season, macro-zones and depth.

		Brycon guatemalensis [Ln (CPUEs No ind/h m^2 + 1)]				
Explanatory variables	N	SS	df	MS	F	p
Intercept		327.10	1	327.10	1352.42	0.000
Season	**549**	**3.13**	**1**	**3.13**	**12.94**	**0.000**
Error		132.78	549	0.24		
Intercept		325.28	1	325.28	1314.89	0.000
Macro-zone	548	0.35	2	0.17	0.70	0.498
Error		135.57	548	0.25		
Intercept		326.14	1	326.14	1437.87	0.000
Depth (m)	**548**	**11.61**	**2**	**5.81**	**25.60**	**0.000**
Error		124.30	548	0.23		
Intercept		325.91	1	325.91	1348.46	0.000
Season		**3.06**	**1**	**3.06**	**12.67**	**0.000**
Macro-zone		0.34	2	0.17	0.70	0.495
Season*Macro-zone	545	0.73	2	0.37	1.51	0.221
Error		131.72	545	0.24		
Intercept		326.74	1	326.74	1489.28	0.000
Season		**3.01**	**1**	**3.01**	**13.70**	**0.000**
Depth (m)		**11.54**	**2**	**5.77**	**26.30**	**0.000**
Season*Depth	**545**	**1.62**	**2**	**0.81**	**3.69**	**0.025**
Error		119.57	545	0.22		
Intercept		321.48	1	321.48	1487.44	0.000
Macro-zone		0.29	2	0.14	0.67	0.513
Depth (m)		**11.43**	**2**	**5.72**	**26.45**	**0.000**
Macro-zone*Depth	**542**	**6.79**	**4**	**1.70**	**7.85**	**0.000**
Error		117.14	542	0.22		
Intercept		322.20	1	322.20	1553.71	0.000
Season		**2.86**	**1**	**2.86**	**13.80**	**0.000**
Macro-zone		0.28	2	0.14	0.67	0.510
Depth (m)		**11.45**	**2**	**5.73**	**27.61**	**0.000**
Season*Macro-zone		0.80	2	0.40	1.94	0.145
Season*Depth		**1.79**	**2**	**0.89**	**4.31**	**0.014**
Macro-zone*Depth		**6.79**	**4**	**1.70**	**8.18**	**0.000**
Season*Macro-zone*Depth	533	1.10	4	0.27	1.32	0.260
Error		110.53	533	0.21		

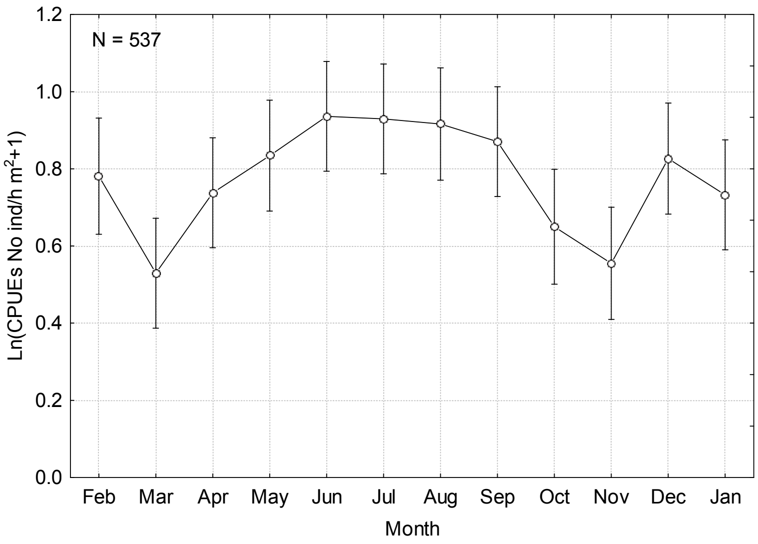


Figure 38. Monthly catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Brycon guatemalensis* during a fishery-independent survey in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

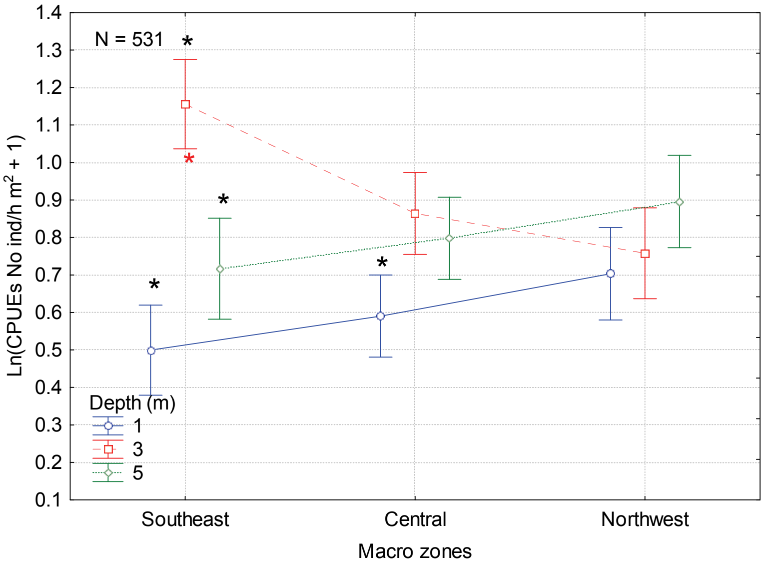


Figure 39. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Brycon guatemalensis* between macro-zones and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

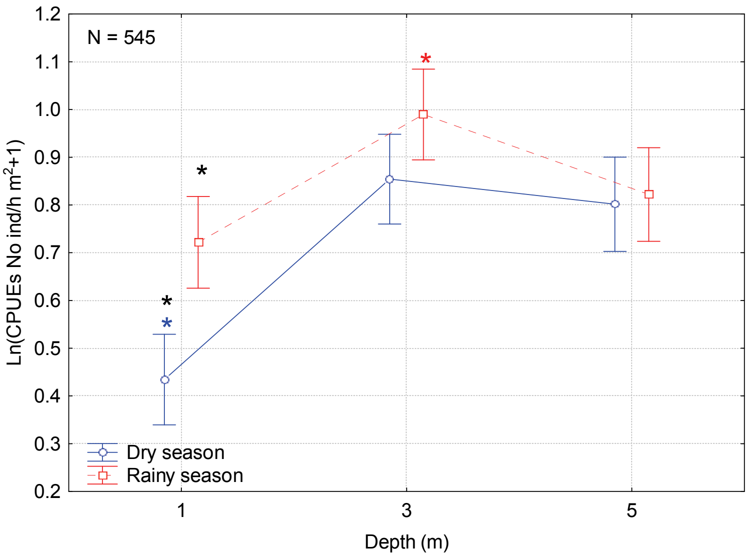


Figure 40. Spatial variations of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Brycon guatemalensis*, between season and depth. Mean ± CI: Vertical bars denote 0.95 confidence intervals. Blue and red * denotes significant differences among depth strata within seasons. Black * denotes significant differences among seasons within depth stratum.

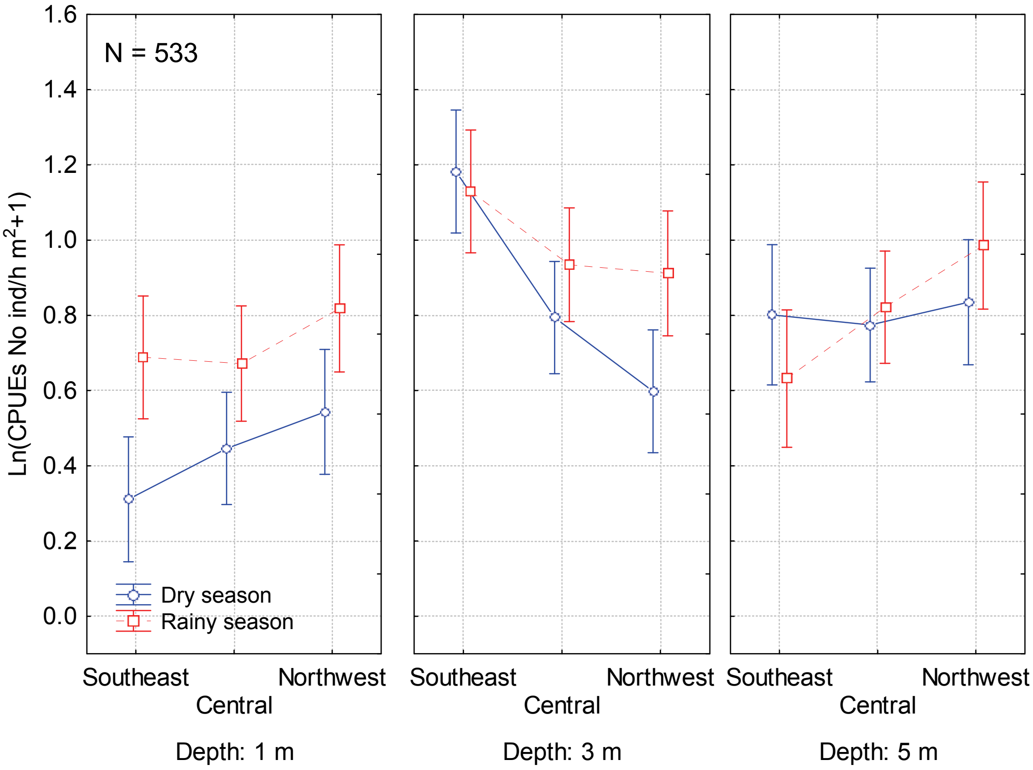


Figure 41. Spatio-temporal variation of catch per unit of fishing effort [Ln(CPUEs No ind/h m^2+1)] of *Brycon guatemalensis*, by depth, macro–zones and season in the Lake Nicaragua. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

3.2.4. Length-frequency distribution

Amphilophus citrinellus

The length frequency distribution departed slightly from normality (Shapiro–Wilk, $p<0.01$), in both sexes, but only male distribution showed some minor positive skewness, indicating lower catchability at smaller size males (Figure 42). The size distribution was significantly different between both sexes (ANOVA: F= 539.89, $p<0.001$), being males larger (20.1 cm ± SD 2.5) than females (18.8 cm ± SD 1.9). The male and female maximum length registered slightly differed 40.5 and 40.9 cm respectively, and the overall mean length caught during the survey was 19.6 cm ± SD 2.3.

The monthly mean length fluctuated along the year showing significant variability (ANOVA: F= 7.48, $p<0.001$), but without a defined pattern. The mean length varied from 19.1 to 20.0 cm (Figure 43), being the larger mean length registered in January 20.0 cm ± SD 2.1 and the smaller 19.1 cm ± 2.3 in February.

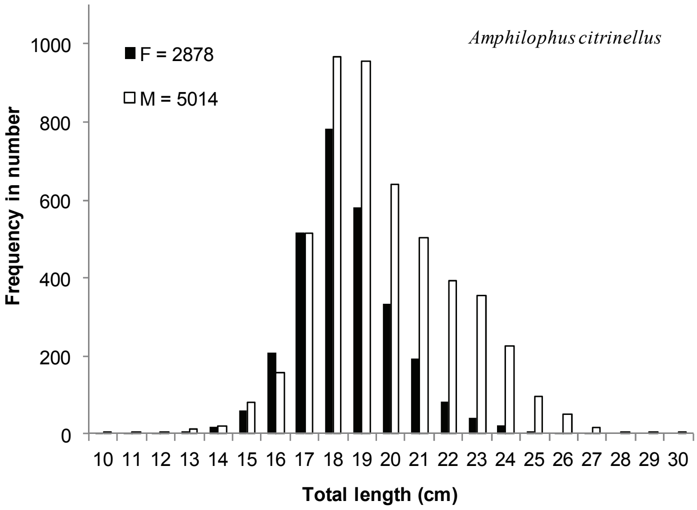


Figure 42. Length frequency distributions (number) of *Amphilophus citrinellus*. F: females and M: males.

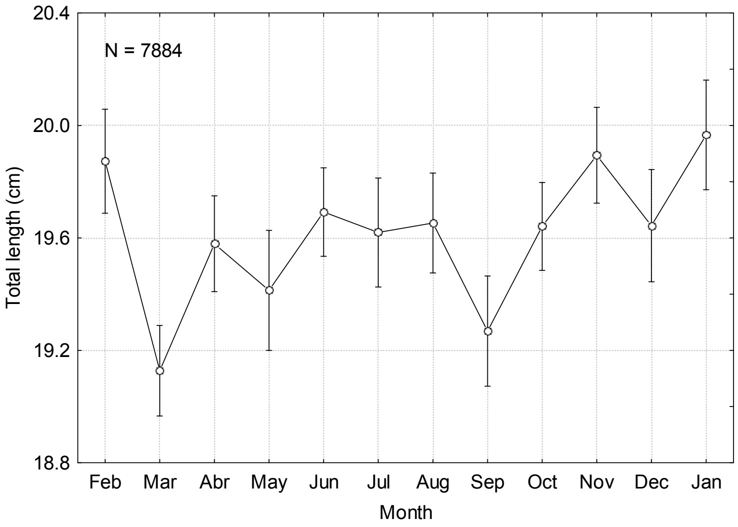


Figure 43. Monthly mean length distributions pattern of *Amphilophus citrinellus* during the fishery-independent survey in the Lake Nicaragua. Vertical bars denote 0.95 confidence intervals.

Length distributions were analyzed considering, the season, macro-zones and depth strata, as factors explaining length variability. There were not differences between seasons, and seasons had not interaction with zones and depths (F= 2.19; p= 0.06; Table 21). On the other hand, significant differences in size were observed among zones and depth, and with the interaction between both (Table 21) indicating size variations between depths but differently in each zone.

Size was significantly different (Post Hoc, p<0.01) among depth strata in the southeast, increasing size with depth stratum (Figure 44). However, in the central zone there were no differences in size between 1 and 3 depth strata, neither among all depths in the northwest zones (Figure 44). The general pattern indicates that smaller sizes are found in the northwest at all depths and in the southeast at 1.0 m, and fishes are larger at deeper waters, mainly in southeast. Figure 45 illustrates this pattern of the mean length distribution in a spatial scale during the analyzed year, where it is observed that, during both season (dry and rainy), larger individuals are distributed toward the southeast and the smaller toward the northwest zone. Spots of largest fishes appeared in the southeast zones during both seasons toward “deeper” waters, especially during rainy season. The northwest part is dominated by specimens with average length of 18.5 cm, while the central area by fishes of one cm above (19.5 cm) and the southeast are found a mixture of all sizes but stratified by depth strata.

The total length of *Amphilophus citrinellus* was significant correlated with the water turbidity of the lake (r = 0.068; p = 0.001; Figure 46), Due to the high dispersion of values (Figure 46) a second analysis was performed with the mean length by water turbidity class and no significant differences were found (GLM F=1.4, p=0.199).

Table 21. Results of the GLMs for *Amphilophus citrinellus.* Total length (cm) as function of season, macro-zones and depth.

	Amphilophus citrinellus: Total length (cm)					
Explanatory variables	n	SS	df	MS	F	p
Intercept		3037236.26	1	3037236.26	550391.45	0.000
Season	7894	12.70	1	12.70	2.30	0.129
Error		43561.62	7894	5.52		
Intercept		2957134.65	1	2957134.65	540461.17	0.000
Macro-zone	**7893**	**387.75**	**2**	**193.88**	**35.43**	**0.000**
Error		43186.57	7893	5.47		
Intercept		2761135.64	1	2761135.64	503540.47	0.000
Depth (m)	**7893**	**293.50**	**2**	**146.75**	**26.76**	**0.000**
Error		43280.82	7893	5.48		
Intercept		2896541.04	1	2896541.04	530087.68	0.000
Season		0.13	1	0.13	0.02	0.880
Macro-zone		**395.78**	**2**	**197.89**	**36.22**	**0.000**
Season*Macro-zone	7890	71.26	2	35.63	6.52	0.001
Error		43113.07	7890	5.46		
Intercept		2755977.13	1	2755977.13	502514.44	0.000
Season		6.50	1	6.50	1.19	0.276
Depth (m)		**287.59**	**2**	**143.80**	**26.22**	**0.000**
Season*Depth	7890	1.16	2	0.58	0.11	0.899
Error		43271.71	7890	5.48		
Intercept		2596395.69	1	2596395.69	481612.70	0.000
Macro-zone		**335.78**	**2**	**167.89**	**31.14**	**0.000**
Depth (m)		**286.64**	**2**	**143.32**	**26.59**	**0.000**
Macro-zone*Depth	**7887**	**344.47**	**4**	**86.12**	**15.97**	**0.000**
Error		42519.17	7887	5.39		
Intercept		2526329.34	1	2526329.34	469321.22	0.000
Season		4.48	1	4.48	0.83	0.362
Macro-zone		**333.44**	**2**	**166.72**	**30.97**	**0.000**
Depth (m)		**267.76**	**2**	**133.88**	**24.87**	**0.000**
Season*Macro-zone		60.19	2	30.09	5.59	0.004
Season*Depth		12.25	2	6.12	1.14	0.321
Macro-zone*Depth		**325.51**	**4**	**81.38**	**15.12**	**0.000**
Season*Macro-zone*Depth	7878	47.09	4	11.77	2.19	0.068
Error		42407	7878	5.38		

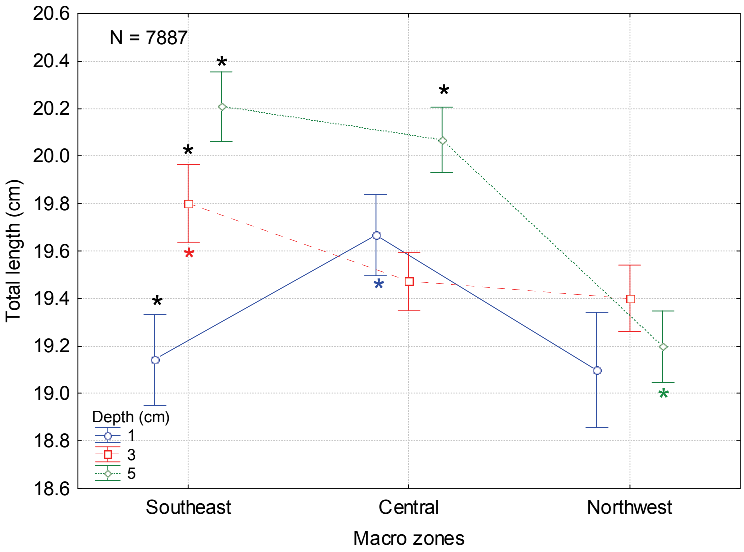


Figure 44. Spatial variations of the mean length of *Amphilophus citrinellus* between macro-zones and depth. Vertical bars denote 0.95 confidence intervals. Blue, green and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

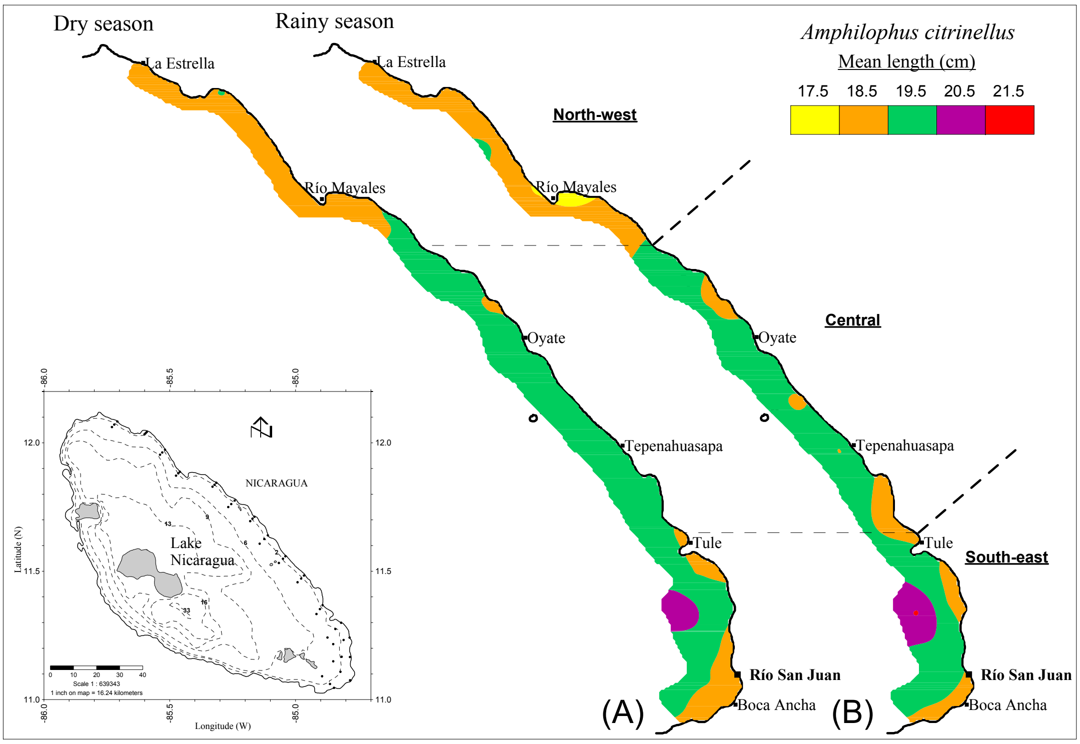


Figure 45. Mean length distributions of *Amphilophus citrinellus* in the eastern part of the Lake Nicaragua.

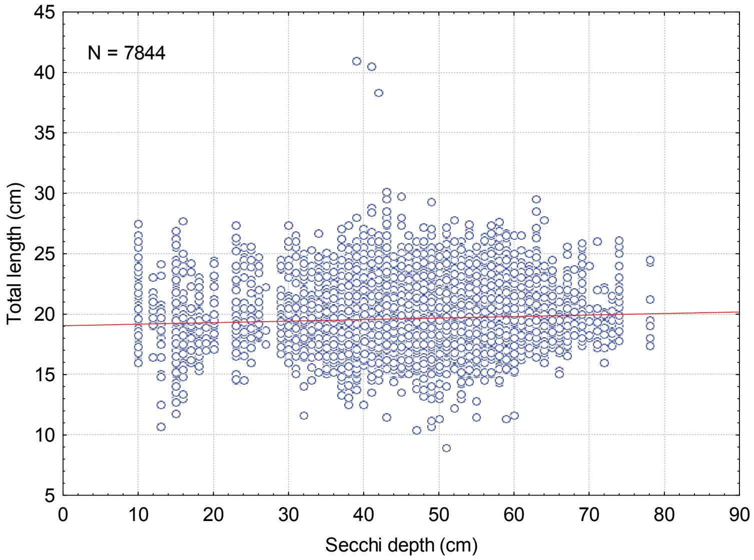


Figure 46. Relationship between total length of *Amphilophus citrinellus* and secchi depth.

Hypsophrys nicaraguensis

The length frequency distributions for both males and females departed slightly from normality (Shaphiro-Wilk, p<0.01), with some positive skewness in females. Catchability was much higher in males (Figure 47). The size distribution differed significantly between both sexes (ANOVA: F= 990.77, p=0.001), and the average length for males was larger (17.3 cm ± SD 1.14) than females (14.3 cm ± SD 1.29). The male and female maximum length registered differed in 6.1 cm being 25.5 and 19.4 cm respectively, and the overall mean length caught during the survey was 16.9 cm ± SD 1.42.

The monthly mean length showed significantly variability during the year (ANOVA: F= 9.49, p<0.001). This mean length increased from May to December from 16.5 cm ± SD 1.47 to 17.9 cm ± SD 1.25, respectively (Figure 48). November showed the larger variability of fish sizes 17.2 cm ± 1.92.

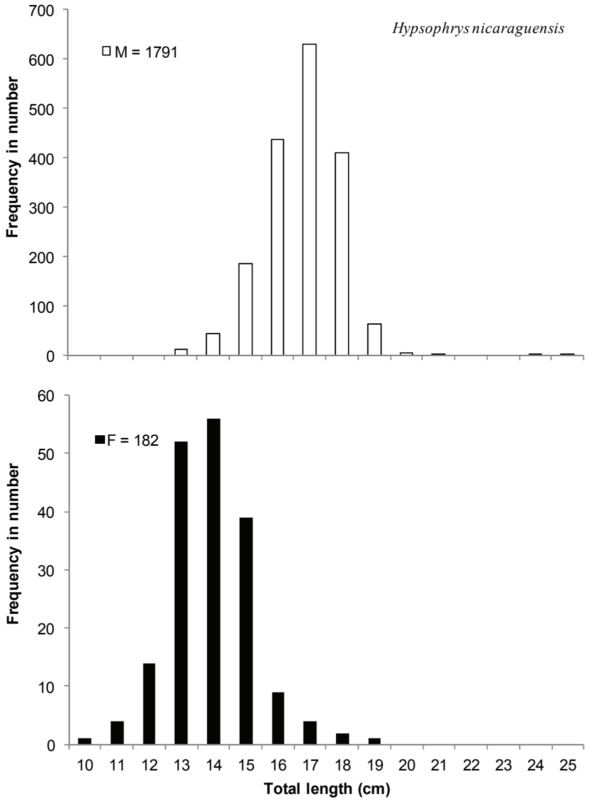


Figure 47. Length frequency distributions (number) of *Hypsophrys nicaraguensis*. F: females and M: males. Note the different Y-axis scale between graphs.

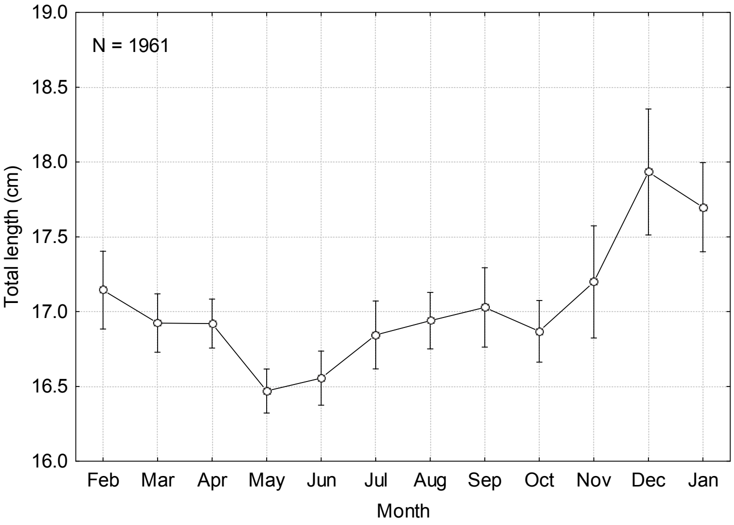


Figure 48. Monthly mean length distributions pattern of *Hypsophrys nicaraguensis* during the fishery-independent survey in the Lake Nicaragua. Vertical bars denote 0.95 confidence intervals.

The size distribution showed significant differences between macro-zones and depth strata, but not between seasons (Table 22). The significant interactions obtained indicate a complex pattern of size variability between macro-zones, depth and season.

Size was significantly higher (Post Hoc, $p<0.05$) at depth 5 stratum in the southeast only, and differences in size were not observed in the central and northwest zones (Figure 49). On the other hand, size was significantly smaller in the southeast zone at depth 1 stratum (Post Hoc, $p<0.05$). Differences in size from southeast to northwest were not observed along each depth stratum, except in the 5 depth strata in the southeast (Figure 49). The general pattern indicates that smaller and larger sizes are found in the southeast in shallower zones (1.0 m) and deeper zones (5.0 m) respectively. Figure 50 illustrates the complexity of the mean length distribution in a spatial, where it is observed that during both seasons larger individuals are distributed mainly towards the southeast and the smaller towards the northwest zone. But patches of larger and smaller fish are scattered along the zones, thus during dry season areas of larger fishes are located between Oyate and Tepenahuasapa rivers, the surrounding area of Tule rivers and offshore (deeper water) in the southeast zone, while during rainy season larger fish appeared distributed in spots along the whole area, but larger spots are observed in the southeast. The entire area appeared dominated by size of 16.5 cm.

The total length of *Hypsophrys nicaraguensis* was significant correlated with the water turbidity of the lake ($p<0.001$) with low coefficient of correlation ($r=0.105$). Due to data dispersion of values (Figure 51) a second analysis was performed with the mean length by water turbidity class, with range of 10 cm, and significant differences were found (GLM $F=3.057$, $p<0.01$). Post Hoc analysis shows differences in fish length ($p<0.05$) only at 60 cm of secchi depth.

Table 22. Results of the GLMs for *Hypsophrys nicaraguensis*. Total length (cm) as function of season, macro-zones and depth.

	Hypsophrys nicaraguensis: Total length (cm)					
Explanatory variables	n	SS	df	MS	F	p
Intercept		558772.56	1	558772.56	275627.31	0.000
Season	1971	1.65	1	1.65	0.82	0.366
Error		3995.76	1971	2.03		
Intercept		560757.20	1	560757.20	278027.12	0.000
Macro-zone	**1970**	**24.09**	**2**	**12.05**	**5.97**	**0.003**
Error		3973.32	1970	2.02		
Intercept		266768.02	1	266768.02	132106.47	0.000
Depth (m)	**1970**	**19.31**	**2**	**9.66**	**4.78**	**0.008**
Error		3978.10	1970	2.02		
Intercept		511292.15	1	511292.15	254548.46	0.000
Season		0.03	1	0.03	0.01	0.909
Macro-zone		**24.97**	**2**	**12.49**	**6.22**	**0.002**
Season*Macro-zone	**1967**	**22.31**	**2**	**11.15**	**5.55**	**0.004**
Error		3950.96	1967	2.01		
Intercept		262003.16	1	262003.16	129727.65	0.000
Season		0.27	1	0.27	0.14	0.712
Depth (m)		**17.07**	**2**	**8.54**	**4.23**	**0.015**
Season*Depth	1967	4.82	2	2.41	1.19	0.304
Error		3972.63	1967	2.02		
Intercept		216687.53	1	216687.53	108280.78	0.000
Macro-zone		**16.40**	**2**	**8.20**	**4.10**	**0.017**
Depth (m)		**24.38**	**2**	**12.19**	**6.09**	**0.002**
Macro-zone*Depth	**1964**	**19.16**	**4**	**4.79**	**2.39**	**0.049**
Error		3930.28	1964	2.00		
Intercept		139667.02	1	139667.02	70060.75	0.000
Season		0.04	1	0.04	0.02	0.892
Macro-zone		10.04	2	5.02	2.52	0.081
Depth (m)		**12.53**	**2**	**6.27**	**3.14**	**0.043**
Season*Macro-zone		2.58	2	1.29	0.65	0.524
Season*Depth		0.96	2	0.48	0.24	0.787
Macro-zone*Depth		13.72	4	3.43	1.72	0.143
Season*Macro-zone*Depth	1955	5.68	4	1.42	0.71	0.584
Error		3897.32	1955	1.99		

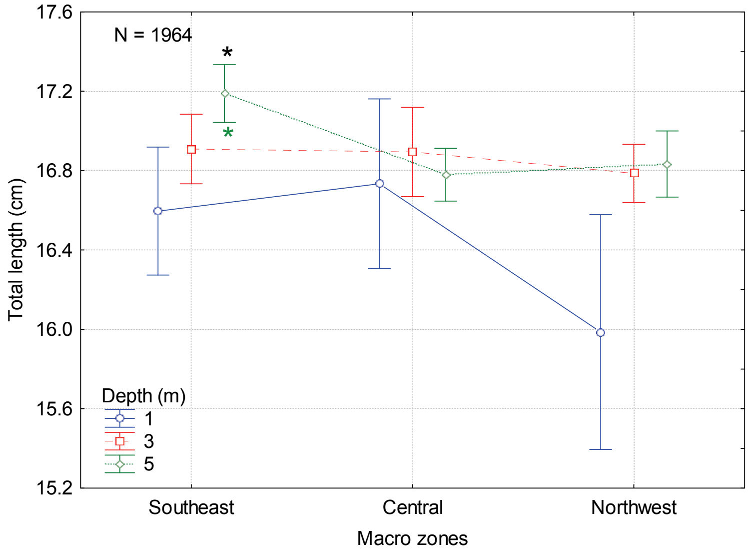


Figure 49. Spatial variations of the mean length of *Hypsophrys nicaraguensis* between macro-zones and depth. Vertical bars denote 0.95 confidence intervals. Green * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

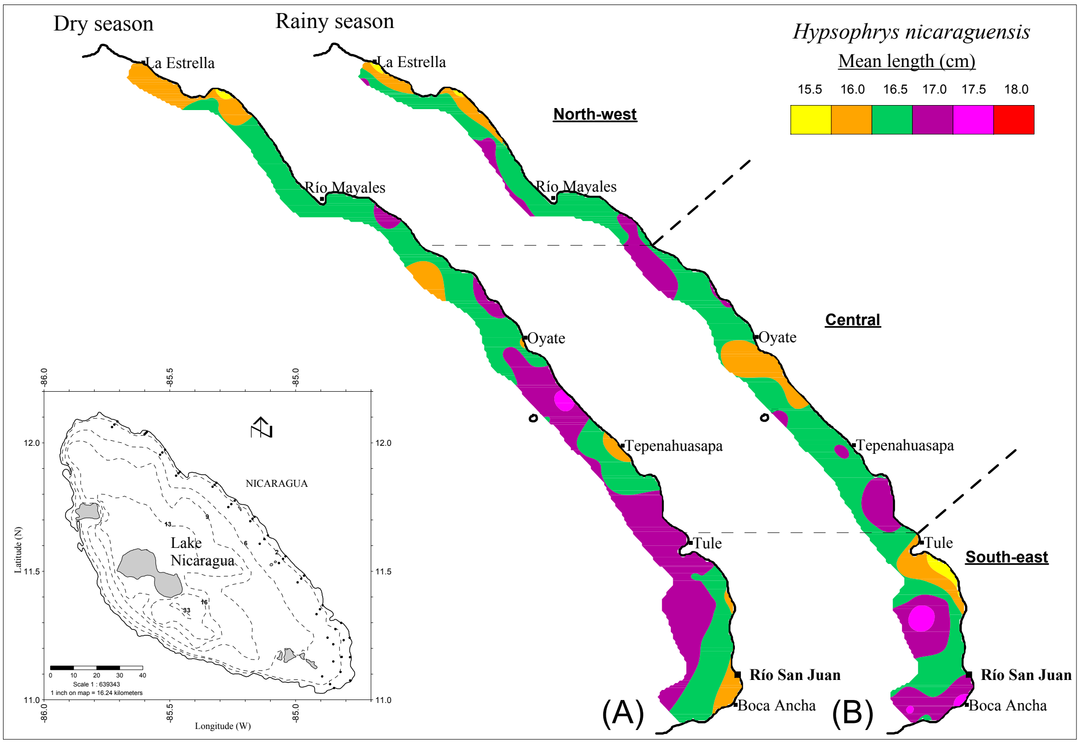


Figure 50. Mean length distributions of *Hypsophrys nicaraguensis* in the eastern part of the Lake Nicaragua.

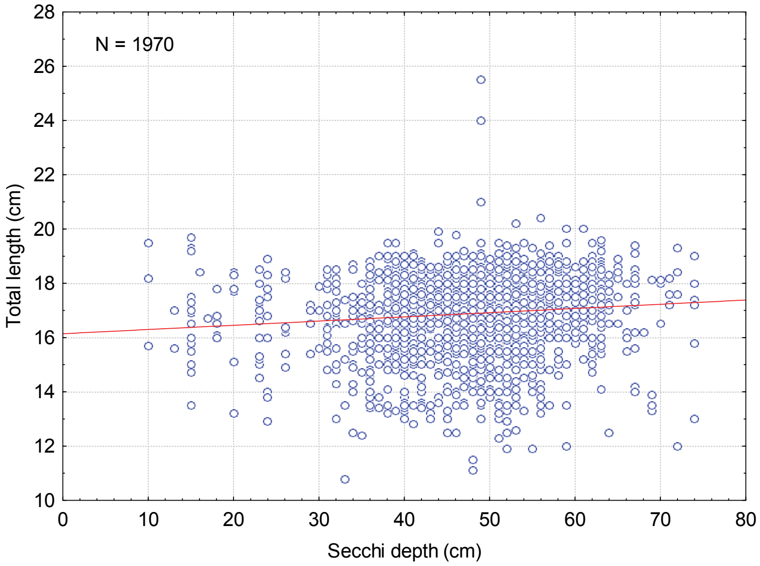


Figure 51. Relationship between total length of *Hypsophrys nicaraguensis* and secchi depth.

Parachromis managuensis

The length frequency distribution of males and females did not follow a normal distribution (Shaphiro-Wilk, $p<0.01$) showing both a positive skewness, and hence a lower catchability at smaller sizes. Thus males below 21 cm and females bellow 19 cm were captured in low numbers (Figure 52). The size distribution was significantly different between both sexes (ANOVA: F= 121.93, $p=0.001$), and the mean length for males was larger (24.6 cm ± SD 2.75) than females (22.7 cm ± SD 2.01). The male and female maximum length registered differed in 7.5 cm being 42.0 and 34.5 cm respectively, and the overall mean length caught during the survey was 23.7 cm ± SD 2.63.

The monthly mean length showed no significant variability during the year (ANOVA: F= 0.94, $p=0.498$) (Figure 53). Significant differences in size distribution were only observed among macro-zones ($F=5.82$, $p<0.01$) and depth strata ($F=4.11$, $p<0.05$), without significant differences between seasons, neither significant interactions were found (Table 23). This indicates that length variability of *Parachromis managuensis* in the study area is explained, separately, by both spatial factors only.

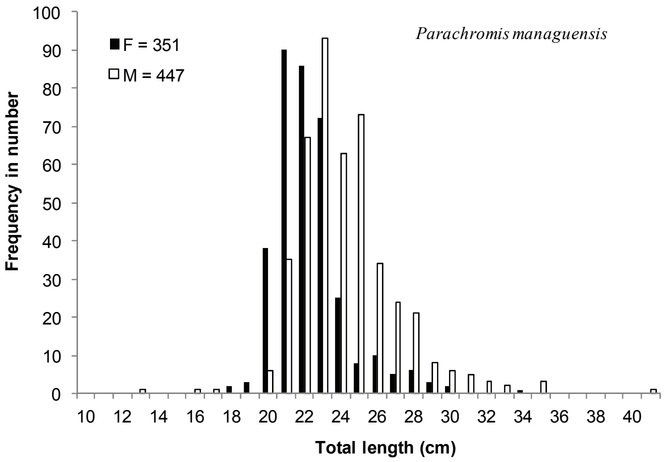


Figure 52. Length frequency distributions (number) of *Parachromis managuensis*. F: females and M: males.

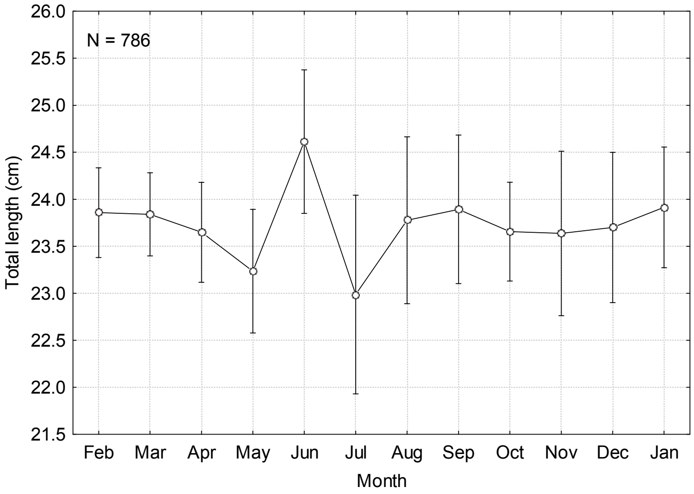


Figure 53. Monthly mean length distributions pattern of *Parachromis managuensis* during the fishery-independent survey in the Lake Nicaragua. Vertical bars denote 0.95 confidence intervals.

Size was significantly higher in the southeast zone (Post Hoc, $p<0.005$), and at depth 1 stratum (Post Hoc, $p<0.05$). Differences in size from southeast to northwest were not observed along each depth stratum (Post Hoc, $p>0.05$) (Figure 54).

The general pattern indicates that smaller sizes are found at depth stratum 3 and 5 and larger size in shallower waters. Figure 55 illustrates the mean length distribution in a spatial scale, where it is observed that, during both seasons (dry and rainy) the average fish sizes of around 22.0 cm dominated most in the study area. Larger individuals than 24.0 cm were located as large spots in the southern part near the shoreline between Tepenahuasapa and Río San Juan, and in small patches in the northern part during dry season; while during rainy season these spots were located nearby rivers mouth in the southeast and central zone. Largest fish sizes (above 26.0 cm) were located mainly in a small spots in the southeast zone.

The total length of *Parachromis managuensis* was significant correlated with the water turbidity of the lake ($p<0.05$) with low coefficient of correlation ($r=0.027$). Due to data dispersion of values (Figure 56) a second analysis was performed with the mean length by water turbidity class, with range of 10 cm, and no significant differences were found (GLM $F=1.425$, $p=0.21$).

Table 23. Results of the GLMs for *Parachromis managuensis*. Total length (cm) as function of season, macro-zones and depth.

	Parachromis managuensis: Total length (cm)					
Explanatory variables	n	SS	df	MS	F	p
Intercept		410091.43	1	410091.43	58992.83	0.000
Season	796	0.90	1	0.90	0.13	0.718
Error		5533.43	796	6.95		
Intercept		368430.10	1	368430.10	53699.02	0.000
Macro-zone	**795**	**79.82**	**2**	**39.91**	**5.82**	**0.003**
Error		5454.51	795	6.86		
Intercept		421911.50	1	421911.50	61233.51	0.000
Depth (m)	**795**	**56.62**	**2**	**28.31**	**4.11**	**0.017**
Error		5477.71	795	6.89		
Intercept		347364.59	1	347364.59	50662.72	0.000
Season		2.18	1	2.18	0.32	0.573
Macro-zone		**86.14**	**2**	**43.07**	**6.28**	**0.002**
Season*Macro-zone	792	24.02	2	12.01	1.75	0.174
Error		5430.28	792	6.86		
Intercept		342488.47	1	342488.47	49667.71	0.000
Season		0.28	1	0.28	0.04	0.841
Depth (m)		**46.60**	**2**	**23.30**	**3.38**	**0.035**
Season*Depth	792	16.29	2	8.14	1.18	0.307
Error		5461.31	792	6.90		
Intercept		316887.52	1	316887.52	46524.57	0.000
Macro-zone		**67.49**	**2**	**33.75**	**4.95**	**0.007**
Depth (m)		**57.19**	**2**	**28.59**	**4.20**	**0.015**
Macro-zone*Depth	789	42.55	4	10.64	1.56	0.183
Error		5374.03	789	6.81		
Intercept		269536.68	1	269536.68	39829.64	0.000
Season		0.19	1	0.19	0.03	0.869
Macro-zone		**66.03**	**2**	**33.02**	**4.88**	**0.008**
Depth (m)		**49.37**	**2**	**24.68**	**3.65**	**0.027**
Season*Macro-zone		20.45	2	10.23	1.51	0.221
Season*Depth		38.96	2	19.48	2.88	0.057
Macro-zone*Depth		24.05	4	6.01	0.89	0.470
Season*Macro-zone*Depth	780	39.31	4	9.83	1.45	0.215
Error		5278.45	780	6.77		

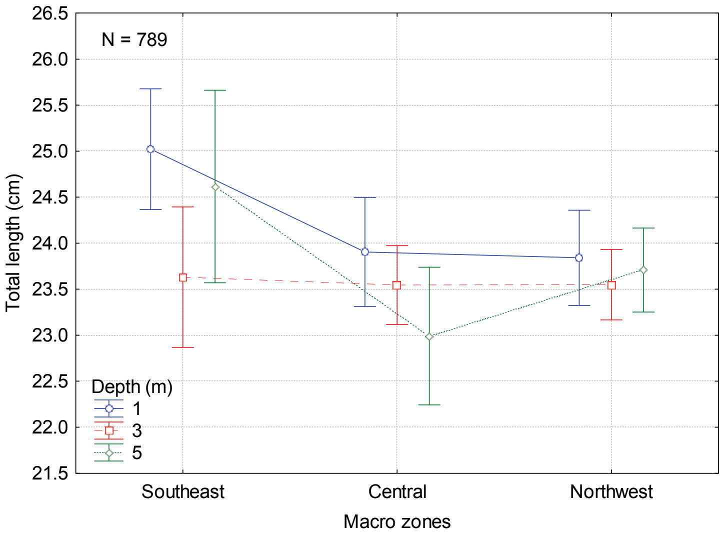


Figure 54. Spatial variations of the mean length of *Parachromis managuensis* between macro-zones and depth. Vertical bars denote 0.95 confidence intervals.

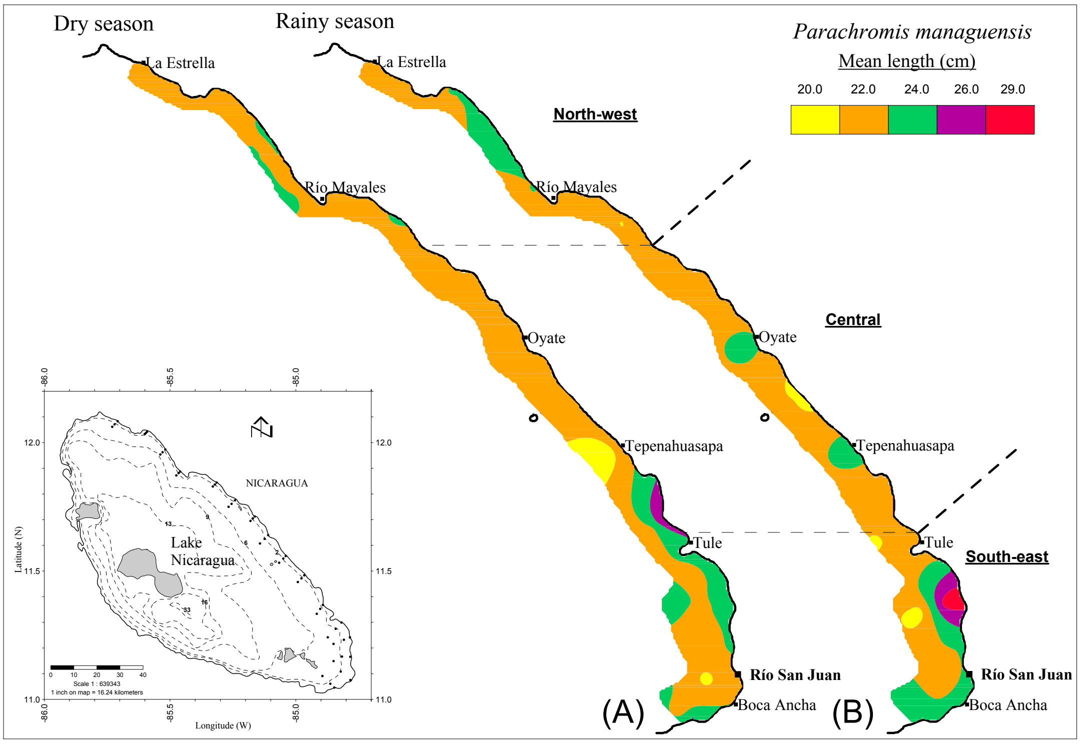


Figure 55. Mean length distributions of *Parachromis managuensis* in the eastern part of the Lake Nicaragua.

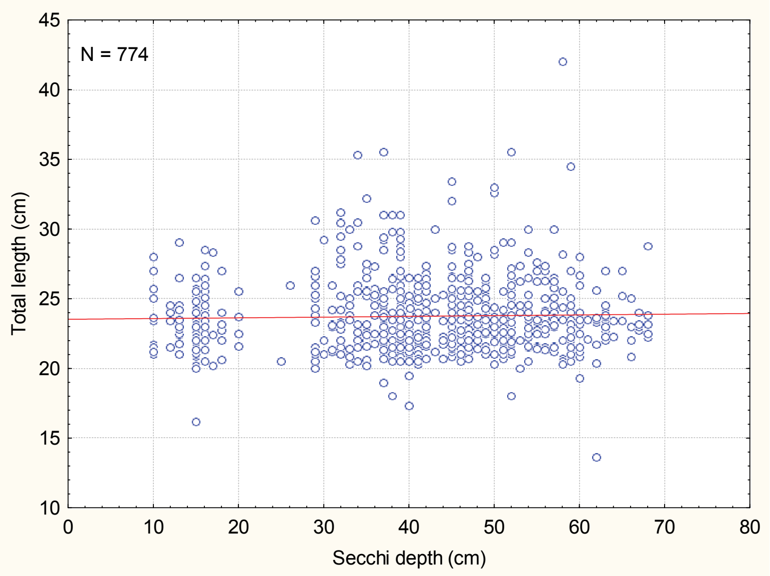


Figure 56. Relationship between total length of *Parachromis managuensis* and secchi depth.

Brycon guatemalensis

The length frequency distribution of both sexes departed from normality (Shaphiro-Wilk, p<0.01) showing a slight positive skewness indicating lower catchability at smaller sizes (Figure 57); thus specimens below 24.0 cm where captured in lower number than expected. Size distribution was significantly different between sexes (ANOVA: F=7.89; p=0.005), being the females larger (mean size 32.7 cm ± SD 5.64) than males (mean size 31.4 cm ± SD 5.0). The maximum length registered for females was 55.5 cm and for males was 49.5 cm. The overall mean length (population mean) of *Brycon guatemalensis* caught during the survey was 32.1 cm ± SD 5.40.

The statistical analysis of the monthly mean length showed significant variability during the year (ANOVA, F=4.113, p<0.001). This mean length varies from 30.8 to 33.0 cm (Figure 58). However, only in September the mean length significantly differ from other months (Post Hoc, p<0.05), but mean length steadily decline from June to September indicating a trend in those months.

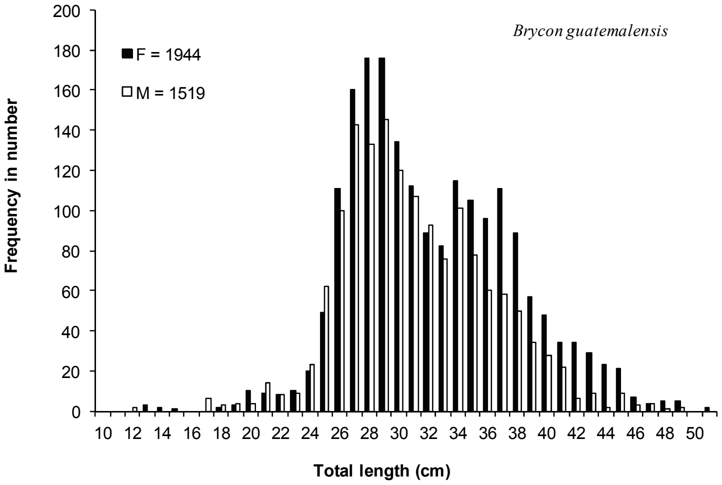


Figure 57. Length frequency distributions (number) of *Brycon guatemalensis*. F: females and M: males.

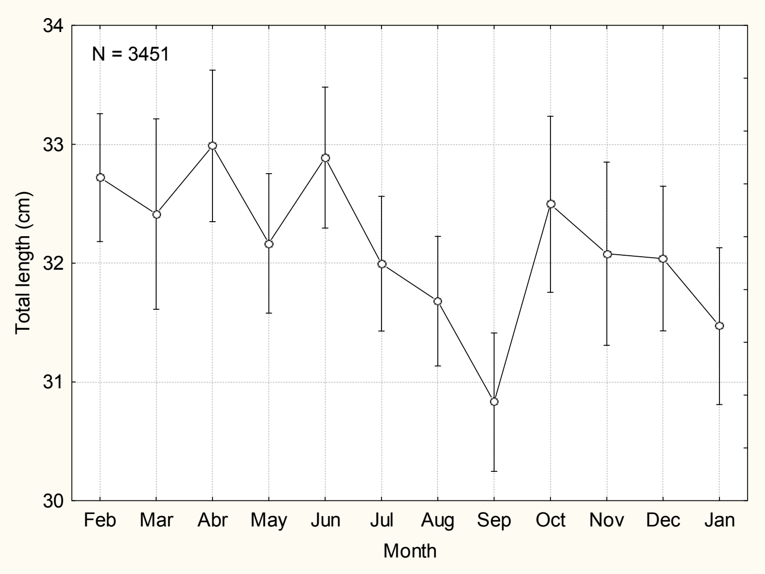


Figure 58. Monthly mean length distributions pattern of *Brycon guatemalensis* during the fishery-independent survey in the Lake Nicaragua. Vertical bars denote 0.95 confidence intervals.

Differences in size distribution were analyzed considering, separately and together, season, macro-zones and depth strata as factors explaining length variability. There were not differences between seasons, and seasons had not interaction with zones and depths (F= 1.75; p= 0.14; Table 24). But otherwise significant differences in size were observed among zones and depth strata (Table 24). Moreover, the interaction between zones and depth was significant (GLM, $p<0.05$, Table 24) indicating size shifts between depths but in differently in each zone.

Table 24. Results of the GLMs for *Brycon guatemalensis*. Total length (cm) as function of season, macro-zones and depth.

	Brycon guatemalensis: Total length (cm)					
Explanatory variables	n	SS	df	MS	F	p
Intercept		3547894	1	3547894	121564.5	0.000
Season	3461	112	1	112	3.8	0.050
Error		101010	3461	29		
Intercept		3550677	1	3550677	126038.9	0.000
Macro-zone	**3460**	**3649**	**2**	**1825**	**64.8**	**0.000**
Error		97473	3460	28		
Intercept		2476208	1	2476208	85846.79	0.000
Depth (m)	**3460**	**1320**	**2**	**660**	**22.88**	**0.000**
Error		99802	3460	29		
Intercept		2375757	1	2375757	86296.18	0.000
Macro-zone		**3162**	**2**	**1581**	**57.42**	**0.000**
Depth (m)		**1944**	**2**	**972**	**35.31**	**0.000**
Macro-zone*Depth	**3454**	**292**	**4**	**73**	**2.66**	**0.031**
Error		95090	3454	28		
Intercept		3504971	1	3504971	124765.4	0.000
Season		47	1	47	1.7	0.196
Macro-zone		**3538**	**2**	**1769**	**63.0**	**0.000**
Season*Macro-zone	3457	297	2	149	5.3	0.005
Error		97116	3457	28		
Intercept		2207227	1	2207227	76524.01	0.000
Season		6	1	6	0.20	0.651
Depth (m)		**1294**	**2**	**647**	**22.43**	**0.000**
Season*Depth	3457	36	2	18	0.63	0.535
Error		99712	3457	29		
Intercept		2057845	1	2057845	74914.31	0.000
Season		5	1	5	0.17	0.684
Macro-zone		**2843**	**2**	**1421**	**51.74**	**0.000**
Depth (m)		**2053**	**2**	**1026**	**37.37**	**0.000**
Season*Macro-zone		150	2	75	2.74	0.065
Season*Depth		16	2	8	0.29	0.747
Macro-zone*Depth		217	4	54	1.98	0.095
Season*Macro-zone*Depth	3445	193	4	48	1.75	0.135
Error		94632	3445	27		

Size was significantly higher (Post Hoc, $p<0.05$) at 5 depth stratum in the northwest and central zones, while there were no differences in size between depth strata 1 and 3, and among all depths in the southeast (Figure 59). Size was also significantly smaller in the northwest zone at all depths and at depth stratum 3 in the central area (Post Hoc, $p<0.05$, Figure 59). The general pattern indicates that size decreased by 4 cm from south to north at all depths and fishes are larger at deeper waters. Figure 60 illustrates this pattern of the mean length distribution in a spatial and environmental scale during February 2005 to January 2006, were it is observed that, during both season (dry and rainy), larger individuals are distributed toward the south-east and the smaller toward the north-west zone, and that larger fishes which appeared particularly during rainy season, are distributed toward “deeper” waters. In the northwest part, specimens with average length smaller than 28.0 cm and as larger a 30.0 cm are present, whereas in the central and south-east the average length of the specimens increase from 32.0 to 38.0 cm and even larger than 38 cm.

The total length of *Brycon guatemalensis* was not correlated with the water turbidity of the lake (r = 0.013; p = 0.444; Figure 61). The analysis performed with the mean length by water turbidity class showed no significant differences (GLM F=2.033, p=0.058).

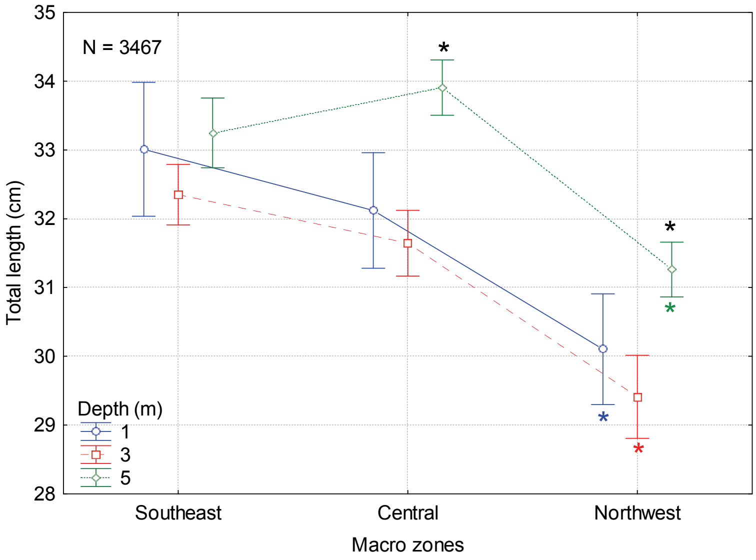


Figure 59. Spatial variations of the mean length of *Brycon guatemalensis* between macro-zones and depth. Vertical bars denote 0.95 confidence intervals. Blue, green and red * denotes significant differences among depth strata within macro-zones. Black * denotes significant differences among macro-zones within depth stratum.

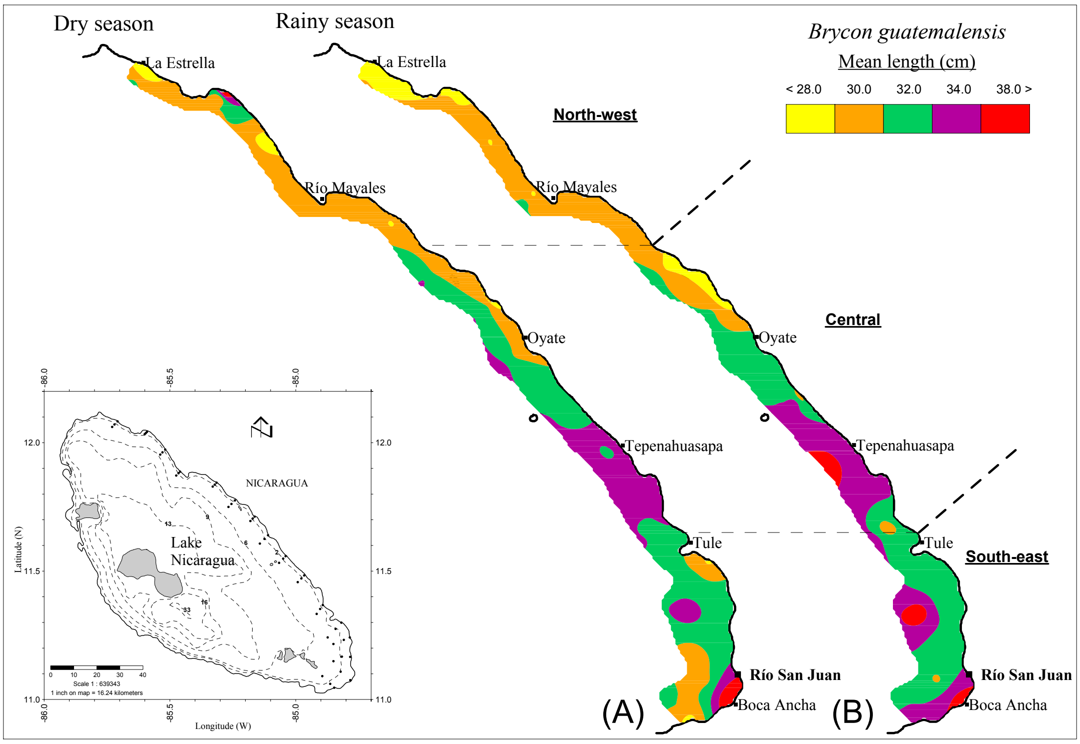


Figure 60. Mean length distributions of *Brycon guatemalensis* in the eastern part of the Lake Nicaragua.

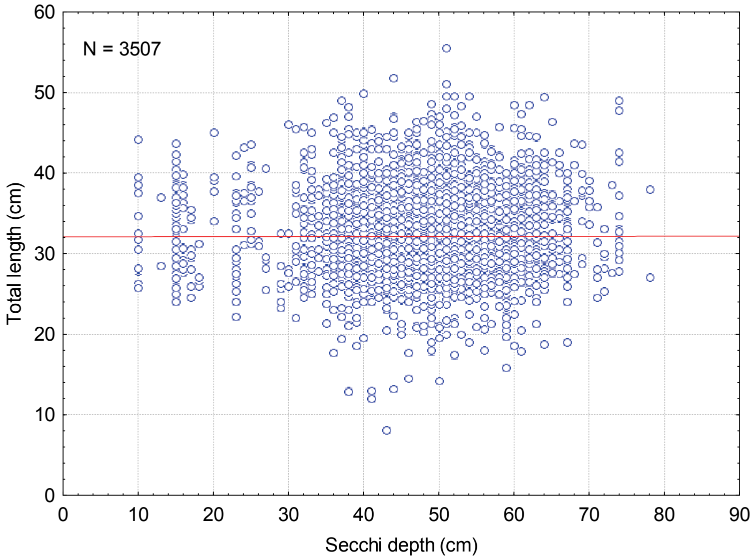


Figure 61. Relationship between total length of *Brycon guatemalensis* and secchi depth.

3.3. Discussion

The richness of fish species in the Lake Nicaragua has been studied previously, which counted till 55 species (Villa, 1982; Astorqui, 1976; Bussing, 1976; Koenig *et al*. 1976; Orellana, 1986). The species diversity studies carried out in 1972 in the Lake Nicaragua indicated that diversity indexes are sensitive to differences in distribution of biomass among species, and demonstrated that fish diversity in the lakes differ between habitats, i.e., between coastal and deeper areas (Koenig *et al*. 1976). In that study the shallow benthic habitat was dominated by *Dorosoma chavesi*, and in decreasing order of biomass were *Cichlasoma longimanus* (*Astatheros longimanus*), *Cichlasoma citrinellum* (*Amphilophus citrinellus*), *Lepisosteus tropicus* (*Astractosteus tropicus*), *Cichlasoma centrarchus*, *Bramocharax bransfordi*, *Neetroplus nematopus* and *Brycon guatemalensis*.

Although the present study does not intend to demonstrate changes in the species richness and assemblage, it is adverted that higher number of species, 26, were identified. This number is considerably lower than most of previous studies, because our study focused only in the eastern side of the lake and used only gillnets, compared with the use of trawl net, bag seine and gillnets in the previous studies. However, it was slightly higher than the number of species (21) identified in 1985-1986 (Orellana, 1986) using also gillnets but with lower mesh size. The differences in catch ratios between previous studies carried out in different zones of the lake (Martínez, 1976; Orellana, 1986; Gadea, 2003) and the present study may be the consequence on using different fishing gear as trawls nets, gillnets and bag seine. But if results from the same gear are compared then it may indicate changes in population structure composition. For example, *Amphilophus citrinellus* represented 23.6 % of the catches in number with gillnets in the coastal areas of the lake (Martínez, 1976), while Orellana (1986) indicated *Dorosoma chavesi* with highest catches ratio (55 %) and only 13 % for *A. citrinellus*. Besides, the author reported 6 % for *Hypsophrys nicaraguensis*, 2 % for *Brycon guatemalensis* and 0.2 % for *Parachromis managuensis*. Gadea (2003) reported, from the extreme southern side of the lake, *B. guatemalensis* as the most important species in the catches (36 %), followed by *A. citrinellus* (27 %), *Atractosteus tropicus* (22 %) and *P. managuensis* (0.5 %). In the present study *A. citrinellus* (43 %) was the most important species (catches in number) followed by *B. guatemalensis* (19 %), *H. nicaraguensis* (11 %), *D. chavesi* (8 %), *A. rostratus* (7 %) and *P. managuensis* (4 %). It seems that the structure of the ichthyic composition and assemblage in the lake has varied since 1972 (Koenig *et al.* 1976) and 1985-1986 (Orellana, 1986). These changes can be related to different level of exploitation of fish stock, thus in 1972, the Guapotes (*P. managuensis* and *P. dovii*), snook (*Centropomus parallelus*) and Sawfish (*Pristis perotteti*) were considered first-class fish whereas Gaspar or Gar (*Atractosteus tropicus*), Mojarra (*A. citrinellus*, *H. nicaraguensis*) and Machaca (*B. guatemalensis*) were considered second-class fish because their low commercialization (Davies & Pierce (1972). In recent years this situation has reversed due to the low abundance of those species once commercialized as first-class. The decreasing abundance in biomass of some species is probably due to the increasing fishing effort as consequence of the growing number of full-time fishers in the lake.

In theory, during a fishing operation with gillnets it is expected an increase of the catches with an increase of the fishing time, i.e., a linear relationship between catches and net soak time. However, the relationship between the catches and fishing effort, expressed in hours, for at least the four main species considered in this study, was asymptotic, which shows in practice a saturation process of the gillnet performance during fishing operation. Hence, the observed operation pattern can be separated in three periods: a first one where catches are very low, which might be related to the disturbances exerted when fishing operation start, and as the fishing hours increase, an increase of catches occur (the second period), reaching a maximum level of catches between 6 and 7 hours. Finally a third period is observed, when a reduction of the catches and CPUEs occur for longer setting times. This last period has been interpreted as a decreasing efficiency of the net when fish accumulate (Kennedy, 1951; Beverton & Holt 1957). This relationship between catches and soak time (effort), has been found in other studies, for example Kennedy (1951) found a clear reduction in the catch per day when nets were allowed to stand for two or three days as compared to their being lifted daily, and Hickford & Schiel (1996) observed about the same numbers of fish caught in 6-hour-day and 15-hour-night settings for four New Zealand reef species, i.e., when catch rates were compared no statistical difference was found between the catch per hour in the long and short settings. Engås (1983) compared catches of blue ling (*Molva dypterygi*a) in gillnets lifted at 1, 2 or 3 day intervals and found no differences in catch per day in two experiments whereas a third experiment showed increasing catch rates with increasing set time.

The fishing gear performance has being related to the net saturation level, because the meshes are occupied by fishes (Hamley, 1975), furthermore, over the fishing period an increasing number of these catching sites may be occupied thereby decreasing the fishing power of the gear over time (Hovgård & Lassen, 2000). These authors have indicated that the interpretation of gillnet CPUEs is hampered by the fact that the gear is characterised by a fixed number of positions where the fish may be caught, i.e., the number of meshes. The net saturation level assumes that the mesh of the net are occupied by fishes (Hamley, 1975; Li & Jiao, 2011), and then saturated. However, visual observation of the girth retained species in this study suggests that nets are saturated at different gear segments depending of the fish species. As the most notorious case *Brycon guatemalensis* was mostly retained at the upper sections of the nets, while lower sections were less occupied by this species and occupied by others. This may suggest that fish swim at basically the same height explaining fish clustering in the net and then saturated at that level, which in time may be related with its benthopelagic behaviour (Froese & Pauly, 2004) and migratory habits (Horn, 1997). On the other hand, because the demersal habitat of most cichlids species (Oldfields, McCrary & McKaye 2006) this are thought to be retained more in the lower level of the net. This observation of fish behaviour may have an interesting implication from a fisheries management and economics point of view, since it can increase gillnet selectivity by using nets of different heights and soaked at different depths. Thus, for example, for catching *B. guatemalensis* fishers would not need the use of net covering the entire water column; instead of that, nets should be shorter and covering only the upper part of the water column which would allow a better and easier fishing operation, reducing costs and bycatch. This empirical observation here pointed out should be considered in multi-specific fisheries, since it would help in the protection of species none commercially but biologically important and to avoid fish discards. Nevertheless, the four species analysed in this chapter showed a very similar saturation point at 6-7 hours. The average soak time was 6.4±0.4 hours showing the validity and appropriateness of the survey design, and hence CPUE was used as abundance index without further transformation (Li & Jiao, 2011).

Gill nets have been widely used in fisheries surveys (Hansen, Schorfhaar & Selgeby, 1998), and CPUE used as an index of fish abundance based on multi-mesh gillnet sampling design, has been used for applied research (European Union, 2000; Sondergaard *et al*., 2005; Diekmann *et al*., 2005). However, the information obtained on the fish stock depends strongly on the choice of sampling methods (Jackson & Harvey, 1997; Jurvelius, Kolari & Leskelä, 2011). Therefore, the use of more than one sampling methods is generally preferred in order to achieve a comprehensive overview of the abundance and spatiotemporal distribution pattern (Kubecka *et al*., 2009). The efficiency of passive types of sampling gear such as gillnets largely depends on both technical and biological factors, including mesh size, net length, soak time, set and life time, gear saturation, fish abundance, morphology, behaviours, the activity of the fish (Beverton & Holt 1957; Hamley, 1975; Olin *et al*., 2004; Rotherham *et al*., 2006). Because of that, gillnet is thought to reduces the accuracy and reliability of CPUE estimates, which may increase the probability of underestimation the real population size and may result in under-exploitation of fish stock (Beverton & Holt 1957; Olin *et al*., 2004; Rotherham *et al*., 2006). Thus, the estimates of fish abundance are accordingly indirect (Hamley, 1975). Because gillnets are considered destructive as they kill most individuals entangled in the meshes if the nets are left for several hours, and that situation has low acceptance by the public and the recreational fishery community (Winfield *et al*., 2009), recently modern hydroacoustics equipment, a sophisticated active fishing technology has evolved (Simmonds & MacLennan, 2005) and frequently applied to sample fish assemblages. This hydroacoustics techniques applied in research on fish abundance in many European lakes have validated CPUE obtained from gillnet sampling. That because the strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes have been observed (Emmrich *et al*., 2012). Thus, very likely in our study the estimated CPUE can be considered as a good index of fish abundance.

However, the behavioural response of each fish assemblages to water turbidity may affect the estimated fish abundance. But a weak or not at all relationship between CPUE and water turbidity was observed. Turbidity may affect fish catchability, i.e., the interaction between fish abundance and the fishing effort (Arreguín-Sánchez, 1996), because of the differences in fish behavioural response to different level of water transparency. From an ecological point of view the change of water transparency is one of the major drivers of lake ecology (Welcomme *et al*., 2010) but the oligomesotrophic (PNUMA-OEA, 1997) characteristic of the Lake Nicaragua seems to preserve good condition for the living resources. From a strictly fishery perspective, the changes in water transparency modifies the net efficiency for some species, through the alteration of fish behaviour. Clearest water allows the fishes to detect the gear reducing fish-net encounters. Moderate levels of turbidity apparently decrease the likelihood that fish will perceive the net material (Kirkland, 1965) increasing catch opportunities. Conversely, reduced light penetration caused by turbidity also alters the fish behaviour by reducing reactive distances, altering foraging behaviour, and decreasing association with substrates, i.e., reducing catch rates (Noggle 1978; Gradall & Swenson 1982; Barrett *et al*., 1992). The reducing reactive distance may applied to *B. guatemalensis* since this is known to be a rapid swimmer because it migratory behaviour (Horn, 1997). This fish need enough visibility to initiate its swimming activity since it seems to swim constantly and sustained, then turbid water do not give the proper condition for this activity, therefore trammel is not expected. However, in our study *B. guatemalensis* catch rate was not affected at all by turbidity, in spite the wide range of turbidity recorded.

The fact of some cichlid species were more caught in turbid waters might be related with the low capacity of those to visualise objects in those waters. Cichlids are probably less adapted to habitat with low water transparency since these fish are visually oriented fish and often associated with transparent water (Lowe-McConnell, 1999; Rodriguez & Lewis, 1997). The low visibility pose has being adverted in haplochromine cichlids in which the decrease of water clarity seems to affect foraging, social interactions (Fryer & Iles, 1972), to hamper mate recognition or even frustrate breeding (Seehausen *et al*., 1998), and also may decrease prey selectivity which result in an increased interspecific competition, that have negative impact on species coexistence (Seehausen *et al*., 2003). Most cichlids are stenotopic (Eccles, 1986), i.e., able to adapt only to a narrow range of environmental conditions, which mean that under unfavourable environmental conditions their distribution and abundance may be restricted. In our study turbidity seems to have affected catch rate of two species only at very high values of turbidity, i.e., less than 10 cm visibility. This situation occurred in less than 5% of the hauls.

Intra-annual variation of the relative abundance index is hypothesised to be strongly influenced by spatiotemporal effects, both horizontal (macro-zones) and vertical (depth), and by environmental factors, i.e., the seasonality of precipitation. Each of these factors independently and significantly determines the abundance index along the studied area. However, the interaction between these factors was in most of the cases also significant indicating a complex fish distribution and seasonal fish movements.

The four species covered in detail in this study are widely distributed in the eastern part of the Lake Nicaragua. The more deterministic factors influencing the spatial distribution of cichlids species was depth stratum and latitude, i.e., macro-zones. These species were more abundant in shallower waters. Depth influences the composition of species in a fish assemblage in floodplain lakes (Rodriguez & Lewis, 1997), due to variation in the hydro-periods (Fernandes, Machado & Penha 2010), i.e., the period of time during which a wetland is covered by water. The greater the depth of a body water, the greater the hydroperiod and, therefore, the greater the time available for the processes of extinction or colonization of the species in the assemblage (MacArthur & Wilson, 1967). The distribution and abundance of cichlids may be also related to the affinity of these species with rocks or rocky areas (Olfields, 2006), that in the lake are located in areas near shore. However, rocky affinity may temporarily change when searching for food in open waters and during spawning season, the last may apply particularly for *H. nicaraguensis* which deposit the eggs in sand depressions (Conkel, 1993).

The horizontal and vertical distribution of abundance of cichlids assemblages is probably influenced by river drainages along the eastern coast and the different ecosystems found in the lake as sandy, muddy and rocky areas, and edge vegetation (INFONAC, 1974). According to INFONAC (1974) most of the lake bottom is muddy, regardless of its depth. However there are several rocky patches in the southeast of Ometepe Island, near the mouth of the Rio Mayales and around the Solentiname Archipelago. Particularly, the cichlids assemblage (*A. citrinellus*, *H. nicaraguensis* and *P. managuensis*) and *B. guatemalensis* higher abundance found in the surrounding area near the mouth of Río Mayales, with monthly average flow is 6.33 m^3/s, might be consequence of the combination of its undiscovered ecological importance for fish development and the rocky areas located near the river mouth. The higher abundance of *A. citrinellus*, *H. nicaraguensis* and *B. guatemalensis* in the extreme southern part of the lake is associated to the influence of the San Juan River, which has an outstanding ecological importance (Bussing, 2002; Villa, 1982; PROCUENCA-SAN JUAN, 2004).

Although seasonality has been shown to affect the distribution and abundance pattern of these three cichlids, its influence was negligible in *A. citrinellus* but certainly important in *H. nicaraguensis* and in less extent in *P. managuensis*. Most studies on seasonal influence on the cichlids abundance have being observed in rivers where dry or rainy periods induce rapid changes in the level of water column, i.e., flooding during rainy season and drying up during dry season. In lentic environments as lakes those effects occur moderately since these are closed systems consisting of defined body water (Welcomme *et al*., 2010). Yet, this moderate influence was evident in our study, particularly for *H. nicaraguensis* and *P. managuensis* that showed lower relative abundance during rainy season. Although these cichlids apparently do not undergo major reproductive migration, they may move in a horizontal plane colonizing other rocky areas along the shore, disperse in the whole area or even move into tributary rivers (Lowe-McConnell, 1999). Some cichlids move out from the lagoon onto the floodplain during the flood at the beginning of the rainy season in Cuiabá River, Brazil (Fernandes, Machado & Penha, 2010). The relative abundances of cichlid assemblages in some neotropical areas were distinct between the seasons, which indicate that neither persistence nor stability was maintained on a seasonal basis (Lourenço *et al*. (2012).

Season and depth are the main factors influencing abundance of *B. guatemalensis*. Largest abundances were found in the southeast and northwest side, during both seasons (dry and rainy), but highest abundances occurred in rainy season at shallower waters, and lower abundance in the central part the area. Seasonality seems to strongly modulate the migratory behaviour of this species from rivers to the lake environment and vice versa. The increasing abundance during rainy season is more evident near the areas of rivers drainage. Rivers have been known to be very important habitat for potamodromous (migrating within freshwater only) species as *B. guatemalensis*, which inhabits the lakes of Nicaragua and exhibit a migratory behaviour into tributary rivers (Drewe *et al*., 2003) to spawn (McLarney *et al*., 2010). The seasonal migratory behaviour is confirmed by a parallel study carried out during 2005 in the San Juan River (RSJ), where major abundances of *B. guatemalensis* were found upstream of the river during dry season, i.e., from November to March (PROCUENCA-SAN JUAN, 2004). This finding indicates that probably the same pattern occur in other tributary rivers located in the eastern side of the lake. Similar pattern was also found in *Brycon behreae*, which during highest flows (rainy season), it comes out of the open regions of Térraba River, Costa Rica, and concentrates in pools located at its shore and in the streams (Ribeiro & Umaña, 2010). Low flows are directly associated to the absence of rainfall, i.e., dry season, whereas high flow is the result of rainfall during rainy season. The low and high abundance of *Brycon behreae* is in line with the pattern of the abundance index observed in *B. guatemalensis* in the lake (open waters), where lower and higher abundance index were found in dry season (low flow) and in rainy season (high flow), respectively. Seasonality has been identified as the main factor influencing the abundance of many other characoid fresh water fishes in other neotropics areas (Kramer, 1978b). According with Magalhães, Batalha & Pereira (2002), large scale events such as dry or rainy seasons usually alter the ecological structure of communities through mortality and mass migrations, but the season have also local effects over the habitat affecting abundance (Inoue & Nunokawa, 2002).

The abundance fluctuation in *A. citrinellus* and *B. guatemalensis* during the dry season, and the lower abundance of *H. nicaraguensis* at the onset of the same period may respond to the particular dynamic of the lake during this season. From October to March strong wind (The Papagayo wind) blows through the gap in the mountain ranges of Central America and over the lakes of Nicaragua (NASA SeaWIFS 2000-2001). This wind dominates the entire southern side of Pacific Nicaragua, with velocity in the order of 7 m/s and occasionally reaching speeds greater than 10 m/s (Brenes, Hernández & Gutiérrez, 1998), and in turn stress over the entire water surface of the lake. The unidirectional wind stress over the entire lake and affect the entire water column of the coastal area because the shallowness of this area. This atmospheric condition might induce the cichlid species to seek for shelter and alter the migration pattern in *B guatemalensis* causing in extreme cases even a movement out of the area. The bad whether condition is probably responsible for some capture failures because well of fishing gear malfunction when trammel the net, well a lack of fish movement. It may explain the occurrences of zero-captures in dry season in the order of 65 %; against 35 % during in rainy season where zero-capture occurrences may be also the result of some strong storms occurred during the period of study. During rainy season the lake water level slowly but steadily increase due to direct rainfall over the lake and the river discharges, the last affecting more the adjacent areas of the river mouth. The changes in the lake ecosystem during rainy seasons are reflected in the gaining depth because the water level rise and the increasing water turbidity because suspended sediments are transported by river flows into the lake. These two factors seems to favour the occurrence in open waters of *B. guatemalensis* but the gradual decline in abundance of *H. nicaraguensis* and *P. managuensis* as they occupy flooded areas in the lake shore. Undoubtedly, fish species in the lake distribute according to depth, being the factor that best explain the distribution pattern within the studied area for all species analysed. In the case of *B. guatemalensis* largest abundance were found at bigger depths, i.e., at 3.0 and 5.0 m strata. But this vertical distribution pattern is also influenced by season. This is an expected pattern giving the rise and fall of the lake water level, as a consequence of dry and rainy season.

There was a clear spatial size distribution in all studied species. Larger fishes are found in the south-east and to a lesser extent in the central zone of the lake, whereas in the north-west area the individuals were smaller. This pattern might be related to the influence of San Juan River (Rio San Juan-RSJ), which is the natural out-flood (drainage) of the lake, connecting the lake with the Caribbean Sea. The river, from an ecological point of view, is the most important river in the region because its extension and habitat diversity, as well the high biodiversity, providing optimal conditions (temperature, solar illumination, currents, oxygen, availability of food etc.) for growing and reproduction of many species (Bussing, 2002;_Villa, 1982). Beside this, it is known that freshwater fishes exhibit home range or homing affinities, daily or seasonal movement pattern or longer-distance migrations, which are considered to be truly “autoecological”, because these patterns are more related with searching for optimal environmental conditions (Matthews, 1998). This behaviour may explain the observed size distribution pattern.

The selectivity of the gear used during the surveys prevent us to discern where the juveniles of each species inhabits, i.e., in the lake or in the River. That because size of *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* and *B. guatemalensis* smaller than 14.0, 11.0, 17.0 and 20.0 cm, respectively, were not taken but the sampling gear used. A study carried out along the San Juan River using gillnets with equal mesh size produced similar results, i.e., very low catches of smaller sizes (PROCUENCA-SAN JUAN, 2004). Nevertheless, it was also observed a differential vertical size distribution. Because the shape of the lake, this may be connected directly with depth preferences (different substrates) or with distance to the shore. In any case it is clear that larger fish are found in the deeper waters studied (3-5 m), excepting for *P. managuensis* which larger size has preferences for shallower water (1 to 3 m depth). In shallow waters or inshore areas of the lake, a relative high proportion of specimens were below the mean length estimated for each species, i.e., 64%, 41%, 70%, 50%, in dry season and 66%, 57%, 83%, and 59%, in rainy season, for *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* and *B. guatemalensis*. This overall pattern of smaller size fish inhabiting in shallower waters, particularly for Mojarras (included *A. citrinellus* and *H. nicaraguensis*) and *B. guatemalensis* is in line with previous studies covering the entire lake, where mean length of mojarras and *Brycon* in the coastal area was 19.0 and 37.6 cm, respectively and in deeper water 21.5 and 46.6 cm, respectively (Orellana, 1986), which may indicate that fishes are recruited to the fisheries in the lake. In spite of larger fish inhabiting mainly the southeast, larger fishing effort are located in the north-west zone. This important aspect will be discussed in Chapter 6.

Larger size ever reported in the lake on *B. guatemalensis* was 61.7 cm captured in the southeast area close to RSJ (Gadea, 2003). This was similar to the recorded maximum size of 59 cm (IGFA, 2001) and in the present study (2005-2006), 55.5 cm, captured in the south-east zone. The results of the most recent study in RSJ showed that most of the specimens captured in the river ranged between 35 to 40 cm, with maximum length captured of 60 cm, mainly captured upstream, i.e., the closer area to the lake, whereas downstream there was a tendency to find smaller size, where recruitment of many species is considered to occur (PROCUENCA-SAN JUAN, 2004). On the other hand, from sport fishing in RSJ have been reported the capture of a specimens of 2.5 kg which is equivalent to 52 cm (MACHACA, 2011), and from Costa Rican rivers were reported specimen up to 50 cm and 4.3 kg (Bussing, 2002). These findings may support the hypothesis that the presence of larger fish in the south-east and central zone are influenced by the San Juan River because the migratory movement of the species upstream towards the lake. The migratory habits upstream of *B. guatemalensis* for spawning or perhaps feeding has been already pointed out (Horn, 1997); very likely associated to the precipitation seasonality (Lowe-McConnel, 1987).

CHAPTER 4: Reproductive Strategy of *Brycon guatemalensis.*

4.1. Introduction

The reproductive strategy is the combination of reproductive traits characteristic of individuals belonging to the same gene pool. Some traits may be inflexible and show little variation, while other traits may be plastic, so an individual can exhibit a wide range in their expression. The different expressions of a trait in response to environmental changes are the tactical responses of the individuals to those changes (Wootton, 1990). On the other hand, Fostier (2008) defines reproductive strategy as the way in which a species allocates or budgets energy to produce viable offspring. In all the definitions found are clearly identified that the aim of each species is to produce the maximum amount of offspring. Teleosts fish have developed a large variety of reproductive strategies and reproductive behaviours, e.g., ranging from mass spawning to parental care, from strict gonochorism (separate sexes) to simultaneous hermaphroditism, and from oviparity to viviparity, and one usually distinguishes the r-strategy, in which energy is invested in a multitude of offspring that receive little or no parental care, and the K-strategy, wherein energy is invested in a few, large offspring that require considerable parental care (Fostier, 2008).

In some marine fishes have been described and identified the most common reproductive strategies related to the oocytes development, ovary organization, recruitment of oocytes and spawning pattern (Murua & Saborido-Rey, 2003). As many marine and brackish teleosts, freshwater fishes exhibit a great variety of reproductive strategies. Teletchea *et al.* (2009) defined 10 homogeneous clusters based on 29 reproductive traits such as oocyte size, egg adhesiveness, age and length at sexual maturity of females and males, absolute fecundity (eggs/females), relative fecundity (eggs/kg), maximum gonado-somatic (GSI) value, spawning (season, duration, temperature, water type, substratum, site) and many others. Within each strategy the variation of the traits outlines the variable reproductive potential of the species, stock or an individual. Thus, the stock reproductive potential can be defined as the capacity of a population to produce viable eggs and can be considered as the main outcome of a reproductive strategy (Trippel, 1999; Murua & Saborido-Rey, 2003).

In tropical fresh water environments, a great diversity of fishes from different families with different reproductive strategies and behaviour is found; including the Characidae, Cyprinidae and Siluriformes families. The Characidae family which includes *Brycon guatemalensis*, is a large and diverse family of freshwater subtropical and tropical fish (Oliveira *et al.,* 2011) which a great diversity of reproductive behaviour. This vary from groups of fishes with terrestrial spawning behaviour that spawn in foam nests (Kramer, 1978a), with non or weakly adhesive eggs (Rizzo *et al*., 1998; 2002), to fish spawning in aquatic environments on aquatic plants, which is the most common pattern (Brederc & Rosen, 1966) or laying the eggs in excavated nests in the sand substratum as in *B. guatemalensis* (Bussing, 2002).

Some comparative analyses have shown that some oogenesis patterns are common to fishes of the same family in Neotropical freshwater fishes (Bazzoli & Rizzo, 1990). The eggs surface has so far been examined only in a few Characiformes and Siluriformes (Rizzo *et al*., 1998) and reproductive strategy (sedentary or migratory) and eggs adhesiveness (adhesive, weakly adhesive and non-adhesive) have been also examined on 12 species of the Characidae family (Rizzo *et al*., 2002). The structure of the jelly coat that provides adhesiveness has been recently studied (Weber *et al.,* 2012).

Reproductive behaviour adopted by the Characidae family has been associated with the diversity of the environmental conditions where the species inhabit. The reproductive tactics differ even between strong resemble species in molecular characteristic, morphology and ecology as *B. guatemalensis* and *B, chagrensis* (PANCANAL, 2011), and with other parental species as *B. behreae* and *B. chagrensis*, *B. petrosus*, e.g., *B. guatemalensis* spawn in sand ground nests, whereas *B. petrosus* in a very similar environmental conditions spawn in humidity land (Bussing, 2002). However, many reproductive characteristics of *B. guatemalensis*, such as the duration and timing of the reproduction in response to environmental conditions, remain still unknown. Besides, the duration and timing of the reproduction is altered within the family in response to environmental conditions, also food availability, predation, inter an intra-specific competition and the species' social system is altered, e.g., some species belonging to the same family spawn in dry season, whereas other in rainy season, the diversity of seasonal patterns in this small group of related species presents some fascinating problems for the comparative study of life history strategies (Kramer, 1978a).

Because the very few information found in literature on *B. guatemalensis* reproductive behaviour, comparative studies of life history strategies are difficult to perform. The objective of the present work is to study the female reproductive strategy and traits of wild Machaca, *B. guatemalensis*, using histology and focusing in three key reproductive parameters in fisheries management: the reproductive cycle, the ontogenic maturation and the fecundity.

4.2. Results

The ovaries of *B. guatemalensis*, as many teleosts, are cystovarian type, i.e., the oocytes are released directly into the lumen of the ovary and then to the oviduct. Then a real lumen is observed as the ovary has a clear ovarian wall or membrane. Inside the ovary, complex folds are observed where the follicles are observed connected to the supporting tissue or stroma, blood vessels and nerves.

4.2.1. Oogenesis

The female gametogenesis is described based on histological analysis carried out on 371 ovaries. The different oocytes development stages were identified and described, and in general it follows a typical teleost gametogenesis. The oocyte development can be divided in several stages. Within the primary growth we have focused only in the most advance stage, the so-called perinucleolar stage. Then we have considered the cortical alveoli, vitellogenesis and follicle maturation stages.

Perinucleolar stage (PG)

The oocytes at this stage were observed in every fish analysed, as corresponding to an iteroparous species. In 66 ovaries only these oocytes were detected, indicating the fish was immature or was in regenerating phase (see 4.2.2. *Reproductive cycle*). Typically these oocytes showed a basophilic blue stained colour (with H&E), a spherical nucleus with multiple nucleolus in the periphery of the nucleoplasm and the perinuclear ring is clearly visible (Figure 62A). The oocytes diameter at this stage ranged from 43.5 to 186.8 µm (Table 25).

Cortical alveoli stage

The cortical alveoli stage (CA) is characterized by the occurrence of visible (under light microscope) vesicles or alveoli spread in the cytoplasm. However, it was noticed that the vesicles or alveoli were not clearly visible in the cytoplasm, having small size (Figure 62 B). This circumstance does not seem to change until the onset of vitellogenesis. To overcome the difficulty of observation of these structures and define clearly this stage, it was necessary to look for other relevant characteristics of the oocytes at this stage, as the increase in size of the oocyte and follicle thickness, with respect to the size and follicle thickness of oocytes in primary growth stages. In 181 ovaries cortical alveoli was the most advanced development stage. But in 187 females CA oocytes were visible within the ovary. The diameter of the oocytes in CA stages ranged from 159.7 to 370.1 µm (Table 25).

Vitellogenesis

Basically the whole vitellogenesis was considered in a single stage (VIT1) ranging from the first occurrence of yolk in the cytoplasm until the first signs of follicle maturation were visible (see next stage). In 42 females this stage was the most advance stage observed within the ovary, but 67 ovaries had oocytes in this stage. During the whole stage the follicle envelops keep a round shape that became irregular when the oocytes reach maturation (VIT2) (Figure 62 C). Yolk progressively accumulates around the nucleus and spread towards de periphery. Clear and large vacuoles are observed as a ring around the yolk. This ring is gradually constrained into the oocyte periphery. During this process the oocytes enlarge from 357.1 to 1140.1 µm (Table 25).

Final vitellogenesis

This is a key vitellogenic stage (VIT2) defined here as an oocyte in which yolk accumulation is basically completed; numerous large yolk globules fill the cytoplasm, the oil droplets are constrained to the periphery of the cytoplasm (Figure 62 C). The VIT2 oocyte should have the necessary receptors for the maturation-inducing hormone and thus is able to progress to follicle maturation, although this is not detectable in histological sections. However, the follicle wall and the chorion itself become irregular at this stage facilitating their recognition. In 82 ovaries this was the most advanced stage, but VIT2 were observed in 104 ovaries. The oocytes at this stage ranged from 555.5 to 2004.2 µm (Table 25).

Follicle maturation

During maturation the lipid and protein yolk droplets coalesce and both seems to increase in size, but the complete fusion of these organelles does not occur. The nucleus initiates its migration from the oocyte centre to the animal pole (Figure 62 D) conforming the germinal vesicle migration (GVM) stage that ends when the germinal vesicle breakdown that for practical purposes we consider within GVM stage. The oocytes in GVM range from 686.5 to 2303.8 µm (Table 25). GVM is the only stage indicating oocyte maturation since no oocytes hydration was evinced through the whole observations.

Although the range variation of oocytes diameter of each developmental stage overlaps (Table 25), significant differences in mean oocyte diameter (ANOVA: F=1180.796, $p<0.05$) was observed (Figure 63).

Table 25. Oocytes diameter of the different oocyte developmental stages (histological determined) in ovaries of *Brycon guatemalensis*.

		Oocytes diameter (µm)		
Stages	N	Min	Max	Mean ± SD
PG	106	43.52	186.85	107.63 ± 27.34
CA	237	159.72	370.13	259.13 ± 39.44
VIT1	226	357.15	1140.06	619.19 ±137.49
VIT2	102	555.48	2004.20	1365.01 ± 350.74
GVM	100	686.52	2303.82	1595.24 ± 411.51
	771			

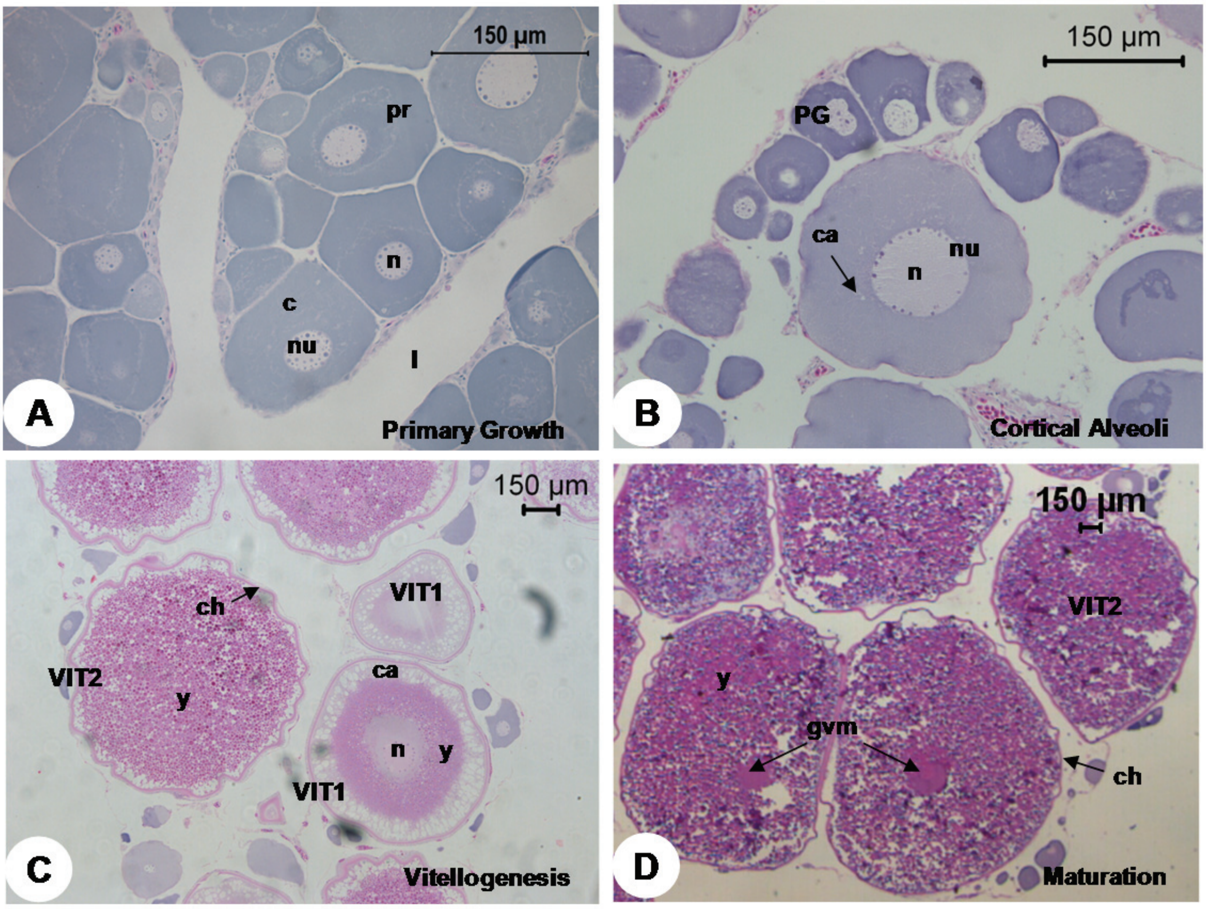


Figure 62. Histological section of the ovary showing **A**: Oocytes in Primary Growth stages (PG) or previtellogenic: c: cytoplasm; n: nucleus; nu: nucleolus; l: lumen; pr: perinuclear ring. **B**: Oocytes in Cortical Alveoli stages (CA). PG: Primary Growth oocytes; ca: cortical alveoli; n: nucleus; nu: nucleolus. **C**: oocytes in Vitellogenesis stage. ch: chorion; n: nucleus; VIT1: initial or early vitellogenesis; VIT2: advanced or late vitellogenesis or advanced vitellogenesis; ca: cortical alveoli; y: yolk. **D**: oocytes in maturation stages. ch: chorion; gvm: germinal vesicle migration or migratory nucleus; VIT2: late vitellogenic oocytes or advanced vitellogenesis; y: yolk.

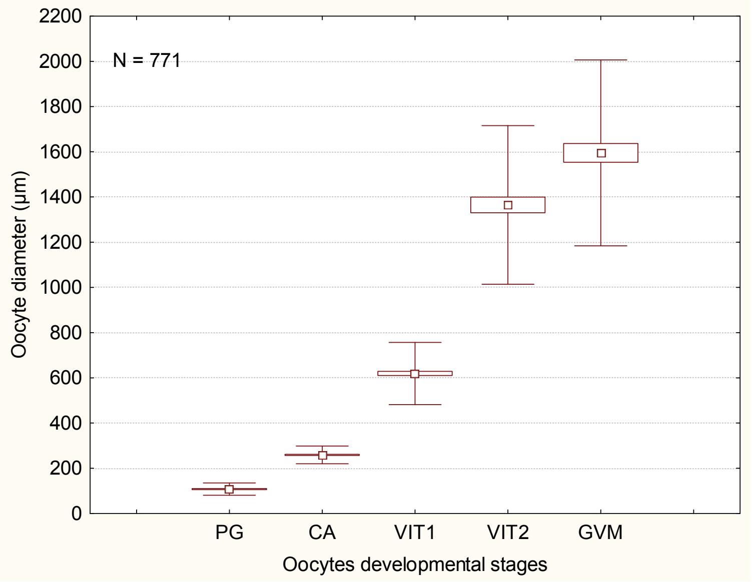


Figure 63. Oocytes development stages in the ovaries of *Brycon guatemalensis*. Mean (midpoint); Mean ± SE (Box); Mean ± SD (Whisker).

The follicle and oocyte envelopes

The oocyte membrane or oolema is visible at light microscope at each stage of development in spite of its thinness. The zona radiata becomes evident during vitellogenesis, with an average of 17 µm of thickness. Rapidly the two layers can be differentiated, the zona radiate interna being stained iridescent red colour with H&E stain and the zona radiata externa, striated (pore canals) layer pink stained (Figure 64 A). In VIT2 oocytes, although there is no degeneration of the zona radiata externa, under the microscopic observation it seems more translucent (Figure 64 B). The follicle layers surrounding the oocyte are observable in all stages of development, but only as small granulosa layer in PG and CA stages. But only when vitellogenesis begun the theca cells becomes discernible, being thinner than the zona radiata (Figure 64 B).

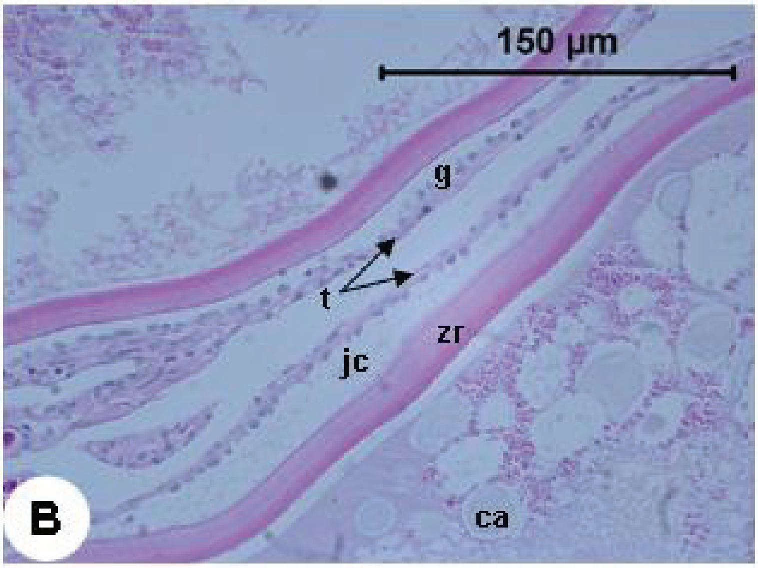


Figure 64. Histological section of the ovary showing the follicle envelops. A and B: ca: cortical alveoli; g: granulosa layer; i: zona radiata internal; jc: jelly coat; ou: zona radiate external; t: theca layer; zr: zona radiata or chorion; y: yolk.

Surrounding mucus

Through histological observation of follicles envelops of oocytes in final vitellogenesis stages (VIT2) it was identified a like mucus jelly coat between the zona radiata and the theca layer (Figure 64 B). This was macroscopically visible as translucent mucus type surrounding the oocytes (Figure 65) within the ovary that hindered the separation of oocytes out the ovary for counting in fecundity analysis, even when washed out with fresh water, indicating that its function very likely is to keep together the clutch of ovulated eggs.

Postovulatory follicle

The postovulatory follicles (POF), which in short are the follicle remaining tissues after ovulation, were observed only in ovaries where dominated oocytes in advanced vitellogenic stages (VIT2). The POF prevalence was very low, observed in three females in August and in one female in September, October and January respectively. In most of the cases these structures were observed in latest stages of degeneration which difficult its correct identification, because can be confused with β-atresia oocytes (Figure 66).

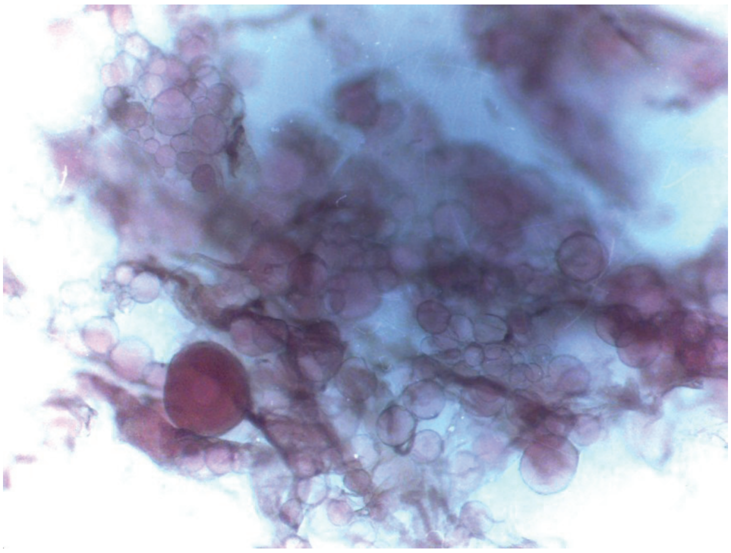


Figure 65. Oocytes surrounded by mucus.

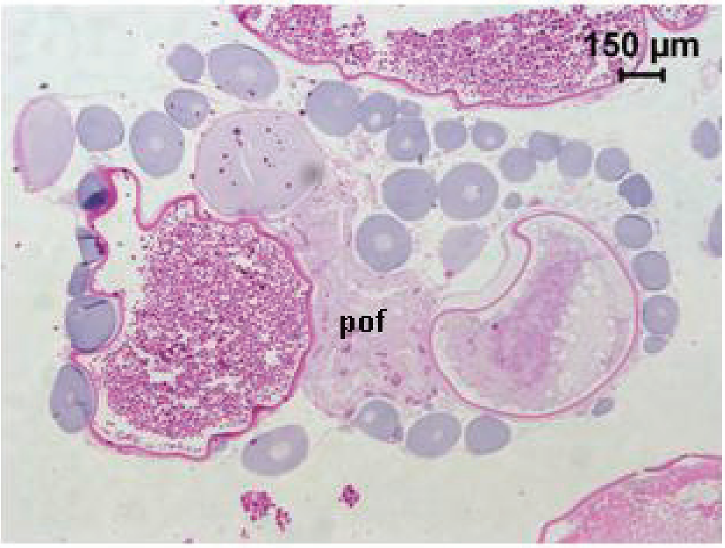


Figure 66. Histological sections of fish ovary tissues showing postovulatory follicle (pof) structures.

Atretic oocytes

Atretic oocytes were found at low prevalence (4.7% of the analysed females) and at different rate of resorption (Figure 67A and B). But most of the atretic oocytes were observed in very late alpha (α) stage. Atretic oocytes were observed in ovaries with VIT2 and GVM as the most advanced stages, but also in one 28 cm female in which the prevailing oocyte stage was cortical alveoli (pre-vitellogenic). Atretic oocytes were evident during the whole spawning period (July to February), and generalized atresia was evidenced in ovaries collected at the end of December and in January, in specimens with advanced yolked oocytes (VIT2). The main characteristic observed was the chorion fragmentation and the complete absence of follicular epithelium.

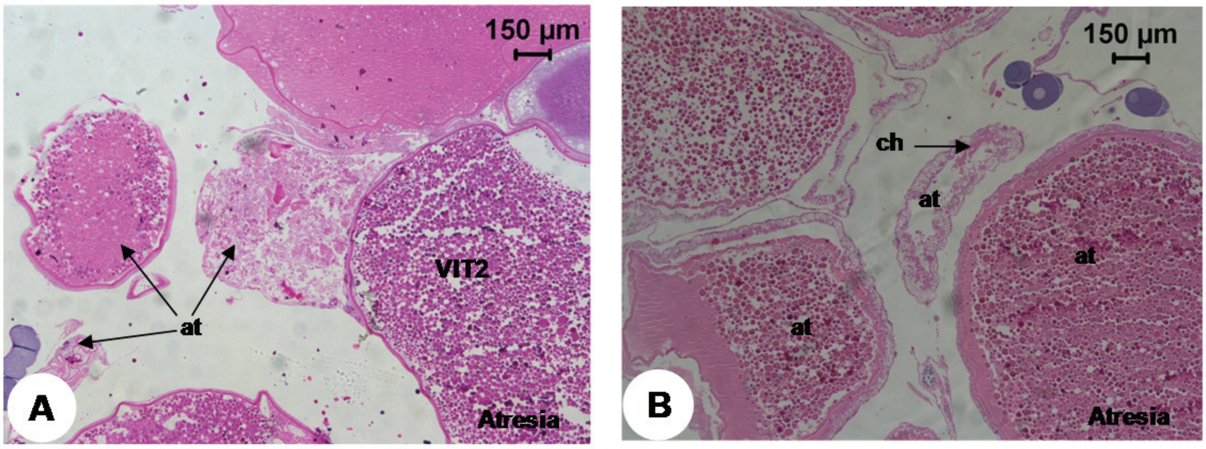


Figure 67. Histological sections showing oocytes in early (A) and late (B) atresia stages. ch: chorion; at: atretic oocyte; VIT2: final vitellogenic oocyte.

4.2.2. Reproductive cycle

On the base of the most advanced oocytes developmental stages in each ovary as being oocyte in PG, CA, VIT1, VIT2, GVM, and the presence of postovulatory follicles (POF) and atretic oocyte identified and described in previous section, females ovaries and consequently the female reproductive phase were categorized as Immature (I), Developing (D), Spawning capable (SC), Actively spawning (AS), Regressing (Rgs) and Regenerating (Rgn) (Table 26).

Table 26. Female reproductive phases as used in this study for *Brycon guatemalensis*.

Reproductive phase	Description	N
Immature (I): Never spawned	The most advanced oocyte stage observed in the ovary is Perinuclear stage (PG)	51
Developing (D): Females in the onset of maturity	Oocytes in cortical alveoli (CA) and/or initial vitellogenic (VIT1) stages are the most advanced stages in the ovaries	209
Spawning Capable (SC): Females are developmentally and physiologically able to spawn in the current annual cycle	The most advanced oocytes stage observed in the ovary is Final vitellogenesis stage (VIT2)	61
Actively Spawning (AS): Imminent spawning during the current annual cycle	The oocyte showing the migratory nucleus or migratory germinal vesicle (Follicle maturation -GVM-) is the most advanced stages observed in the ovary: Post-ovulatory follicles might be present as well	21
Regressing (Rgs): Recent spawning cessation	Atretic oocytes present in ovaries with VIT2 and GVM oocytes	15
Regenerating (Rgn): Females sexually mature but reproductively inactive, reorganizing the ovary for the next breeding season	Perinucleolar oocytes are present but muscle bundles, enlarged blood vessels, thick ovarian wall are observed	14
	Total	371

Temporal dynamic

The reproductive cycle is described analyzing the reproductive phases along one year, from February 2005 to January 2006. During this period, females in Developing were the most observed phase (61.4% of all mature females), and were the most frequent in all analysed months except April and May (Figure 68). The spawning season, defined by the presence of spawning capable and actively spawning females, was relatively long, extending from July (during the rainy season) till February (during the dry period). The highest proportion of specimens in SC phase were observed in July and August (28.8 and 32.7%, respectively), decreasing the spawning activity, although still high, in September to December (14.8 % on average) while the lowest activity was observed in January-February (4.7%). The proportion of specimens in the AS fluctuated along the spawning season, but major peak was observed in October (17.6 %) and the lowest in September (2.0 %). While regressing (Rgs) females were observed all along the spawning season, regenerating (Rgn) coherently observed from February to August (except March). However, due to low sample size in March-June the analysis should be interpreted with caution, especially as spawning may initiate earlier.

Postovulatory follicles (POF) were observed in only 6 out (7.3 %) of 82 ovaries in SC and AS phases, and they were collected in August (n=3), September, October and January (n=1 in each of them). In most of cases these structures were at very advanced degeneration stage. Atretic oocytes were observed in 15 (4.7 %) out 320 mature specimens, one in D phase (in August) corresponding to a specimen of 28 cm length; nine in SC phase (from July to January) and five in AS phase (in February, August, October and December), all these specimens ranged from 29 to 44 cm length. Massive atresia was only observed in two specimens in SC phase of 31.4 and 33.4 cm length collected in December and January, respectively, most of the atretic oocytes were observed in very late alpha (α) atresia.

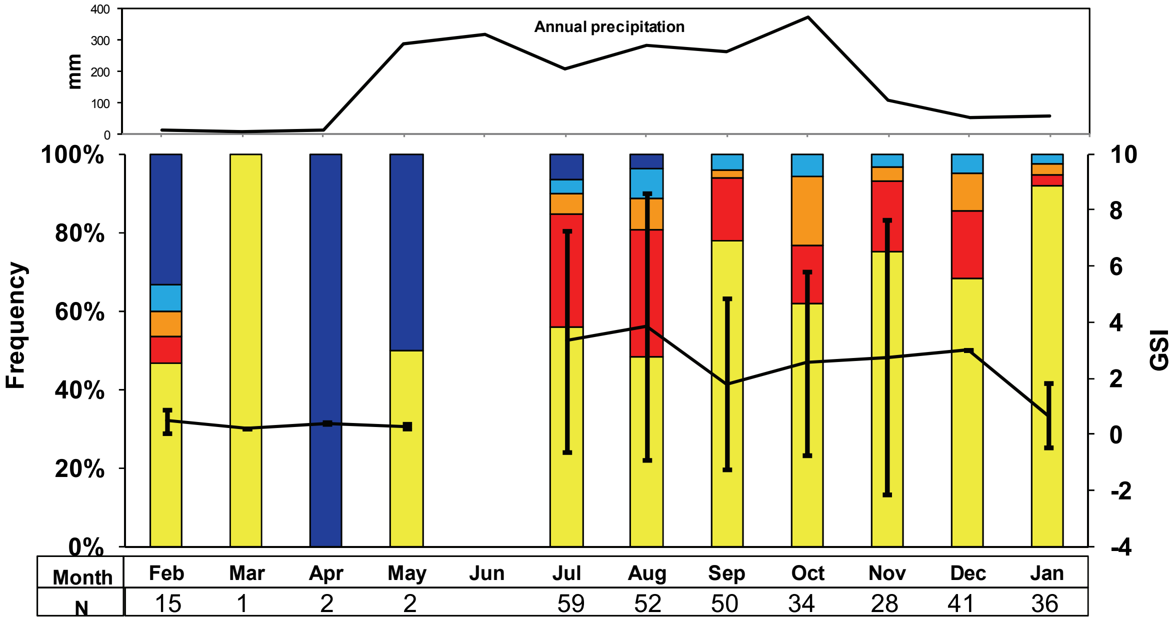


Figure 68. Frequency of incidence of reproductive phases for mature females of *Brycon guatemalensis* (N=320; Bars). Reproductive phases: Developing-D (yellow); Spawning Capable-SC (red); Actively Spawning-AS (light orange); Regressing-Rgs (blue sky); Regenerating-Rgn (blue). Mean monthly variation Gonadosomatic index (GSI: N=240) (solid black line) and standard deviation (whiskers). Upper panel shows annual precipitation in millimetres (mm).

Gonadosomatic index

The mean value of Gonadosomatic index (GSI) oscillated from 0.24 to 3.87 during the annual reproductive cycle (Figure 68), being higher from July to December, coinciding with the spawning season. The GSI decreased from December to May, when the number of female in SC and AS phase decreased and females in Rgn phase increased. The GSI pattern coincides with the SC frequency, with the highest values observed in July-August (above 3), decreasing to an average of 2.5 from September to December. Nevertheless, GSI did not vary significantly among month (ANOVA: F= 1.833, p> 0.05). However, GSI differences were significant when dry (November to April) and rainy (May to October) periods were compared (F= 4.566, p< 0.05), being higher during rainy periods (Figure 69).

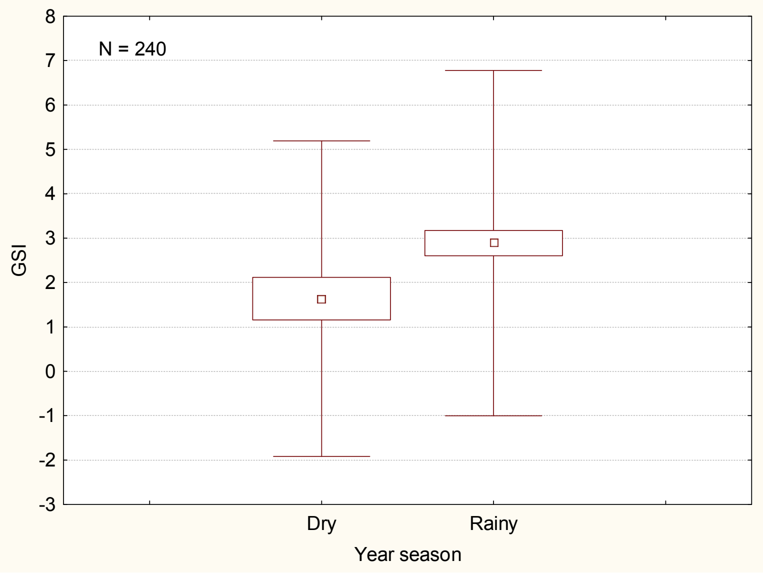


Figure 69. Gonado-somatic indexes (GSI) variation in *Brycon guatemalensis* in relation with the dry and rainy periods of the year. Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker).

The relationships between the somatic variable GSI and female body length are shown in Figure 70, and the obtained statistical parameters in Table 27. The linear regression pooling all reproductive phases (N=239: D, SC, AS and Rgn) was significant ($p<0.05$), but with rather low determination coefficient ($r^2= 0.08$), due to the high variability of GSI at size (Figure 70 A), likely because differences associated to reproductive phases, thus separate regression analysis was performed for each phase (Figure 70 B). The determination coefficient in each case analysed was very low and no significant relationship were obtained, except in the D phase (Table 27), but still with low determination coefficient (r^2=0.05). The relationship between GSI and body length of females in SC and AS phases (N=69) was higher, r^2= 0.24, and significant ($p < 0.05$) (Figure 70 C).

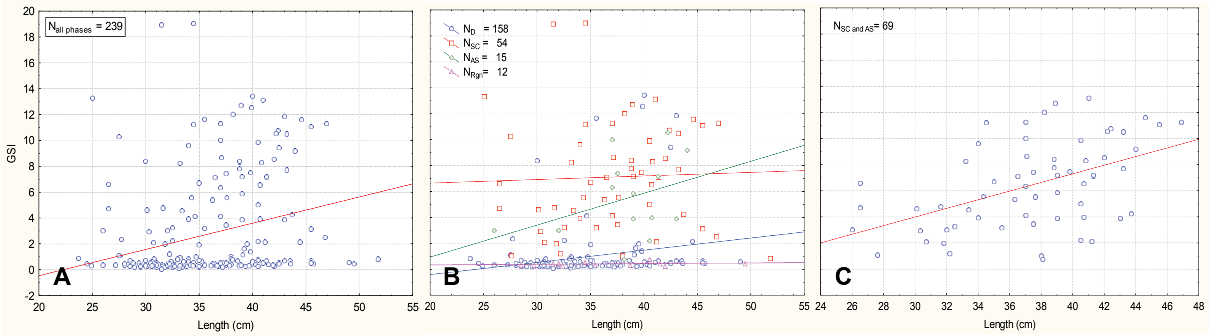


Figure 70. Relationship between GSI and length, considering the reproductive phases: Developing (D), Spawning capable (SC), Actively spawning (AS) and Regenerating (Rgn) phases.

Table 27. Statistical parameters of the relationship between gonadosomatic index (GSI) and length (cm) for females of *Brycon guatemalensis*: Number on specimens in the analysis (N); coefficient of determination (r^2), statistical significant test (p-value) and the linear regression equation.

	Length (cm)				
	Reproductive phase	N	r^2	p-value	Regression equation
GSI	All phases	239	0.079	0.000	y = -4.527 + 0.203*x
	Developing (D)	158	0.047	0.004	y = -2.289 + 0.094*x
	Spawning capable (SC)	54	0.002	0.784	y = 6.094 + 0.027*x
	Actively spawning (AS)	15	0.156	0.146	y = -3.979 + 0.246*x
	Regenerating (Rgn)	12	0.045	0.505	y = 0.232 + 0.005*x
	SC and AS	69	0.238	0.000	y = -5.922 +0.330*x

Condition factor

The condition factor (K) ranged from 0.23 to 0.44 and the mean K varied significantly (ANOVA: F= 4.23, $p< 0.05$) among months (Figure 71 A). Tuckey HSD results showed significant differences ($p<0.01$) between July and December, October and November, and October and December. The highest K is observed in March (0.36), and at the onset of the spawning season (July) the fish condition is still relatively high (0.33±0.03), but decrease toward September (0.32±0.03) with a recovering in October (0.34±0.04). The lower K value is observed in December (0.30±0.03) coinciding with the almost cessation of the spawning season. Except for October a decreasing trend in K ($r^2=0.47$, $p>0.05$) is observed during the main spawning season (July to December) (Figure 71 B).

The analysis of seasonal variation of K, considering both dry (November to April) and rainy (May to October) periods, shows significant variation (ANOVA: F= 16.98, $p< 0.05$) (Figure 72) being higher during rainy periods.

The relationship between K and the female body length, considering all the reproductive phases together (Figure 73 A and Table 28) was not significant ($r^2=0.001$, $p>0.05$) neither considering the phases separately (Figure 73 B and Table 28) except for females at SC phase (N=61) where a significant but poor relationship was observed (Table 28). The relationship between K and gutted weight show very low coefficient of determination ($r^2= 0.016$) but statistically significant level ($p<0.05$). This analysis indicates that changes of gutted weight do not reflect important changes in the condition factor.

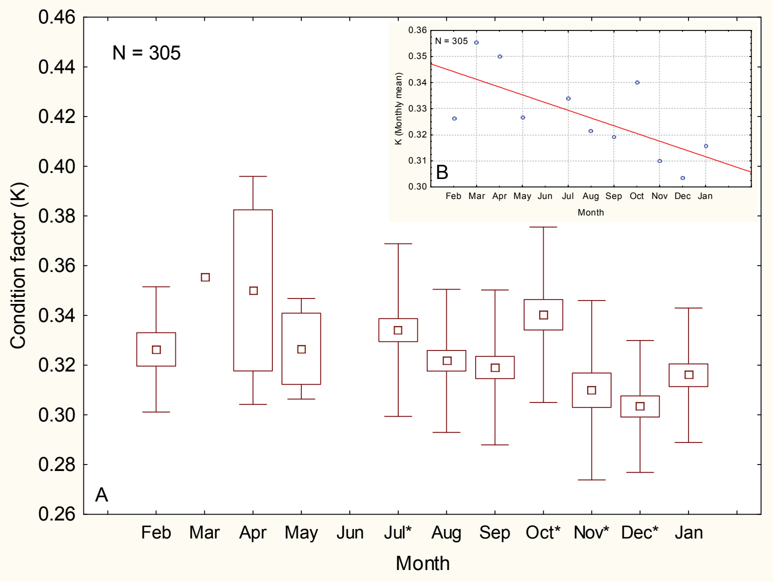


Figure 71. Mean monthly variation of condition factor (K) in *Brycon guatemalensis*. Mean (mid point); Mean ±SE; Mean ±SD. * Month with significant differences.

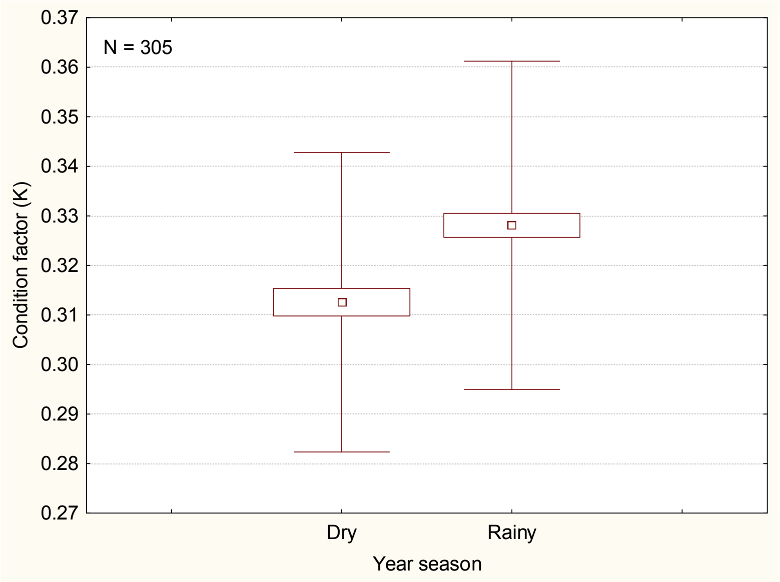


Figure 72. Seasonal variation in the condition factors (K) of *Brycon guatemalensis*. Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker).

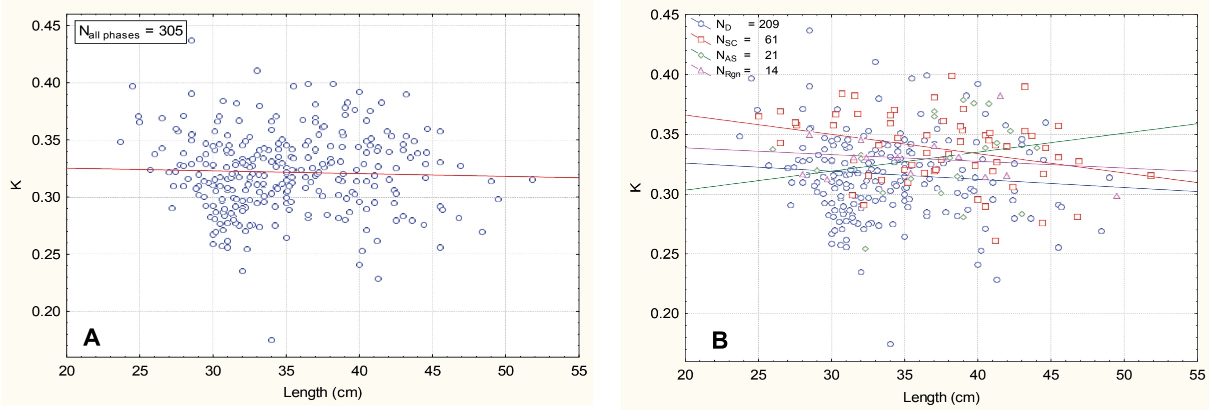


Figure 73. Relationship between K and length, considering the reproductive phases: Developing (D), Spawning capable (SC), Actively spawning (AS) and Regenerating (Rgn) phases.

Table 28. Statistical parameters of the relationship between condition factor (K) and length (cm) for females of *Brycon guatemalensis*: Number on specimens in the analysis (N); coefficient of determination (r^2), statistical significant test (p-value) and the linear regression equation.

	Length (cm)				
	Reproductive phase	N	r^2	p-value	Regression equation
K	All phases	305	0.001	0.524	y = 0.330 - 0.0002*x
	Developing (D)	209	0.009	0.142	y = 0.339 - 0.0006*x
	Spawning capable (SC)	61	0.101	0.012	y = 0.398 - 0.0016*x
	Actively spawning (AS)	21	0.049	0.334	y = 0.271 + 0.0015*x
	Regenerating (Rgn)	14	0.027	0.57	y = 0.349 + 0.0005*x

GSI and K relationship

The regression analysis between both indexes (GSI and K) even though it was statistically significant presented low determination coefficient (r^2=0.085, p< 0.001). The scatterplots shows the high data dispersion of both K and GSI (Figure 74) and indicate also their high variability. In spite of this variability it seems that two groups can be differentiated, a larger group of specimens with lower gonad weight per unit of body weight (less than 2), which are in the developing phase, having a wide range of K, and a group of specimens with higher GSI (in a more advanced developmental phase) that stretch the K-values range as GSI increase. GLM analysis between these two somatic indexes considering the reproductive phases as factor shows higher determination coefficient (r^2=0.49, p< 0.001). It indicates that variations in K induce significant changes in GSI depending on the reproductive phase of the female (Table 29).

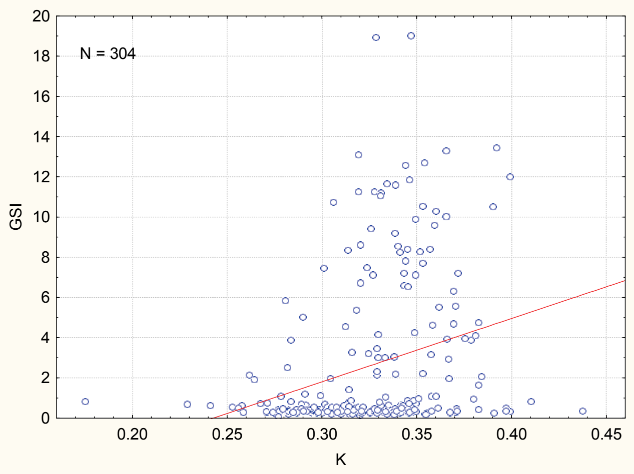


Figure 74. Relationship between both condition factor (K) and gonado-somatic (GSI) indexes in *Brycon guatemalensis*. N =304; r^2=0.085; p < 0.001; y = -7.623 + 31.493*x.

Table 29. Results of the GLM (ANCOVA) to analyse the effect of the reproductive phases in the relationship between condition factor (K) and gonado-somatic (GSI) index of *B. guatemalensis*.

Effect	SS	df	MS	F	p
Intercept	0.012	1	0.012	0.002	0.968
Condition factor (K)	30.596	1	30.596	4.152	0.043
Reproductive phases	1502.485	3	500.828	67.961	<0.001
Error	1812.860	246	7.369		

The monthly overall trend of both somatic indexes, K and GSI, describe, apparently, an inverse pattern, i.e., higher K-values coincide with lower GSI-values and vice versa. This pattern is more clearly evinced from December to March, when the specimens rapidly improved its condition, in terms of gaining body weight (length-weight factor) or energetic content, but loosed gonad weight (Figure 75). During the resting period, i.e., February-May when mean GSI attained the lowest values, monthly mean K increased to the maximum values recorded (Figure 75). Mean GSI increased to a high value rapidly from May to July and then generally decrease in two steps: July-September and October-January. Mean K also largely decreased during this period but with a recovering peak also in October. A summary of the somatic parameters (GSI and K), and body length is presented in Table 30. The linear regression between K and GSI showed no significant relationship for the whole period neither for the spawning season ($p>0.05$). However, a further exploration of the data showed that GSI was significantly affected by condition two months earlier ($r^2=0.66$, $p<0.05$).

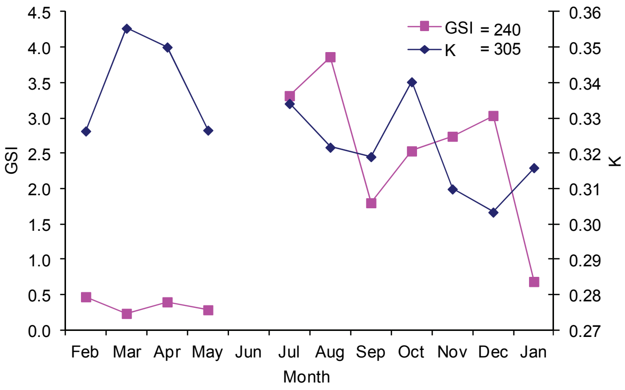


Figure 75. Monthly pattern of the gonadosomatic indexes (GSI) and condition factor (K) in females of *Brycon guatemalensis*.

Table 30. Monthly data of the somatic variables, gonado-somatic indexes (GSI) and condition factor (K), for *Brycon guatemalensis* (February 2005-January 2006).

			GSI			Condition factor (K)		
Month	N	Body length (cm)	N	Range	Mean	N	Range	Mean
Feb	40	29.0 - 42.0	12	0.22 - 1.63	0.47	14	0.28 - 0.38	0.33
Mar	10	28.6 - 28.6	1	0.24 - 0.24	0.24	1	0.35 - 0.35	0.36
Apr	11	35.4 - 41.5	2	0.38 - 0.42	0.40	2	0.32 - 0.38	0.35
May	8	29.7 - 30.1	2	0.24 - 0.34	0.29	2	0.31 - 0.34	0.33
Jun								
Jul	61	24.9 - 49.5	56	0.22 - 13.44	3.32	56	0.23 - 0.44	0.33
Aug	55	27.5 - 51.8	46	0.24 - 18.94	3.87	48	0.26 - 0.38	0.32
Sep	55	23.7 - 43.0	48	0.13 - 11.86	1.80	48	0.26 - 0.39	0.32
Oct	42	24.5 - 45.7	33	0.31 - 10.55	2.54	33	0.27 - 0.41	0.34
Nov	40	27.3 - 49.0	26	0.06 - 19.03	2.74	27	0.24 - 0.39	0.31
Dec	1	27.0 - 48.4	1	3.03 - 3.04	3.04	39	0.23 - 0.35	0.30
Jan	13	25.7 - 45.5	13	0.27 - 4.55	0.69	35	0.25 - 0.37	0.32
	336		240			305		

Spawning fraction

The spawning fraction (Sf) fluctuated throughout the spawning season, being highest in August (0.44), but the overall trend described a significant decreasing pattern (r^2=0.56, $p<0.05$), from July to February (Figure 76). The monthly spawning fraction fluctuations indicates that some other factors than temporal are influencing the spawning activity. In Table 31 is presented a detail of the spawning fraction with regard to the female size composition.

Considering that female size may influence spawning fraction, it was conducted regression analyses between spawning fraction (Sf) and month by three females length classes: smaller (< 33cm), medium (33–43 cm) and larger size (>43 cm). These analyses showed also a decreasing pattern from July to February for the three size classes (Figure 77), but significant decrease was observed only in females of medium size (r^2=0.68, $p<0.05$) (Table 32).The Sf between those length classes showed significant differences (ANOVA F=9.97, $p<0.01$), being lower in smaller females and higher in larger females (Figure 78).

Spawning fraction and gonadosomatic index (Figure 79) were positively and significantly related with a high determination coefficient (r^2 = 0.85; p <0.05).

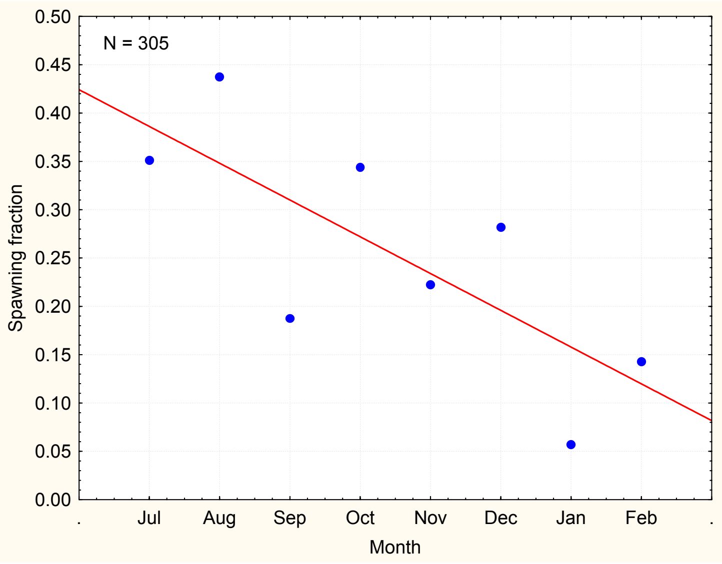


Figure 76. Monthly spawning fraction of *Brycon guatemalensis*

Table 31. Total number of females of *Brycon guatemalensis* analysed during the month of the spawning season. D: Developing; SC: Spawning capable; AS: Actively spawning; Rgn: Regenerating phases.

	Month	D+SC+AS+Rgn	SC+AS	Spawning fraction	Size range (cm)
Spawning season	July	57	20	0.35	24.9-49.5
	August	48	21	0.44	27.5-51.8
	September	48	9	0.19	23.7-43.0
	October	32	11	0.34	24.5-45.7
	November	27	6	0.22	27.3-49.0
	December	39	11	0.28	27.0-48.4
	January	35	2	0.06	25.7-45.5
	February	14	2	0.14	29.0-42.0
	March	1	0	-	28.6
	April	2	0	-	35.4-41.5
	May	2	0	-	29.7-30.1
	Total	305	82	-	-

Table 32. Statistical parameter results from the regression analysis between spawning fraction (Sf) and month, and three fish length classes.

Length class (cm)	r^2	p
<33	0.07	0.61
33-43	0.68	0.01
>43	0.02	0.84

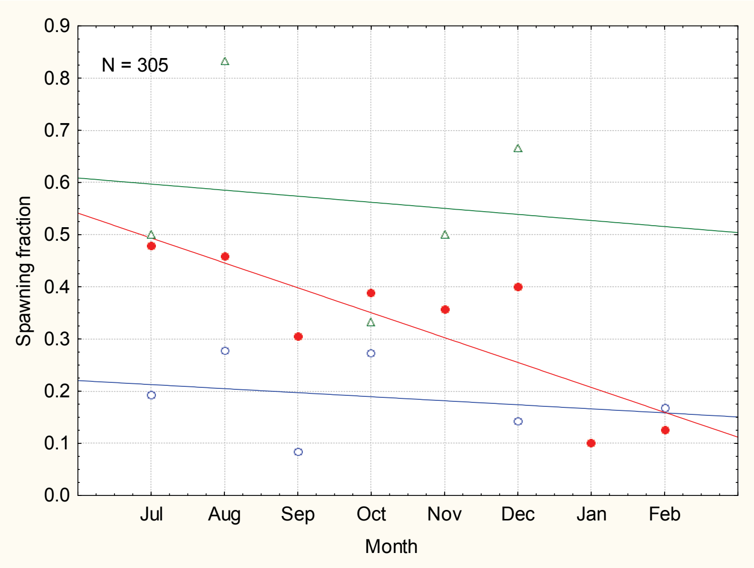


Figure 77. Monthly spawning fraction (Sf) of *Brycon guatemalensis* by length classes. < 33 cm (open circle and dashed line); 33 to 43 cm (solid black circle and solid line) and > 43 cm (open triangle and dotted line).

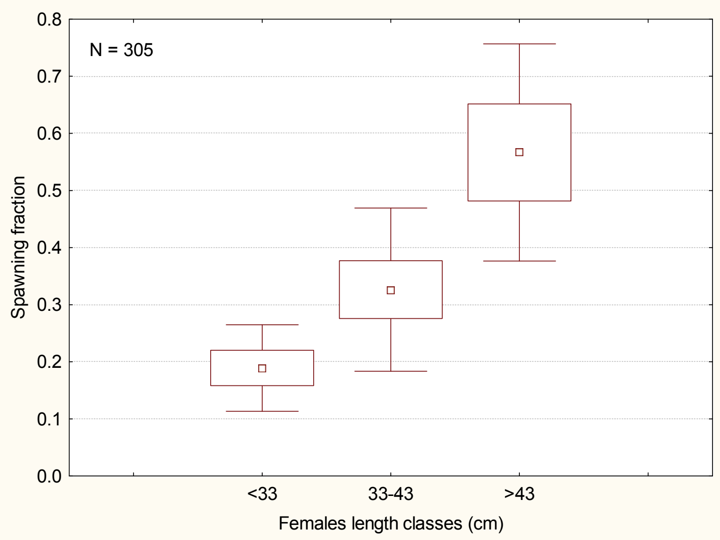


Figure 78. Mean variability of the spawning fraction in relation with the female length classes. Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker).

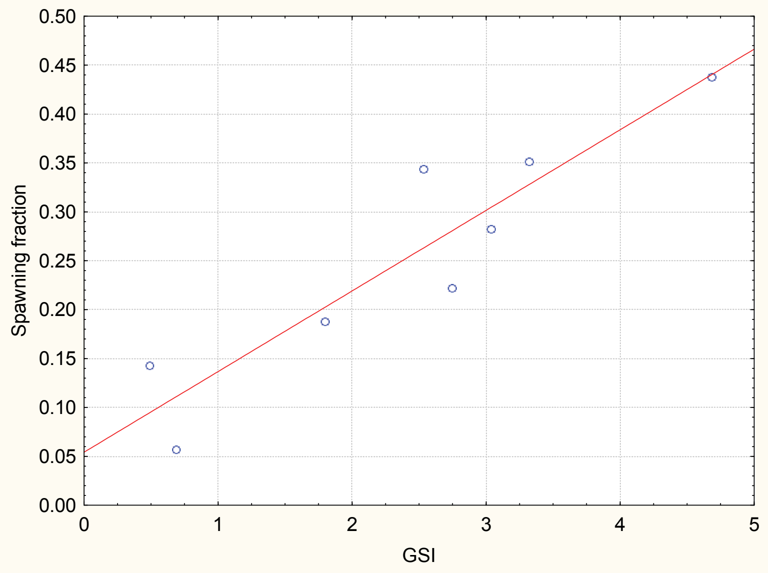


Figure 79. Relationship between the Gonadosomatic index (GSI) and the Spawning fraction of *Brycon guatemalensis*: $r^2 = 0.8491$; $p = 0.0011$; $y = 0.054 + 0.082*x$.

4.2.3. Maturity ogive

Maturity was determined i) macroscopically at the time of the sampling trough the visual inspection of the whole ovaries and ii) microscopically using histological sections. Maturity ogives were then determined by each method and compared.

Macroscopic observations

The size ranges of the immature and mature population almost completely overlap, and even the smaller females sampled were unexpectedly mature, while large females were abnormally immature (Figure 80 A). Yet, statistically significant variation (ANOVA: F= 321.799, $p < 0.05$) are observed in the mean length of both states, being the mean length for immature specimens 30.6 cm and for the mature 35.5 cm. The values attained from logistic regression are presented in Table 33. Using the parameters of the logistic regression, the L_{50} estimated based on the macroscopic observation was 34.9 cm and Figure 81 shows the proportion of mature females at length which fitted significantly to a logistic regression curve ($p<0.001$).A detail analysis is presented when compare this result with the microscopic results.

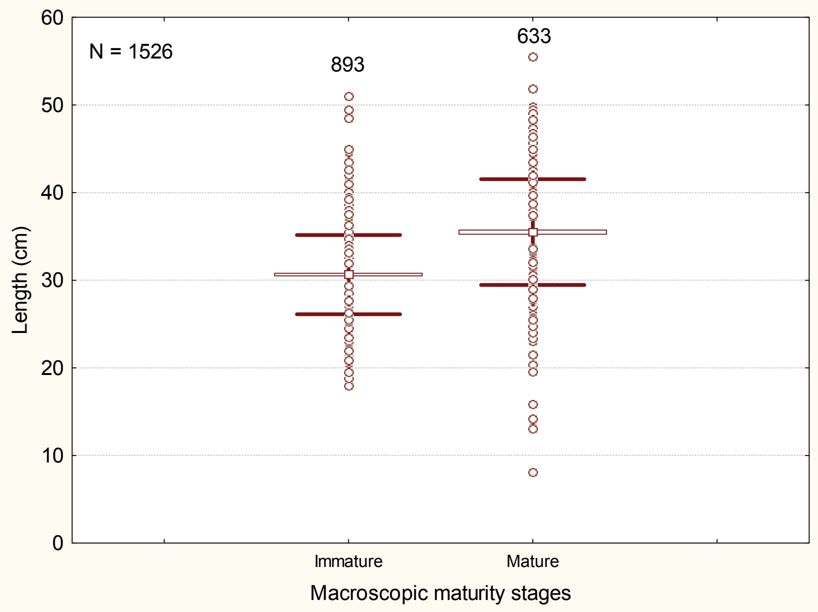


Figure 80. Macroscopic observation of immature and mature gonad stages of *Brycon guatemalensis*. Open circle the data set; Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker).

Table 33. Values attained for the logistic regression curve, based on macroscopic observation of the ovaries

	Coefficient of the logistic curve	
	a	b
Estimated values	-6.111	0.175
Standard Error	0.389	0.012
t(369)	-15.717	15.051
p-level	<0.001	<0.001
Wald's Chi-square	247.01	226.54

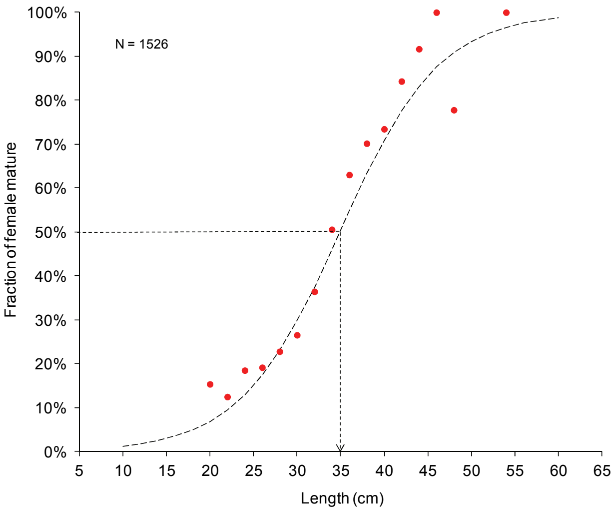


Figure 81. Macroscopic maturity ogives estimated for *Brycon guatemalensis*. Arrows indicate L_{50} = 34.9 cm; red circle represent the females proportion.

Microscopic observations

Based on the whole set of data from the histological analysis (371 ovaries) the proportion of mature females at size was estimated. The size range for immature and mature individuals overlapped between 22 and 35 cm, and consistently smaller and larger females were immature and mature respectively and the mean length for immature specimen was 26.6 cm and for mature 34.8 cm (Figure 82). The statistical analysis evinced significant differences (ANOVA: F= 146.593, $p< 0.05$) in the mean length between immature and mature specimen. The values attained from logistic regression are presented in Table 34. and the portion of mature females fitted significantly ($p< 0.001$) to a logistic regression curve (Figure 83) The estimated length at 50% maturity of female *B. guatemalensis* was 27.3 cm.

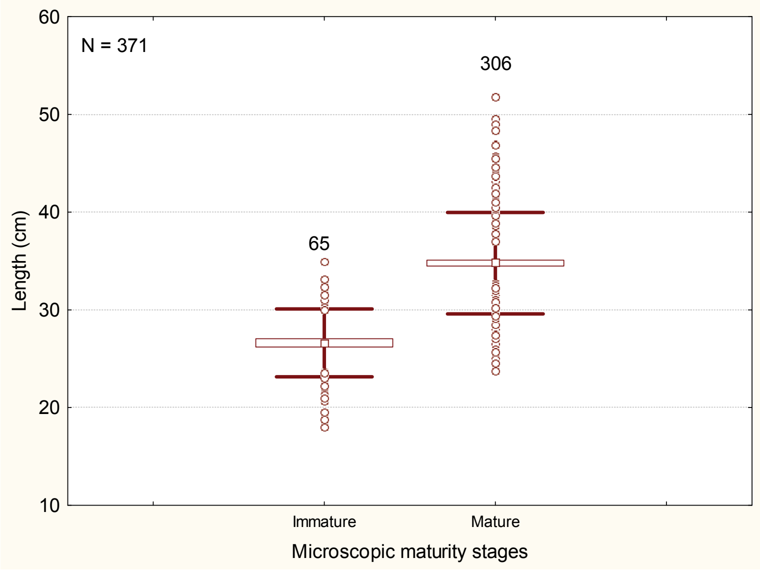


Figure 82. Microscopic observation of immature and mature gonad stages of *Brycon guatemalensis*. Open circle the data set; Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker).

Table 34. Values attained for the logistic regression curve, based on histological observation of the ovaries

	Coefficient of the logistic curve	
	a	b
Estimated values	-15.196	0.557
Standard Error	2.103	0.073
t (369)	-7.226	7.658
p-level	<0.001	<0.001
Wald's Chi-square	52.22	58.65

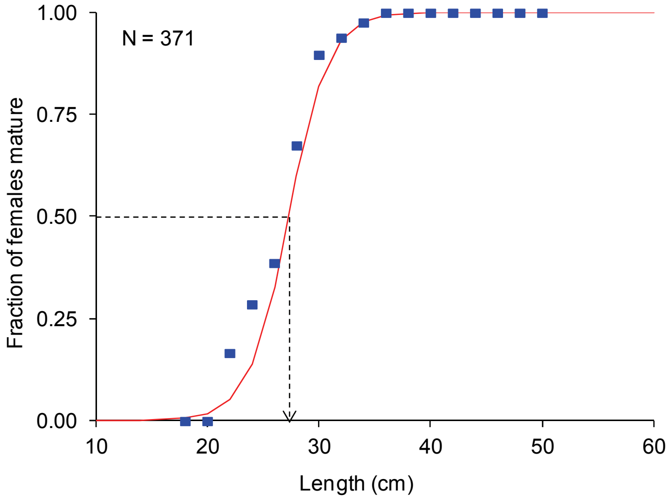


Figure 83. Maturity ogive estimated for *Brycon guatemalensis*. Arrows indicate L_{50} = 27.3 cm; blue colour square represent the females proportion.

The L_{50} estimated based on macroscopic observation was 34.9 cm, whereas the microscopic one was 27.3 cm. In Figure 84 the macros and microscopic maturity ogives are shown for comparison. Maturity ogives were significantly different between methods (z=-4.267; p<0.05) (Table 35). The microscopic ogive seems to be more consistent with a coherent and increasing proportion of mature females at size. The macroscopic ogive yields abnormal values at smaller sizes as well at larger sizes (especially at 50 cm size class).

Table 35. Results of the GLM performed to evaluate the differences between macroscopic and microscopic methods for the L_{50} estimation of Brycon guatemalensis.

Parameter	Estimate	SE	z	p
Intercept	-6.111	0.388	-15.731	< 0.05
Slope	0.175	0.012	15.065	< 0.05
Method	-9.085	2.129	-4.267	< 0.05
Interaction Length-Method	0.382	0.073	5.210	< 0.05

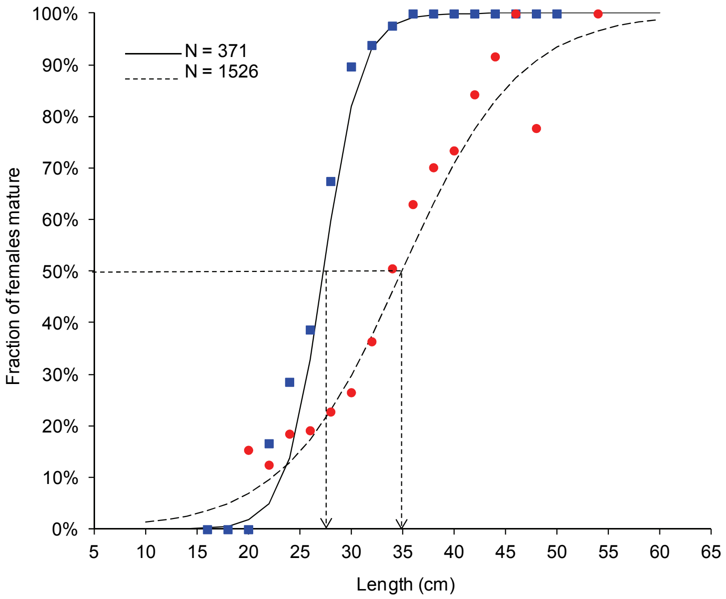


Figure 84. Two maturity ogives estimated for *Brycon guatemalensis*. Macroscopic ogives (dashed line) and female proportion (solid red circle); Microscopic ogives (solid line) and female proportion (solid blue square). Arrows indicate $L_{50\ \mathrm{Macroscopic}}$=34.9 cm; $L_{50\ \mathrm{Microscopic}}$= 27.3 cm.

4.2.4. Fecundity

To determine fecundity type, the oocyte growth dynamic was studied in detail in 53 females in SC and AS phases to assess if oocyte recruitment ends prior to spawning (determinate) or rather continue after the onset of spawning (indeterminate). The oocyte size frequency along the season and trends in the number of developing oocytes were, thus, analysed.

Oocyte growth dynamic and recruitment

The pooled oocyte size frequency in females in spawning capable and actively spawning phase show the presence of two oocytes populations, the most abundant composed by smaller oocytes (< 400 µm diameter), in primary growth (PG) and cortical alveoli (AC) stages (Figure 85 A), and a population of largest and developing oocytes ranging between 1800 to 2500 µm, with a mode equal to 2150 µm (Figure 85 B), mainly composed by oocytes in advanced or late vitellogenic (VIT2) and germinal vesicle migratory (GVM) stages. There is a clear and large gap between both oocyte cohorts.

The frequency of oocytes diameter in the smaller and larger oocytes fluctuate with the ongoing spawning season (Figure 86 A), but particularly the mode of larger oocytes (2150 µm), the one VIT2 and GVM stages decrease from July to August and notably increase in October (Figure 86 B).

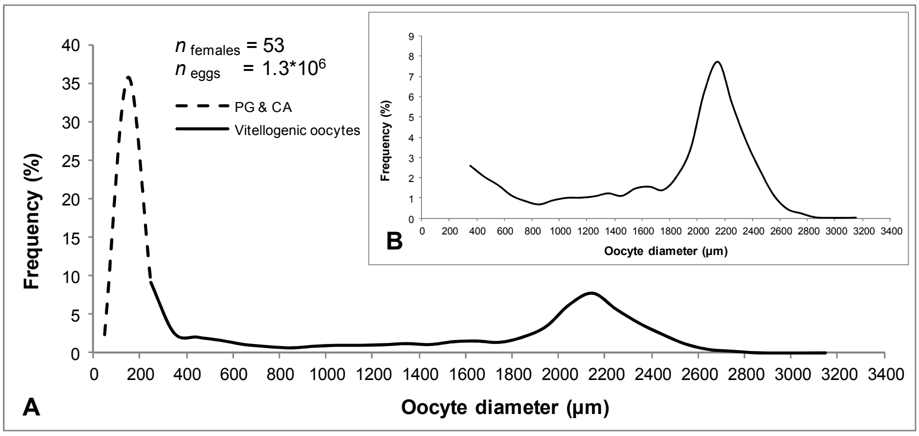


Figure 85. Oocyte-size frequency distribution in mature ovaries in advanced vitellogenic stages of *Brycon guatemalensis*. A) Main panel: The whole oocytes size-range distribution, and B) Inlet panel: The vitellogenic oocytes size-range distribution (N = counting oocytes 32,908).

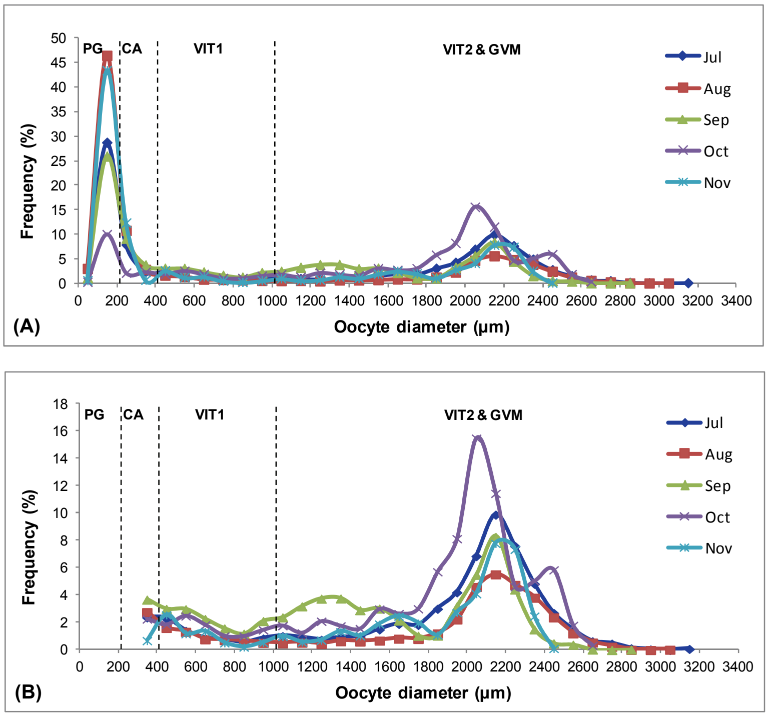


Figure 86. Oocyte-sizes frequency distribution along the spawning season (July to November) observed in mature ovaries (advanced vitellogenic stages -VIT2) of *Brycon guatemalensis*. A) whole oocyte distribution pattern and B) pattern of larger oocytes.

Apart from the reservoir of smaller oocytes in PG and AC stages, the individual frequency distribution of the oocytes larger than 400 µm observed in twelve females selected by date along the spawning season shows that the oocyte growth at final maturation differ considerably between females (Figure 87). Thus, the average diameter of VIT2 and GVM was notably different without a clear temporal pattern and the shape of the distribution varied from peaked (Sept 5, Dec 12) to rounded (Aug 15, Jan 22) and even a wide distribution (Jul 23, Oct 7). However, the mean diameter of oocytes larger than 1000 µm showed no significant differences from July to November (F=0.35, p=0.84; Figure 88). In addition, the mean diameter of the 10 % largest oocytes showed significant differences during the same periods (F=7.005, p< 0.001; Figure 89 A) and the mean diameter of these decreased notably (r^2=0.72) but not significantly (p=0.06) due to low data points (Figure 89 B).

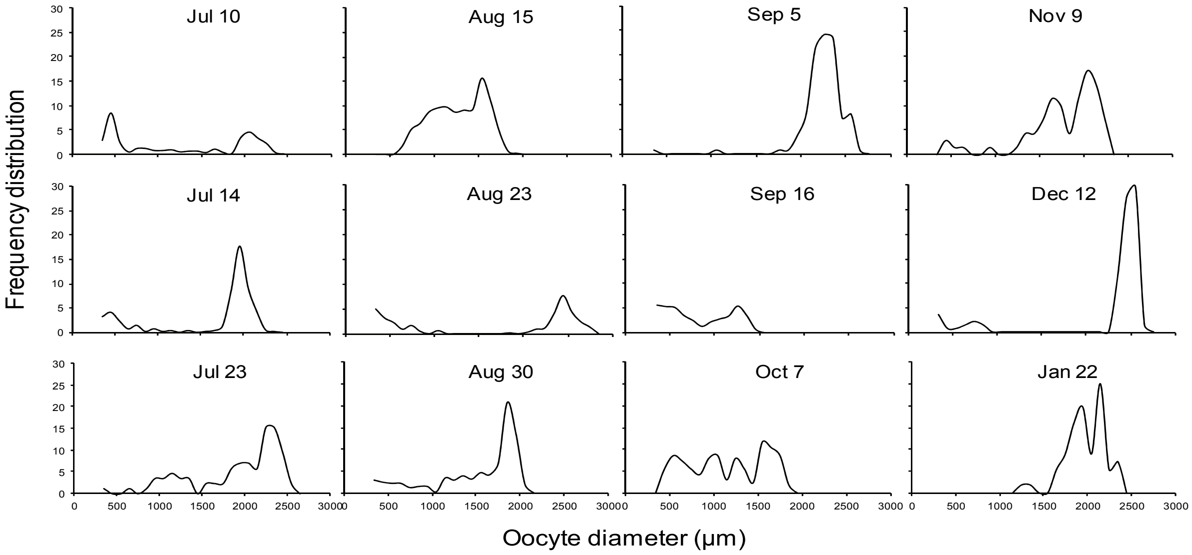


Figure 87. Frequency distribution of oocytes diameter in twelve ripened ovaries examined during the spawning season. Each draw represents the ripened ovary from one female of *Brycon guatemalensis*, which follows a sequential order of collecting days from July 2005 to January of 2006.

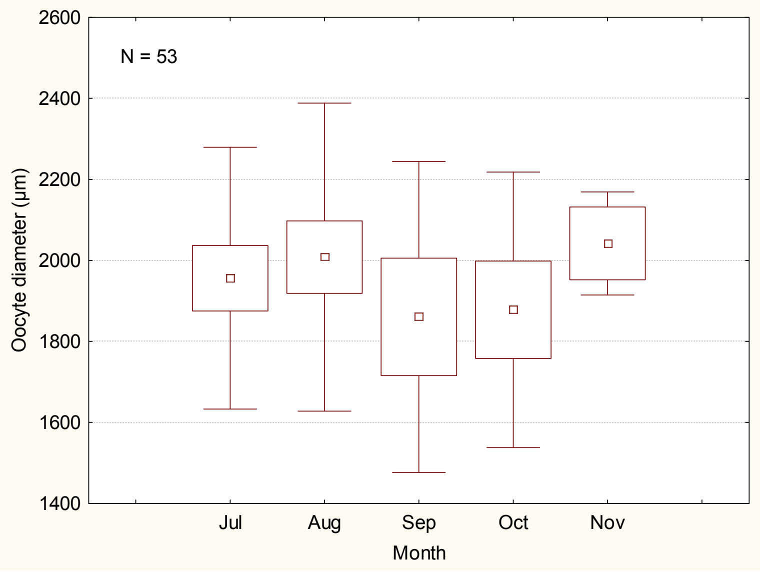


Figure 88. Monthly variability of the mean oocytes diameter larger than 1000 µm. Mean (mid point); Mean ±SE (box); Mean ±SD (whisker).

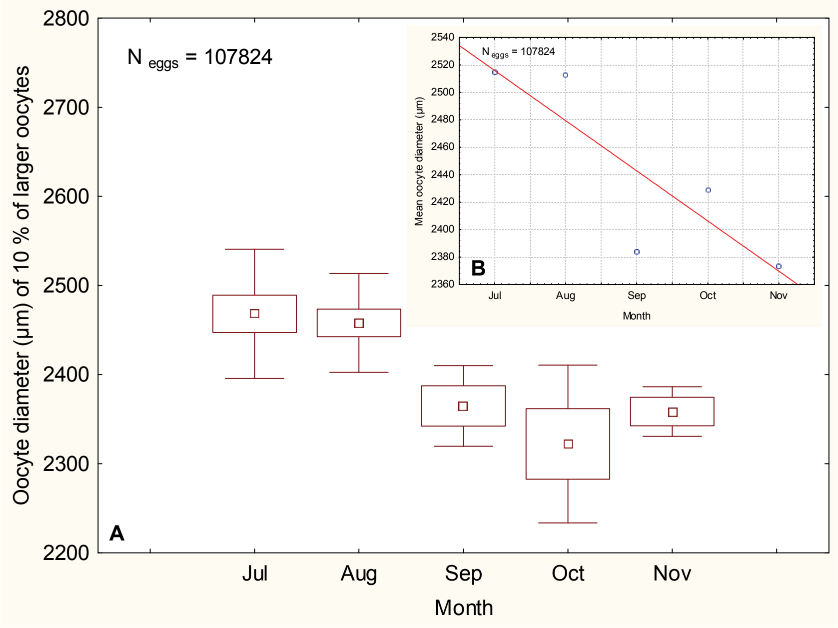


Figure 89. The monthly pattern of the oocyte diameter (µm), considering the 10 % of largest oocytes in *Brycon guatemalensis*. A: ANOVA.-Mean (mid point); Mean ±SE (box); Mean ±SD (whisker); B: Regression.

Thus three cohorts of oocytes can be identified in SC and AS ovaries (Figure 90): a leading cohort composed by VIT2 and GMV stages; a secondary cohort composed by oocytes in early vitellogenesis; and a cohort composed by pre-vitellogenic oocytes. The leading cohort mean diameter increased from 1000 to more than 2500 µm through the spawning season while the other two cohorts did not grow, remaining its mean diameter constant around 500 and 150 µm, respectively.

The relationship between the oocyte diameter of the leading cohort with the female length was significant ($p<0.001$) with low determination coefficient ($r^2=0.24$), indicating that although larger females produce larger oocytes, high variability in the mean oocyte diameter exist among females on similar sizes (Figure 91).

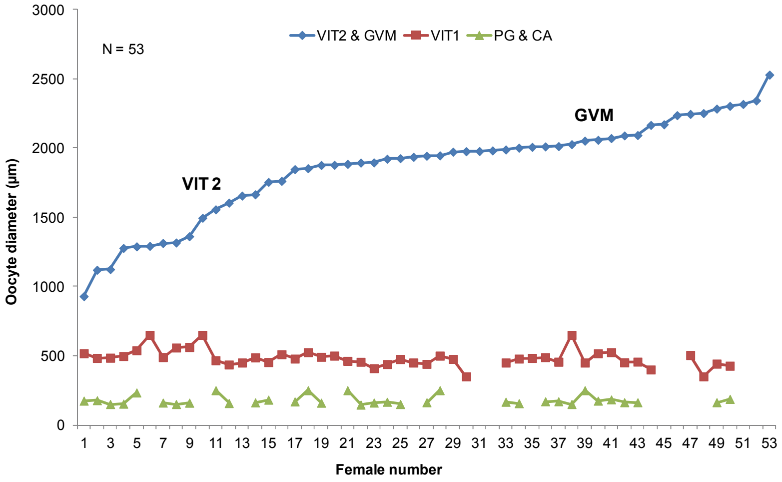


Figure 90. Oocyte diameter progression of three oocyte cohorts identified in ovaries in advanced vitellogenesis stages of *Brycon guatemalensis* along the spawning season. The number of females is ordered by the mean size of the leading cohort.

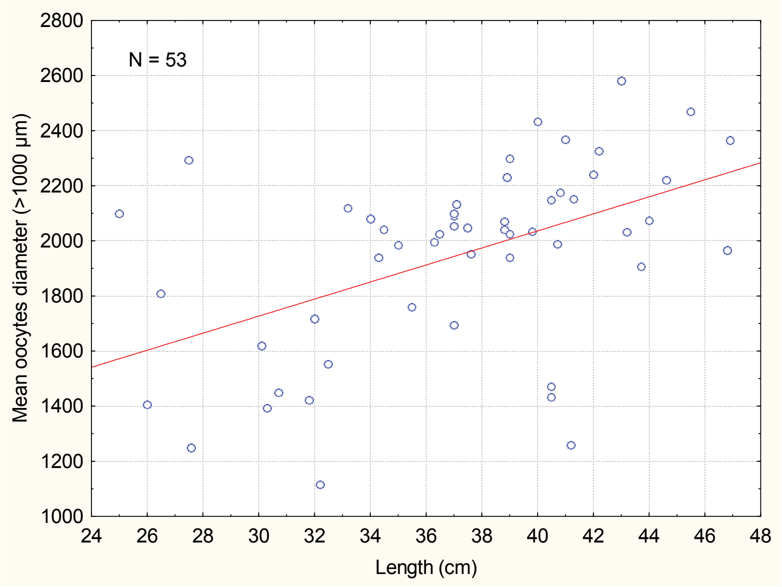


Figure 91. Relationship between the mean oocytes diameter of the leading oocytes cohorts with female body length of *Brycon guatemalensis*.

GVM oocytes are, by definition, close to be spawn and hence can be used as proxy for batch fecundity. The number of oocytes in GVM largely differ from the stock of oocytes in VIT2 stages (ANOVA: F=59.21, p<0.001) in 47 females where both stages were present (Table 36). The ratio between the numbers of oocytes in VIT2 over GVM ranged between 0.007 and 3.788 (Mean 0.159 ± SD 0.824). This ratio significantly decrease (r^2= 0.18, p<

0.01) with the female length (Figure **92**). However, except six specimens where this ratio was above 1, in the majority of the females the ratio was well below 0.5.

The number of developing oocytes (NDO) ranged from 41 to 35,615 oocytes (mean 5,642.8± SD 6,922.8), and the relative number of developing oocytes per gram of gutted body weight (RNDO) varied from 0.04 to 45.07 oocytes/g (mean 7.3± SD 8.3). The NDO and RNDO increased from 7,790.50 (±SE 1,717.03) and 9.95 (± SE 1.9) oocytes/g in July to 8,834.12 (± SE 1,868.18) and 11.8 (± SE 2.35) oocytes/g in August respectively and then, both significantly decreased (F=3.94, $p<0.05$) until 1,935.59 (± SE 429.12) and 2.27 (± SE 0.54) oocytes/g in November (Figure 93).

Therefore, three line of evidences allow to conclude that *B. guatemalensis* has determinate fecundity: i) the decrease in the number of oocytes within the ovary along the spawning season, ii) the clear gap between the leading cohort and the underdeveloped cohorts in females in SC phase and iii) the fact that secondary cohorts did not show any signs of growth indicating that very likely this cohort was not to be spawned during the current reproductive cycle. Moreover, the number of GVM oocytes, those ready to be spawned, is considerably higher than the stock of VIT2 oocytes, which should act as reservoir for next batches. It indicates that very likely only one batch is produced. In conclusion, potential annual fecundity (Fp) can be estimated from the number of oocytes in leading oocytes cohort, i.e., oocytes larger than 1000 µm diameter.

Table 36. Number of oocytes in advanced or late vitellogenic (VIT2) and germinal vesicle migratory (GVM) stages in ovaries of *Brycon guatemalensis*.

Oocyte stages	N	Min	Max	Mean ± SD
VIT2	47	47	14290	1874 ± 2213
GVM	47	722	36160	9996 ± 6889

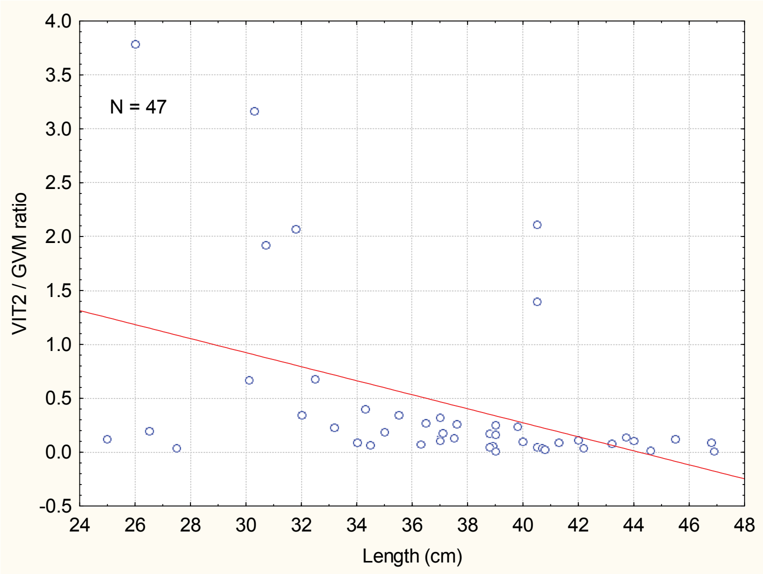


Figure 92. VIT2-GVM ratio and female length relationship based upon 47 ovaries.

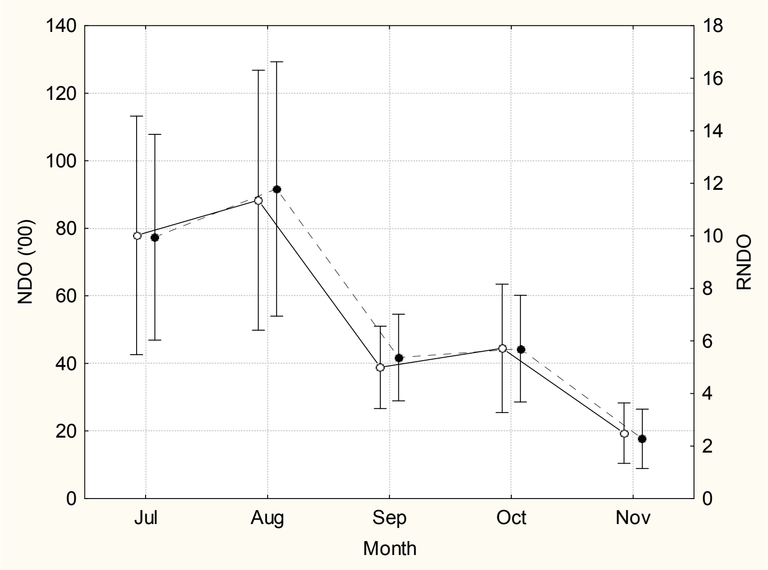


Figure 93. Monthly variation of the number of developing oocytes (NDO: solid line) and the relative number of developing oocytes (RNDO: dashed line). Whiskers denote 0.95 confidence intervals.

Potential annual fecundity (F_p)

Potential annual fecundity (Fp) estimated ranged from 701.8 to 36,569.0 oocytes with a mean of 11,013 ± SD 6,697.5, and was significantly and positive related with the female body length fitting to a power function (regression: N= 48, $r^2=0.71$, $p<0.001$; $y= 0.0626x^{3.3094}$) (Figure 94 A), and with female gutted weight fitted to a linear function (regression: N= 48, $r^2=0.67$, $p<0.001$; $y= -619.59 + 15.306\ x$) (Figure 94 B). In both relationship, the values of the Fp seems like more scattered as the size and weight of the fish increases. Besides, Fp was no significant related with the condition factor (K) ($r^2=0.0024$; $p=0.73$).

Fp was positive and significantly correlated with the mean oocyte diameter of the leading cohort ($r=0.71$, $p<0.001$; Linear equation $y= -14112 + 12.828\ x$) (Figure 95). The Fp and the relative potential annual fecundity ($Fp_{relative}$), along the spawning season (Figure 96), did not show significant variations between months (F= 0.456; p= 0.77 and F=0.81; p=0.81, respectively). However, it is noticed that less range variability of both (Fp and Fp relative) occurred in July (at the onset of the spawning season), while larger variability in egg production is observed in November.

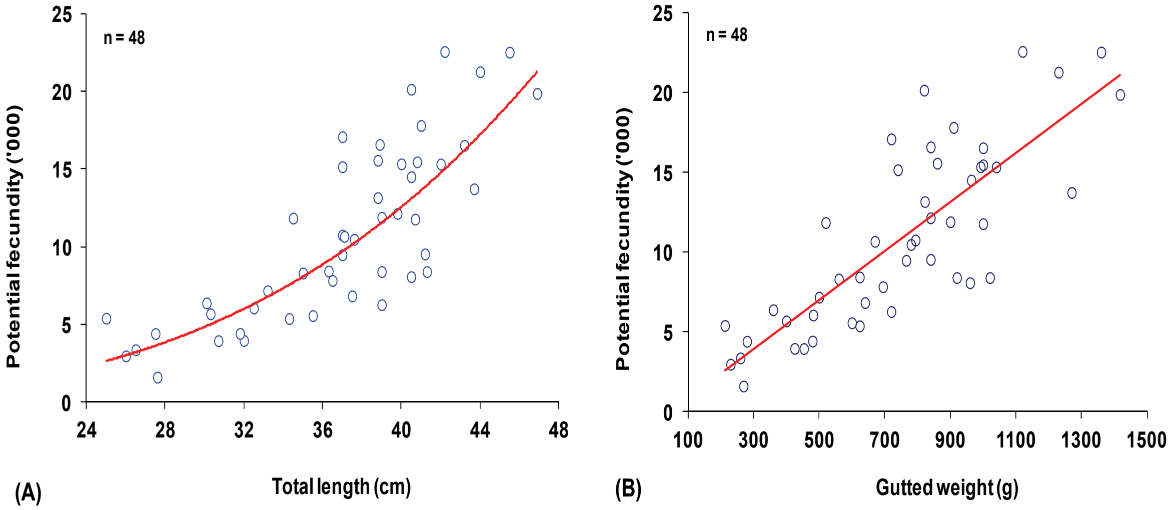


Figure 94. The potential annual fecundity as: (A) function of the total body length (The power equation $y= 0.0626x^{3.3094}$); (B) function of gutted weight (Linear equation $y= -619.59 + 15.306\ x$) of *Brycon guatemalensis* captured along the east coast of the Lake of Nicaragua from July to November (N= 48).

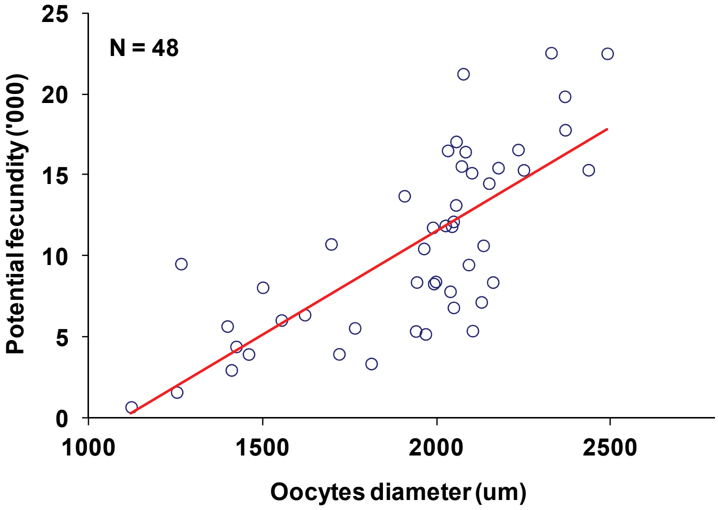


Figure 95. The potential annual fecundity as function of the oocytes diameter of *Brycon guatemalensis* captured along the east coast of the Lake of Nicaragua from July to November (N=48). Linear equation y= -14112 + 12.828 x

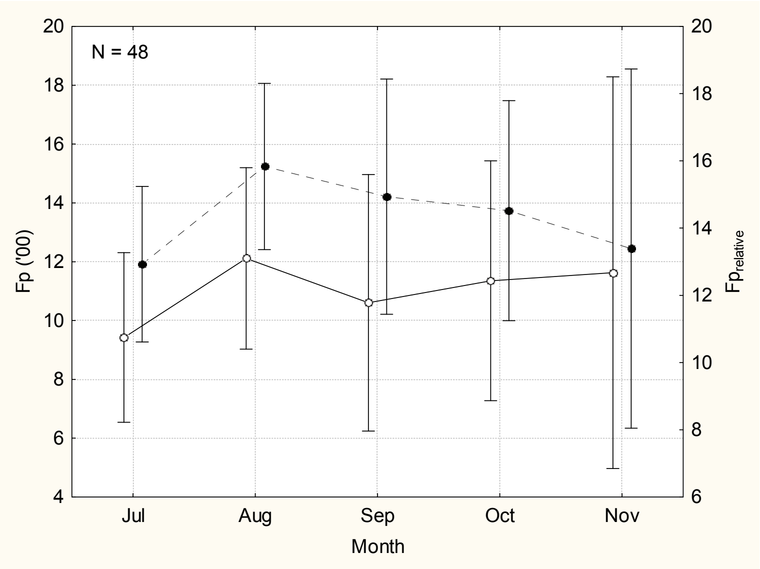


Figure 96. Monthly variation of the potential annual fecundity (Fp: solid line) and relative potential annual fecundity ($Fp_{relative}$: dashed line) of *Brycon guatemalensis* during the spawning season. Mean (midpoint); Mean ±SE (whisker).

Oocyte density (NG) estimation

The mean oocyte diameter (OD) of the leading cohort, i.e., oocytes above 1000 µm, obtained from gravimetric method, and the oocyte density (NO= number of oocytes per gram of ovary weight) attained after calculations, were both related fitting in a power regression line. The relationship between these variables (Figure 97) was significant (p-value <0.001) and the regression shows a high determination coefficient (r^2=0.97) (Table 37). Thus, the autodiametric approach can be easily taken for *Brycon guatemalensis*, following the next equation:

$$\mathrm{Fp} = a \times \mathrm{OD}^{b} \text{ x OW (g)}$$

Where OD is the mean oocyte diameter and OW the ovary weight (OW), and “a” and “b” the parameters of the DO-NO relationship (Table 37).

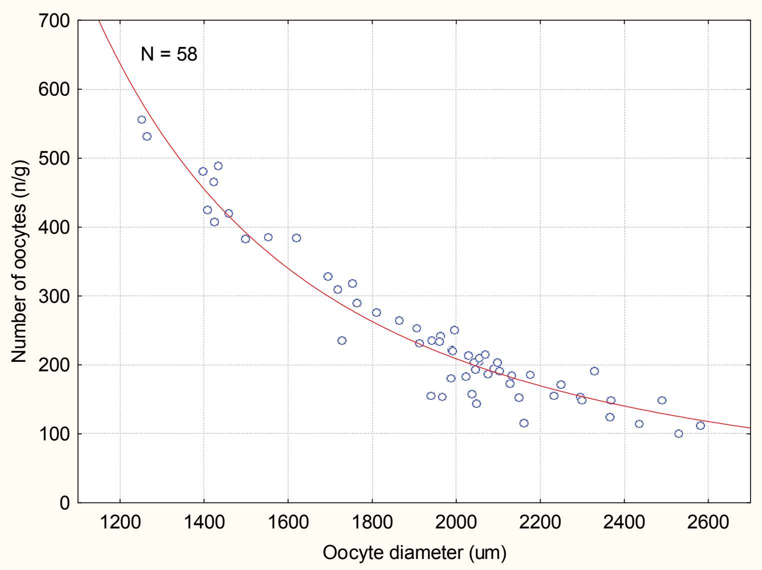


Figure 97. Relationship and fitted curve between oocyte diameter (µm) and oocyte density (number of oocytes per gram of ovary weight) of *Brycon guatemalensis*.

Table 37. Statistical parameters from the relationship between oocyte diameter (OD) and oocyte density (OG) for *Brycon guatemalensis*.

Relationship	n	df	p	r^2	a	b
OD & NO	58	2	< 0.001	0.97	3.341E+09	-2.182

4.3. Discussion

Reproductive studies on *Brycon guatemalensis* are scarce and limited to nesting behaviour (Greenfield & Thomerson, 1997; Bussing, 2002) and to its larval development in captivity (Molina, 2006). It prevents a comparison with previous results, except if compared with some other genus of the family where similar studies have been conducted and with species from other latitudes. Thus, the present analysis of reproductive strategy of *B. guatemalensis* constitutes the most comprehensive study conducted to date in this species, and the first study made in the lake of Nicaragua.

Oocyte development

The oocytes in cortical alveoli stages presented few vesicles in the cytoplasm, which is one of the three components that characterizes the stage in teleosts fish (Begovac & Wallace, 1988; Selman, Wallace & Barr, 1986, Selman & Wallace, 1989; Selman, Wallace & Player, 1991), but these vesicles can appear in oocytes at these stages just before the beginning of vitellogenesis as in *Lampetra planeri* (Busson-Mabillot, 1967), appear in very low number as in *Trisopterus luscu*s (Alonso-Fernández, 2011) or even do not form as in dogfish *Scoliodon sorrakowah* (Guraya, 1982; 1986).

The oocytes final maturation (OM) ends with the migration of the germinal vesicle (GVM) to the animal pole, without eggs hydration. This oocytes feature encompass with its particular reproductive strategy as eggs sink to the bottom after releasing, because of their negative buoyancy, become sticky and agglomerate (Molina, 2006), and are deposited in excavated nests made up in sandy bottoms (Greenfield & Thomerson, 1997; Bussing, 2002). The eggs hydration are characterized by the rapid increases of eggs volume (Wallace & Selman, 1985) and have been described to occur in most pelagic eggs of marine fishes, but also occur in brackish, marine and in less extent in freshwater species with non-floating or demersal eggs (Thorsen & Fyhn, 1996). Comparatively, the water uptake of marine benthophils mature eggs range from 74 to 82 % and the corresponding increase in volume from 1.3 to 3.0, while in those freshwater benthophils eggs the water uptake is considerable less (56 to 85 %) and 1.0 to 1.8 increase in volume (Craik & Harvey, 1984; Cerdá, Fabra & Raldúa, 2007). In spite of the absence of an evident hydration, the *B. guatemalensis* eggs increase 1.6-fold in volume during final maturation, which is in the range for freshwater benthophilics eggs previously mentioned. Moreover, the maximum diameter recorded in our study from histological section, 2.3 mm, is close to the measured eggs diameter under laboratory condition, just before hatching, 2.5 mm (Molina, 2006). However, the average oocyte diameter at OM in our study was smaller, 1.6 mm, and similar to *B. petrosus* whose eggs measured 1.6-1.9 mm (Kramer, 1978a). The increase in oocyte size during OM in our study ranged 0.23 and 0.30 mm, similar to many others freshwater teleosts fishes whose eggs diameter, during germinal vesicle breaks down (GVBD), increases in less than one mm, e.g., in common killifish *Fundulus heteroclitus* (1.4 to 2.0 mm), *Fundulus grandis* (1.6 to 2.2 mm), *Fundulus majalis* (1.7 to 2.5 mm), *Cyprinodon variegates* (0.85 to 1.2 mm), *Chasmodes saburrae* (0.80 to 1.00 mm), *Dormitator maculates* (0.28 to 0.30 mm), or *Gobionellus boleosoma* (0.25 to 0.33 mm) (Skoblina, 2010). For these species, oocytes increased in average 33% in size (142% in volume, i.e., 2.4-fold), while the egg increase in *B. guatemalensis* was 16% in size (56% in volume, i.e., 1.6-fold), i.e., within the variation freshwater teleosts but well below the average.

Eggs of *B. guatemalensis* are released surrounded by mucus, produced within the ovary, that is visually observed when enter in contact with water. This mucus formation occur in some teleosts during vitellogenesis, when their epithelial organization is disrupted, the organelles fragmented, and the cells are transformed into an irregular mass of "mucosomes" which, on contact with water following oviposition, swells to form an adhesive coat of mucopolysaccharides and mucoproteins that causes the eggs to adhere to the nests wall and to each other (McMillan, 2007). Rizzo *et al.* (2002) present a list of 12 species of the Characidae family in which are categorized the eggs adhesiveness of each species in 1. Adhesive; 2. Weakly adhesive; and 3. Non-adhesive. Following the presented categories, the eggs adhesiveness characteristic of *B. guatemalensis* could be included in the category of adhesive eggs, since the surrounding mucus stuck the eggs firmly to each other and formed a coherent egg mass, whereas its close parent *B. petrosus* is in the category of weakly adhesive eggs and spawn out of water on damp gravel at the edge of a riffle (Kramer, 1978a).

Reproductive cycle

The more clear spawning evidence was the observation of GVM since postovulatory follicle (POF) frequency was very low. The POF duration may be temperature-dependent, because the metabolic rate of poikilotherms, like fish, may be directly affected by ambient (Hunter & Macewicz, 1985), and varies between species (Fitzhugh & Hettler, 1995). These can be rapidly deteriorate and become undetectable within few days (Hunter & Golber, 1980) or up to 48 hours in common snook at 29 ºC, (Ronald, 2002) or even in 15 hours at high water temperature of 28 to 30 ºC as in *Callionymus enneactis* (Takita *et al*., 1983). This is likely the reason for the low frequency of POF in ovaries of *B. guatemalensis* observed during this study, since water temperatures in the Lake Nicaragua has an average temperature of 28.6 ºC (Hernández-Portocarrero & Saborido-Rey, 2007). The presence-absence of POF in the ovaries of *B. guatemalensis* seems to be also influenced by the time of the day the samples were collected in the wild, this asseveration is based in the fact that in tropical areas the water temperature rapidly increase as sunrise, in two or more degrees, thus it seems to be advisable to collect samples before sunrise to increase POF frequency. One last consideration to the low frequency of POF is that spawning ground did not overlap with the fishing ground where females were collected because it migratory behaviour to spawn (Horn, 1997; Drewe *et al*., 2003; McLarney, *et al*., 2010). More importantly is to determine the diel periodicity, i.e., the synchronicity of individual spawn times, which varies considerably among species (Lowerre-Barbieri *et al.,* 2011a). The sampling in this study was conducted in the morning (around dawn). If spawning consistently at the afternoon and POF degenerates in few hours, it may explain the low prevalence of POF. Fish must be sampled at given intervals over 24–48 h (Hunter & Macewicz, 1985) to assess the full range of times over which fish spawn.

According to our results *B. guatemalensis* exhibits a protracted spawning season lasting 8 months (from July to February), with the highest activity between July and November. The proportion of spawning fraction (Sf) estimated on the prevalence of the spawning capable and actively spawning females over all mature females was supported on the defined spawning season, the dominant presence of developing phase over the rest of the phases, the negligible presence of POF and the evidence that highest spawning event take place in July and August. This method has been used in species with determinate fecundity as *Trisopterus luscus* (Alonso-Fernández, 2011), and differ with the most common methods used for indeterminate fecundity and batch spawner species as *Merluccius merluccius* (Korta *et al*., 2010). Other characids fishes inhabiting mildly seasonal environments display considerable diversity in the reproductive timing, ranging from an extremely brief period (1 or 2 days per year) as *Bryconamericus emperador*, through moderately long breeding seasons (2 month) as *B. petrosus* and 4 month as *Hyphessobrycon panamensis* to essentially continuous breeding in *Roeboides* and *Gephyrocharax* (Kramer, 1978a). The reproductive period of characids such as *Salminus hilarii*, *Bryconamericus emperador* and *Piabucina panamensis* in Brazil respond to the rainfall season (spring to late summer), river flood and high water temperature (Honji *et al*., 2009) which provide a suitable environment for survival of the offspring, but particularly the rainfall intensity is the most important synchronizing factor in tropical fish reproduction (Lowe-McConnel, 1987; Andrade & Braga, 2005). The influence of this environmental parameter is also evinced in *B. guatemalensis*, since in the present study it has been observed that spawning onset coincides with the rainfall and completely cesses in dry season. However, unlike *B. guatemalensis*, other species like *Hyphessobrycon panamensis* and *B. petrosus* mature and spawn during the dry season, between November and April and from January to March, respectively (Kramer, 1978a; 1978b).

Somatic indexes

Highest values of GSI were observed from July to December without a clear peak during this period. The lowest values were recorded during dry months indicating the complete spawning cessation; the end of spawning is also confirmed by the generalised follicular atresia in December and January. On the contrary, both GSI mean and variance largely fluctuated during spawning season. In species with determinate fecundity, as *Trisopterus luscus*, GSI sharply decrease as spawning progress without further eggs replacement (Alonso-Fernández *et al*., 2008). Large fluctuation in GSI is likely associated to the presence of different reproductive phases and different fish sizes in the spawning stock, i.e., an asynchronicity in the spawning activity within the mature stock. The influence of fish size on gonad development has been evinced in the northern anchovy *Engraulis mordax* in which small fish usually have a lower GSI than larger one and this effect increases with ovary development (Hunter & Golber, 1980). Shepherd & Grimes (1984) found in weakfish (*Cynoscion regalis*) that GSI was size-dependent and that larger fish develops their gonad earlier than smaller fish and therefore spawn earlier. However, Lowerre-Barbieri, Chittenden

& Barbieri (1996) did not found that evidence in weakfish based in GSI data, and attributed this relationship to a temporary presence of the species in the study area, because migratory behaviour. In our study, spawning activity shifted considerably among female size classes, and the decrease in the activity along the spawning season was also related with fish size, i.e., smaller females have an earlier spawning cessation, coupled to the finalization of the rainy season (November), while larger females have a more extended spawning season, till February, and this may explain the protracted spawning season of the species. This spawning structuring, already observed in other species (Alonso-Fernández & Saborido-Rey, 2011) may explains the observed variations in GSI for the whole population.

Mean GSI ranges from 1% to 4% being relatively low in comparison with other freshwater fish of the Characidae family as *Oligosarcus jenynsii* (1% to 8%) and *Oligosarcus robustus* (1% to 10%) (Nunes, Pellanda & Hartz, 2004), which might indicate a relatively lower energy investment in reproduction, but bioenergetics studies would be necessary to test this hypothesis.

From January to April, when generally no reproduction takes place, the fish condition sharply improve in terms of gaining body weight, probably due to intense feeding and to the low spending energy, reduced to nourishment and swimming activity, as shown in other species (Dutil, Lambert & Chabot, 2003). The intense feeding during these months could be a strategy to accumulate energy during periods when food is available to be subsequently allocated to reproduction as reserves used on vitellogenesis (Barbieri, Hartz & Verani, 1996). However, from May to December, when the condition of the fishes largely fluctuates, it experiments small but significant decrease. The decrease of K in May is the first evidence of energy utilization and might be related to the onset of ripening, since variations in K primarily reflect state of sexual maturity (Williams, 2000). The decline of K the following months is attributed to the yolk accumulation (vitellogenesis), since as pointed out before, GSI is higher in July. Lowest condition when gonad is fully developed indicates a major resource transfer to the gonads during the reproductive period (Vazzoler, 1996). The fact of condition decreasing along spawning season indicates a continuous use of stored energy, as a capital breeder (Alonso-Fernández & Saborido-Rey, 2012). The condition factor, K, decreased rapidly when the eggs are released in salmonid fish (Brown trout, *Salmo trutta*, rainbow trout, *Oncorhynchus mykiss* and chinook salmon, *O. tshawytscha*) (Barnham & Baxter, 2003).

Based on the available energy reserves in cod, Dutil & Lambert (2000) found that two distinct groups of fish participate in reproduction: early spawners having lower fat reserves and late spawners having good condition fish. In *B. guatemalensis*, the decreasing tendency of K till September followed by a recuperation of the physiological condition in October support the idea of size structuring of the spawning activity as discussed earlier, i.e., some females are early spawners and cease their reproductive activity while others continue spawning and become later spawners.

Lizama & Ambrosio (2002) compared the condition factor of nine species of Characidae family and found greater differences in K along the year, however in all species K decreased with the onset of the spawning and in most of them highest K occur in the smallest fish length. This pattern is unclear in *B. guatemalensis* since K in smaller and larger females showed a high variance, except in female close to spawn, i.e., spawning capable phase, in which highest K occur in smaller females. The decoupling pattern of both GSI and K along the spawning season and the influence of fish size, support the idea of size structuring spawning discussed earlier, which induce a population asynchrony, mainly in the spawning cessation.

The seasonal patterns observed in *B. guatemalensis* contribute to confirm the high diversity of seasonal patterns found in the Characidae family, revealing the complexity of its life history, and support the hypothesis that reproductive seasonality in the characids is controlled by the environmental condition and body size (Kramer, 1978a). In our study the rainy season seems to be the trigger of spawning season and the duration and timing of the spawning are female size-dependent. One fact that favours the size segregation of spawning activity is the competition for breeding sites (Kramer, 1978a), since *B. guatemalensis* needs to excavate holes (nests) in sandy bottoms for placing the eggs (Greenfield & Thomerson, 1997; Bussing, 2002) and therefore sand ground is a limited resource. Also inter-specific competition for breeding sites may exist with, for example, *Cichlasoma citrinellum* (recently: *Amphilophus citrinellum*) which breed in sand grounds between depths from 3.0 to 6.0 m, in a 30 cm holes (McKaye, 1977). Thus, competition for the suitable environment for releasing eggs can take place and migrations may occur. Segregation in timing of spawning may be a clear advantage reducing competition. However, further studies are needed since discrepancies exist about *B. guatemalensis* spawning grounds, e.g., Horn (1997) mentioned the migratory habits upstream (towards the lakes) of *B. guatemalensis* for spawning or perhaps feeding, on the contrary McLarney *et al*. (2010) indicate that this species inhabits the lakes of Nicaragua and moves into tributaries to spawn.

Maturity

Maturity has been poorly studied in *B. guatemalensis* and other species of the Characidae family. Maturity ogives and the corresponding size at 50% maturity are commonly used in fisheries management in many ways, but mostly to estimate spawning stock biomass and to establish a minimum landing size, and often biological reference points are also based on these estimations. In data limited stocks L_{50} can be critical to establish size-based indicators (SBIs) as management procedure (Shin *et al*., 2005). In the Lake Nicaragua there is no specific regulation for *B. guatemalensis*. Hence, a proper estimation of L_{50} is required.

The L_{50} macroscopically determined in the present study was 34.9 cm, which was close to L_{50} (34.6 cm) estimated from an empirical relationship between length at first maturity and asymptotic length (Froese & Binohlan, 2000). However, these values are well above the L_{50} microscopically estimated, 27, 3 cm. Macroscopic classifications of the gonad stages methods produce many uncertainties and interpretation errors should be assessed when macroscopic classification of gonads stages are carried out, that because boundaries, between different development stages, are subjectively estimated (Williams, 2007). The misclassifications and uncertainties may introduce bias in the L_{50} estimation. The sub or over-estimation of L_{50} can induce unreliable management measures that should ensure the protection of the immature stock. Also the onset and cessation of the spawning season, i.e., the duration of the season, can be wrongly estimated if females at immature and recovery phases are confounding, as often occur when maturity is staged macroscopically (Murua *et al*., 2003; Domínguez-Petit *et al*., 2008).

To reduce errors in macroscopic staging, it has been recommended to estimate maturity ogive only during the spawning season (Hunter & Macewicz, 2003). However, in spite in this study maturity ogive was estimated in different periods including the spawning season, still unreliable results were obtained. Moreover, the size distribution of immature and mature females complete overlap, and even the smaller fish sampled were determined as mature. The uncertainties of macroscopic observations indicate that relying on this procedure is no longer feasible especially when the results have an implication for the management regulations.

Histological (microscopic) determination of L_{50} in *B. guatemalensis*, considering in the analysis whole year period or the spawning season only, showed no differences, and was estimated in 27.3 cm. The lack of discrepancy of these results supports the robustness of the microscopic method, which generates less biased estimates of maturity (Hunter *et al*., 1992).

The great majority of species studied in Paraná River, included species of Characidae family, reach maturity with less than 20 cm in length (Agostinho, Vazzoler & Thomaz, 1995), e.g., L_{50} in *Brycon opalinus* were about 18 cm (Gomiero & Braga, 2007). Differences in length at maturity between Paraná River and the lake environments have been observed in *Prochilodus lineatus*, that mature at larger sizes in lakes (Agostinho *et al*., 1993), indicating that different stocks can occur in similar environments. However, larger L_{50} has been reported for *B. hilarii*, 26.6 cm (Vicentin, Costa & Súarez, 2012). Size at maturity is known to be a highly plastic parameter sensible to growth rate, food availability and feeding capacity, including foraging behaviour (Saborido-Rey & Kjesbu, 2005). Consequently it often changes under external pressure, such as intensive fishing or environmental factors (Trippel 1995; Dominguez-Petit *et al*., 2008; Cook & Heath, 2005). Although it normally shows density-dependent phenotypic plasticity, genetic changes have been also reported (Pérez-Rodriguez, Morgan & Saborido-Rey, 2009). Shifts in maturation severely determine the population dynamics (Saborido-Rey & Trippel, 2013). There are not historical data on maturity in *Brycon guatemalensis*, and then it is not possible to analyse changes in length at maturity. Therefore, it is highly advisable to conduct maturity studies on regular basis in *B. guatemalensis* in the lake and in the main tributaries.

Fecundity

A number of evidences analyzed indicated that *B. guatemalensis* shows determinate fecundity. The presence of a major gap between the reservoir of small unyolked (primary growth) oocytes and the dominant population of larger and more advanced development oocytes stages or leading cohort, in mature ovaries, indicates that the ovary dynamic of *B. guatemalensis* adjust to the “group-synchronous” type ovary organization described by

Wallace & Selman (1981) which has been associated with iteroparous species with determinate fecundity (Hunter & Macewicz, 1985; Murua & Saborido-Rey, 2003). At the same time the decreasing tendency of the number of oocytes present in the ovary during the spawning season (NDO and RNDO) indicates a lack of oocyte recruitment to the leading cohort during the spawning confirming the determinate fecundity in *B. guatemalensis*. The leading cohort, i.e., oocytes in VIT2 or GVM clearly dominate the oocyte frequency in spawning capable females, although a second cohort of developing oocytes, at initial vitellogenesis stage (VIT1), was present in the majority of spawning capable females. But the modal progression pattern of both oocytes cohorts differs notably, and while the leading cohort develops, the second remains at the same small diameter, generating also a clear size gap of more than 1 mm between these cohorts. The second cohort was probably the one entering in atresia at the end of the spawning season (December and January). Moreover, the number of oocytes of the leading cohort was five times larger on average than the number of oocytes in the secondary cohort. Because oocytes of the leading cohort entered in GVM at the same time, it probably indicates that *B. guatemalensis* spawn only one batch in each breeding season, i.e., it is a total spawner (Murua & Saborido-Rey, 2003). If a second batch is spawned (recruited from the few oocytes of the secondary cohort) it must be considerably smaller in numbers. Nevertheless, in six specimens the number of oocytes in the secondary cohort was 1.5-3.5 times larger than the leading cohort. There are two possible explanations, either some specimens spawn more than two batches, or, more likely, in those specimens the oocyte recruitment from VIT1 to VIT2 was not yet finalized, underestimating the size of the leading cohort. Therefore, the estimated number of oocytes in the leading cohort, the one closer to be spawned and composed by larger oocytes (>1000 µm) should be considered as the potential annual fecundity.

The potential annual fecundity was highly variable, between 700 and 35,500 eggs (mean 11,013 ± 6,697), well above the fecundity of other characids as *Bryconamericus iheringii* in which fecundity range from 370 to 1600 (933.71 ± 303.10) and *Bryconamericus stramineus* from 98 to 1100 (371.3 ± 244.6) (Lampert, Azevedo & Bernhardt, 2004; 2007), although the size structure of both populations differs notably with *Brycon* to establish a sound comparison. But fecundity was in the same order as in *Salminus hilarii* (Characidae family) with a similar female size range (Honji *et al*., 2009). Atresia occurred along the spawning season with very low incidence (4 %), and generalised atresia was observed only in two females at the end of the spawning period (December and January, respectively) coinciding with the cessation of the spawning season, which is typical in most of seasonal spawning fish (Hunter & Macewicz, 1985). The low prevalence of atresia can be the result of a rapid turnover rate that makes difficult to find this structure in a standard field sampling. However, given the known duration of atretic stages in other species which always are above several days (Hunter & Macewicz, 1985; Miranda *et al.,* 1999; Witthames, Thorsen & Kjesbu 2010), unlikely rapid atresia degeneration may explain the low prevalence. The low number of generalised atresia might indicate reproductive success, since, the high incidence of atresia has been linked to a reproductive failure, e.g., in Fathead Minnows (*Pimephales promelas*) was established a critical threshold value of 20% as indicative of potentially impaired reproduction (McCormick, Stokes & Hermanutz, 1989). Although atresia has been acknowledged as mechanism to regulate fecundity (Hay & Brett, 1988), the low prevalence seems to not affect fecundity, and therefore we can conclude that atretic losses did not constitute an important fraction to be considered in the potential annual fecundity.

Fecundity is considered to be a key factor in population dynamics (Hilborn & Walters, 1992; Marshall *et al*., 2003) that evolves temporally and spatially within a given species. Fecundity is a highly plastic trait, showing inter and intra-specific variations. Differences in fecundity among species often reflect different reproductive strategies (Pitcher & Hart, 1982; Wootton, 1984; Murua & Saborido-Rey, 2003). Within a certain species, fecundity could vary in response to particular environmental conditions of a specific habitat, as latitudinal variability (Witthames *et al*., 1995). Even annual and long-term changes in fecundity were reported within a fish stock (Horwood, Bannister & Howlett, 1986; Rijnsdorp, 1991; Kjesbu *et al.*, 1998) and changes among successive reproductive periods and between individuals with same size in the same reproductive period (Vazzoler, 1996). Generally, it is known that fecundity is proportional to female size/age and condition (Kjesbu *et al.* 1991; Marshall *et al.* 1998, 1999; Cooper *et al.,* 2013). It is the case of *B. guatemalensis* in our study where fecundity was positively determined by fish size and weight, but allometric coefficient obtained with the relationship between fecundity and fish size was well above three indicating that larger females produce more eggs than predicted by weight, i.e., showing higher reproductive potential. The importance of stock reproductive potential is further discussed in Chapter 6.

Although fish weight is a reliable indicator of the capacity of oocytes production also, it depends on many biotic (e.g., food availability) and abiotic (e.g., environmental stress) factors, and may vary along the year (Bagenal, 1967), being fish size a more reliable predictor of fecundity (Thorsen, Marchall & Kjesbu, 2006). However, this seems to be species-dependent since the fecundity and fish weight shows a better relationship in *Bryconamericus iheringii*, whereas in *Bryconamericus stramineus* no differences were obtained between fecundity and female size and weight (Lampert, Azevedo & Bernhardt, 2004; 2007). Moreover, larger females produce also bigger oocytes, as shown by the fairly good correlation between fecundity and oocyte diameter, also found in other determinate fecundity species as Dover sole (Hunter *et al*., 1992). These findings may have importance understanding recruitment process in *B. guatemalensis*, since larger eggs presumable produce larger larvae with higher possibilities of surviving (Hislop, 1984), as they grow faster and are more resistant to starvation (Berkeley, Chapman & Sogard, 2004b). The diameter of fully mature oocytes of a 42 cm female from this study (2.17 ± 1.36 mm) was similar to that reported for a same size fish keep under controlled condition (2.31 ± 0.08 mm, Molina, 2006), but considerably larger than *Salminus hilari* which, in wild, produce eggs of no more than 1.4 mm (Takahashi, 2006).

The individual distribution pattern of the oocytes development stages, observed in each females along the spawning season, evidence the spawning asynchrony among females and partially explain the protracted of the spawning period (6-8 month). Although fishes of determinate fecundity typically have short spawning seasons (1-2 month), and protracted spawning seasons are typical from fish with indeterminate fecundity, also species with determinate fecundity show long seasons (six month) as Dover sole (Hunter *et al*., 1992). In *B. guatemalensis* the protracted spawning season can be the consequence of differences in reproductive behaviour among different size classes, both in terms of reproductive timing, condition, egg production and egg quality as shown above, that may indicate intra-specific spawning competition, which may explain the occurrence of the greatest reproductive event of the species in July. Kramer (1978a) studied six species of the Characidae family, and indicated some competition level in relation to the duration and timing of the reproductive period. Nevertheless, females spawning late in the season seem to perform worst, as indicated by the decrease in egg size in *B. guatemalensis* as spawning season progress. Normally females have high energy reserves early in the spawning season and thus may have more resources to produce more yolked and larger oocytes (Lowerre-Barbieri, Chittenden & Barbieri, 1996). With the ongoing spawning season of *Brycon* the frequency of larger oocytes becomes lower, which could be a response of the decrease of energy supply reflected in the condition factor decline, but also to changes in the environmental condition, from rainy to dry season, which might induced oocyte maturation at smaller size.

The potential annual fecundity of *B. guatemalensis* could be estimated by using the calibration curve obtained from the relationship of the oocyte diameter (OD) and the number of oocytes per gram of ovary weight (NO) since both set of observation fit well and were highly correlated. This correlation type named *the auto-diametric fecundity method* was developed by Thorsen & Kjesbu (2001) to estimate the potential fecundity of Atlantic cod, and has been applied with successful result in other species, especially those with group-synchronous ovary development and determinate fecundity from northern latitudes (Lambert, 2008; Alonso-Fernández *et al.*, 2009; Witthames *et al.*, 2009; Thorsen *et al.,* 2010). The method has also being applied in species characterized by asynchronous oocyte development and determinate fecundity (Alonso-Fernández *et al.*, 2009; Alonso-Fernández, 2011). The application of the *auto-diametric fecundity method* will ease considerably the routine estimation of fecundity and hence improve our knowledge on egg production and reproductive potential.

The reproductive strategy study on *B. guatemalensis* should contribute to improve fishery management and therefore the sustainability of its exploitation (See Chapter 5 and 6). This is the first time that reproductive cycle, and particularly spawning season, is defined based on a detailed histological analyses. Our findings can lead to adoption of closed season that currently is not implemented. A better estimate of L_{50} on histological bases shows that it matures at lower size (27.3 cm) than the one reported based on macroscopic observations, which has a great implication for assessment and management. Finally, it has been shown that larger females own larger reproductive potential. Hence, these results are used to evaluate the impact of fishing on the spawning stock size or biomass (SSB) and the stock reproductive potential (SRP) to be applied in the management of the species, in the next chapter.

CHAPTER 5: Reproduction in Fisheries Management

5.1. Introduction

In order to make sustainable the fishery activity, the fisheries management action requires the good understanding of the methods of exploitation of fish stock and the biological response capacity of the stock to a defined level of exploitation. The establishment of a minimum landing size (MLS) is one of the most common management measures to prevent overexploitation, particularly in data limited stocks exploited by the small-scale fisheries. Often this technical measure is reinforced with regulations on fishing gears mesh size. Generally, legal mesh size is determined combining gear selectivity and length-at-maturation (L_{50}) of the target species. The last aim is the protection of the immature or juvenile component of the stock, a measure that often is considered enough to ensure the sustainability of the fishery since it allows the fish to reach maturation and spawn at least once.

Although the protection of juveniles and the spawning stock biomass has been the focus of sustainable fisheries management, there is increasing evidence that these efforts are not sufficient to avoid overexploitation (Saborido-Rey & Trippel, 2013). The demonstrated higher contribution of larger fish to stock productivity has shown that conserving sufficient reproductive potential of the exploited stock is a determinant factor for stock sustainability (Berkeley *et al.,* 2004a; 2004b, Bobko & Berkeley, 2004; Birkeland & Dayton, 2005; Kjesbu, 1989); Trippel, 1999; Winters, Wheeler & Stansbury, 1993; Lambert, 2008). Thus, it is essential to implement stock reproductive potential into assessment advice for harvested marine species (Morgan *et al*., 2012) protecting the most productive stock fraction through management actions. Therefore, a management measure, now required to achieve maximum sustainable yield (MSY), should ensure the conservation of stock productivity which is linked to egg production and stock structure, both affecting the estimation of MSY (Cerviño *et al*., 2012).

Gillnets are the most common fishing gears used in small-scale fisheries (Hovgård & Lassen, 2000). Gillnets are known to have a dome-shaped selectivity curve, which reflects size-specific probabilities of capture that increase from near 0 to a maximum before declining symmetrically with further increases in fish size to values near or equal to 0 (Hamley, 1975).

Thus gillnet shows a higher selectivity in comparison with bottom trawl (Martín, Sartor & García-Rodríguez, 1999) and can be controlled to avoid catch fish below and above given sizes, i.e., on a desirable size range (Gulland, 1983). In the Lake Nicaragua gillnets are widely used and due to high species diversity and richness (Koenig *et al*., 1976; Bussing 1976, and see Chapter 3), many different species can be caught by the same gillnet. Fisheries in the lake target 31 species caught with different fishing gears (trawl, bag seine and gillnet), and out of these, 19 are caught mostly by gillnets (Orellana, 1986). In the eastern side of the Lake, where most of the fishery is found, 24 species are fished by gillnets (Hernández-Portocarrero & Saborido-Rey, 2007). *Brycon guatemalensis* or Machaca is one of the most fished species because of its high biomass (Orellana, 1986; see Chapter 3). Overall, the fisheries management measures in the Lake Nicaragua mainly consist in the regulation of the mesh-size derived from catches and effort data, abundance of the species, indirect estimations of biomass (Orellana, 1986; Gadea, 2003) and by combining the results of the size at 50% maturity (macroscopic determination) with gillnet selectivity (Hernández-Portocarrero & Saborido-Rey, 2007).

Selectivity studies are requested for a proper management, as optimal mesh size contribute in obtaining the maximum yield (McCombie, 1961), protecting small fish and minimizing escapement of injured or dying fish (French & Dunn, 1973). Gillnet selectivity, usually described by curves, one for each mesh size, show how the probability of catching a fish changes according to its size (Hamley & Regier, 1973), nevertheless fish population are heterogeneous not only in size, but also in age, sex, condition, behaviour, habitat, etc., subsequently each individual is not equally vulnerable to the same fishing method. Fishing involves several aspects: time and space overlapping of fish and fishing activity, fish interaction with fishing gear and finally fish probability being caught by gears (Hamley, 1975). Despite most of selectivity studies are focused on relationship between fish and mesh size, some studies demonstrated the influence of other factors like fish behaviour (Clark, 1960) or maturity stage and fish shape (McCombie & Berst, 1969) on gillnets selectivity patterns. As the environmental factors influence the reproductive dynamic and behaviour of the species (Kramer, 1978a; Honji, *et al*., 2009; Andrade & Braga, 2005; Lowe-McConnell, 1987), these factors should be also considered in selectivity studies.

From chapter 4 we know that females annual reproductive cycle of *Brycon guatemalensis* is characterized by the presence of developing phase along the year, and a protracted spawning season from July to December, with a higher spawning fraction occurring in July and August. Also that fecundity studies indicated it has determinate fecundity, and that larger female has a higher reproductive potential both in terms of quantity, i.e., egg production and quality, i.e., larger eggs.

The data collected from females of *B. guatemalensis* in the lake are used in the present study to introduce several aspect of the biology of the species that contribute to improve the management, such as the influence of reproductive strategies and tactics of the females on the catches and vice-versa the effect of the gillnets on the immature portions of the stock, the spawning stock size or biomass (SSB) and the stock reproductive potential (SRP). Besides, the influence of reproductive behaviour pattern on catches and its relation with the dry and rainy season of the year is also studied. Finally, some alternative management measurements are provided.

5.2. Results

In this section, it is analyzed the gillnet selectivity effect on i) the population size structure of *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* and *Brycon guatemalensis*, on both sexes, and ii) on the length at 50 % maturity of these species. The effect of each net mesh size on the reproductive phases and egg production is also analyzed but only in *B. guatemalensis*.

5.2.1. Gillnet selectivity

Gear selectivity analyses were performed on *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* and *Brycon guatemalensis*. Four nets of mesh size 75, 100, 125 and 150 mm stretch mesh were used (see Chapter 2, Material and methods for details). Table 38 shows the estimated parameters of the selectivity curves for each species and the observed and estimated values of the catch. The number of specimens captured for *H. nicaraguensis* and *P. managuensis* in the largest net (150 mm) was very low and thus abundance was not estimated. The optimum length (OL) and selection factor (SF) estimated in all mesh size was lower for *H. nicaraguensis*, followed by *A. citrinellus*, *P. managuensis* and being the highest in *B. guatemalensis*, and particularly the SF decreases with the increasing mesh size (Table 38). The differences of SF estimated in the 75 mm mesh size are smaller between *A. citrinellus* and *H. nicaraguensis* (0.5) which are species similar in body height and shapes, and much higher (1.6) between *P. managuensis* and *B. guatemalensis*.

Males of *A. citrinellus*, *H. nicaraguensis* and *P. managuensis* were captured in higher number in each net during the whole study period (Table 39), except in the case of *P. managuensis* in which male and females were captured in similar number in the smaller net of 75 mm (Figure 98). Especially high value was observed in *H. nicaraguensis* in the 75 mm net. On the contrary females of *B. guatemalensis* were more often caught in all gillnets although sex ratio was, nevertheless more similar than in the other species (Table 39). Figure 98 shows the catches by month, sex and mesh size (with the 125 ad 150 mm nets pooled as one) for each species. Males and females catches of *A. citrinellus* fluctuated without a clear trend, both along the year and among nets. Similarly *H. nicaraguensis* catches fluctuated, but showing a decreasing trend with lower values towards the rainy season of the year, especially in males.

Table 38. Observed parameter of the captured specimens (male and females) and the estimated parameters from the gillnet selectivity analysis, by mesh size net tested in the Lake Nicaragua.

		Mesh size of the net (mm)			
Species/ Parameters	**Total**	**75**	**100**	**125**	**150**
Amphilophus citrinellus	**Observed**				
Number of specimens (♂+♀)	6745	5198	1322	197	28
Observed mean length in cm		18.4	21.7	22.5	23.5
Size range in cm		11-27	12-29	15-30	19-29
Observed modal length in cm		18.0	23.0	23.0	25.0
	Estimated				
Abundance (A)	8154	5674	1865	612	3
Estimated mean length in cm		18.6	20.7	22.4	29.0
Standard Deviation		1.869	2.801	1.514	--
Optimum length (OL) in cm		17.9	23.8	29.8	35.7
Selection factor (SF) for each net		6.142	7.219	5.027	--
Selection factor (SF) whole set of net	5.952				
Hypsophrys nicaraguensis	**Observed**				
Number of specimens (♂+♀)	1653	1419	214	18	2
Observed mean length in cm		16.7	16.3	17.0	16.0
Size range in cm		11-20	12-21	15-18	16.0
Observed modal length in cm		17.0	16.0	18.0	--
	Estimated				
Abundance (A)	2229	1595	634	--	--
Estimated mean length in cm		16.7	16.1	--	--
Standard Deviation		1.380	1.007	--	--
Optimum length (OL) in cm		15.9	21.2	26.5	--
Selection factor (SF) for each net		6.661	4.477	--	--
Selection factor (SF) whole set of net	5.300				
Parachromis managuensis	**Observed**				
Number of specimens (♂+♀)	724	655	62	6	1
Observed mean length in cm		23.2	28.2	31.4	31.0
Size range in cm		19-30	20-35	22-35	31.0
Observed modal length in cm		23.0	28.0	35.0	--
	Estimated				
Abundance (A)	871	762	99	10	--
Estimated mean length in cm		23.1	27.1	33.2	--
Standard Deviation		2.2	2.9	1.3	--
Optimum length (OL) in cm		22.8	30.3	37.9	--
Selection factor (SF) for each net		7.922	7.382	--	--
Selection factor (SF) whole set of net	7.586				
Brycon guatemalensis	**Observed**				
Number of specimens (♂+♀)	2927	1769	929	164	65
Observed mean length in cm		29.1	35.6	39.8	41.8
Size range in cm		17-48	18-45	22-49	27-51
Observed modal length in cm		29.0	34.0	40.0	45.0
	Estimated				
Abundance (A)	4476	2759	1312	285	120
Estimated mean length in cm		29.6	36.0	39.6	45.9
Standard Deviation		2.8	4.1	2.8	1.3
Optimum length (OL) in cm		26.7	35.6	44.4	53.3
Selection factor (SF) for each net		9.517	9.129	8.291	--
Selection factor (SF) whole set of net	8.801				

For this species catches of both sexes decreased notably in the largest mesh size net. Somehow a similar pattern is observed in *P. managuensis* in the 75 mm net where catches of both sexes decreased during the dry season and the lower catches were observed at the beginning of rainy season. From that period catches increased at the same level in both sexes, with unusual high values in October. Different to the observed in cichlids, in *B. guatemalensis* female were captured in higher number than males, but the decreasing pattern toward the rainy season was also observed in both sexes in the two largest mesh sizes nets, while there was not a clear pattern in the 75 mm net.

Table 39. Average sex ratio (male: female) for each species captured in the Lake Nicaragua and mesh size net.

Species / Mesh size net	Sex ratio (♂ : ♀) 75 mm	 100 mm	 >125 mm
Amphilophus citrinellus	1.4 : 1	3.9 : 1	5.3 : 1
Hypsophrys nicaraguensis	22.8 : 1	4.9 : 1	--
Parachromis managuensis	1.1 : 1	2.3 : 1	--
Brycon guatemalensis	1 : 1.2	1 : 1.5	1 : 1.5

The selectivity curves for the different gillnet combination by species were obtained by plotting the probabilities of captures against fish size (Figure 99). Differences in width reflects the fish size range captured and hence the efficiency of the net. The nets captured the wider size range of *A. citrinellus* and *B. guatemalensis* while narrower size ranges were captured of *H. nicaraguensis* and *P. managuensis*.

The size distributions of estimated abundance for the four species, male and female together, are shown in Figure 100. *H. nicaraguensis* shows the smaller sizes and narrower size range but relative high abundance, *A. citrinellus* and *P. managuensis* shows similar size range (10 cm) but towards largest size in the latest. *B. guatemalensis* is the largest fish among the four species analyzed, with the wider size range, but also with the largest minimum size captured. *H. nicaraguensis* and *P. managuensis* were most captured in the 75 and 100 mm nets, *A. citrinellus* was captured in higher portion in these two nets but also in the 125 mm nets, whereas *B. guatemalensis* was captured in all nets. In summary, selectivity factor was quite different for these species.

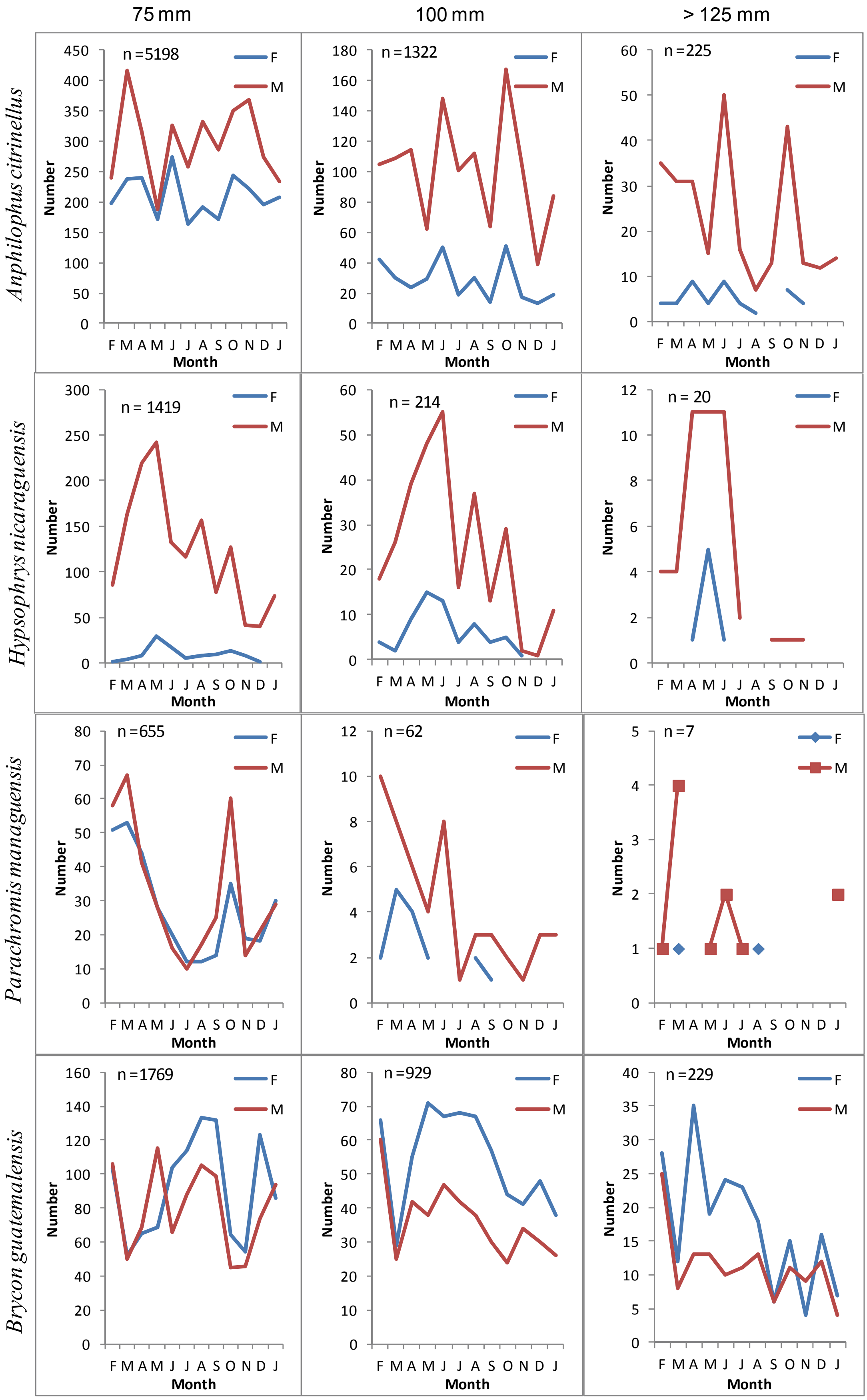
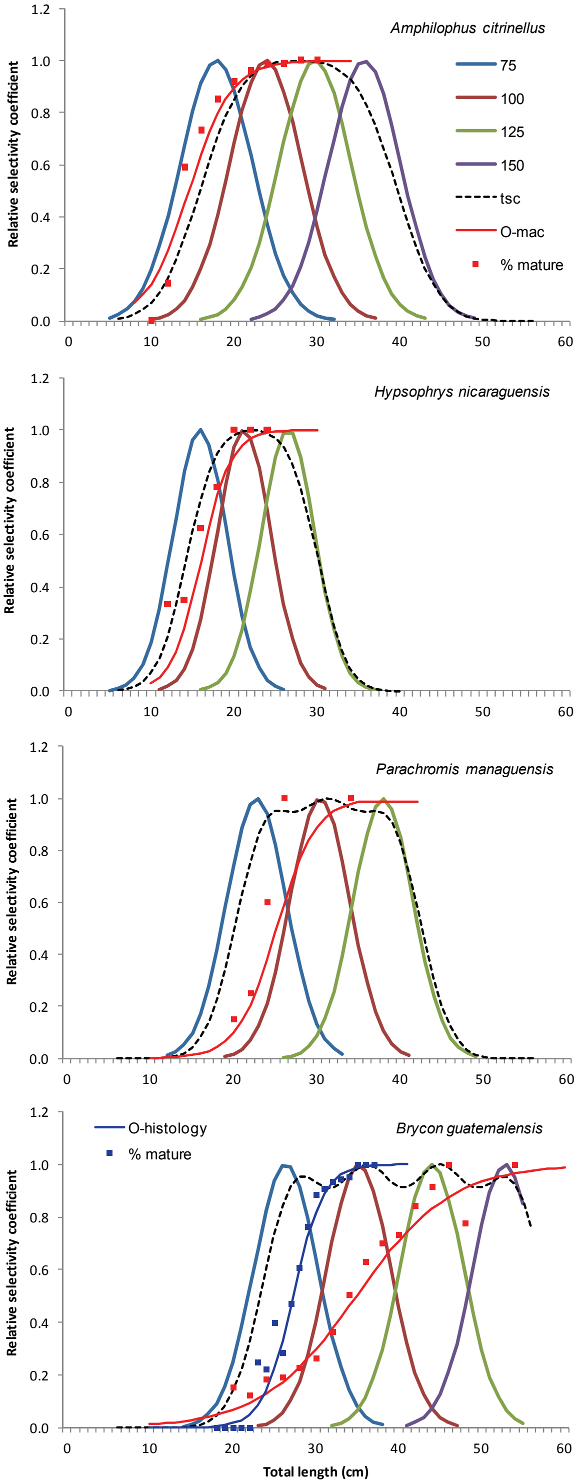


Figure 98. Monthly patterns of captures, showing the male and female capture in numbers, by species and mesh size of the nets.



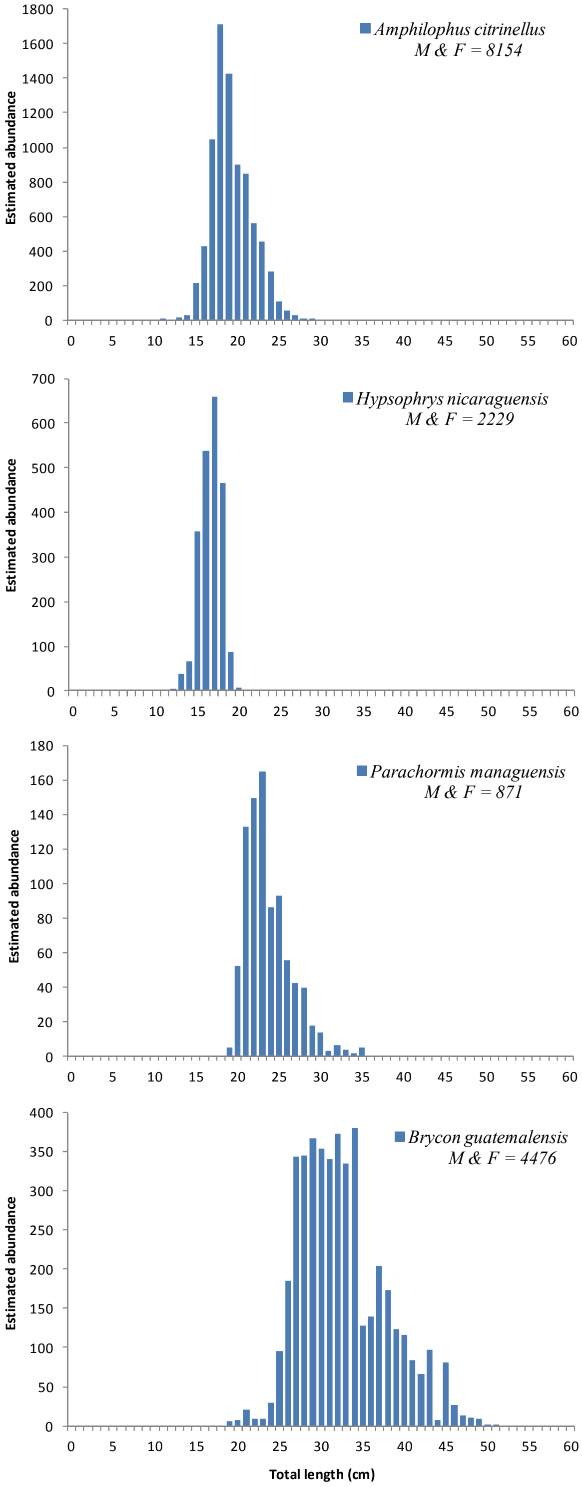


Figure 99. The relative selectivity curves of four mesh sizes tested: 75, 100, 125, and 150 mm stretch mesh, the total selectivity curve (thick dashed lines), O-mac (macroscopic ogives) and O-histology (microscopic ogives) for each species.

Figure 100. Length-frequency distribution of estimated abundance of males and females of *A. citrinellus, H. nicaraguensis*, *P. managuensis* and *B. guatemalensis*.

5.2.1.1. Selectivity and maturation

The macroscopic maturity ogives of *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* and *B. guatemalensis* are shown in Figure 101. The length at 50 % maturity (L_{50}) estimated for *A. citrinellus* and *H. nicaraguensis* were based on male data, while for *P. managuensis* and *B. guatemalensis* on female data (see Material and Methods). The data fitted significantly to a logistic regression ($p<0.01$), although in *H. nicaraguensis* there was a general lack of immature fish, as it was, in less extent, in *A. citrinellus*. The corresponding size at 50% of maturity (L_{50}) for each species is shown in Table 40.

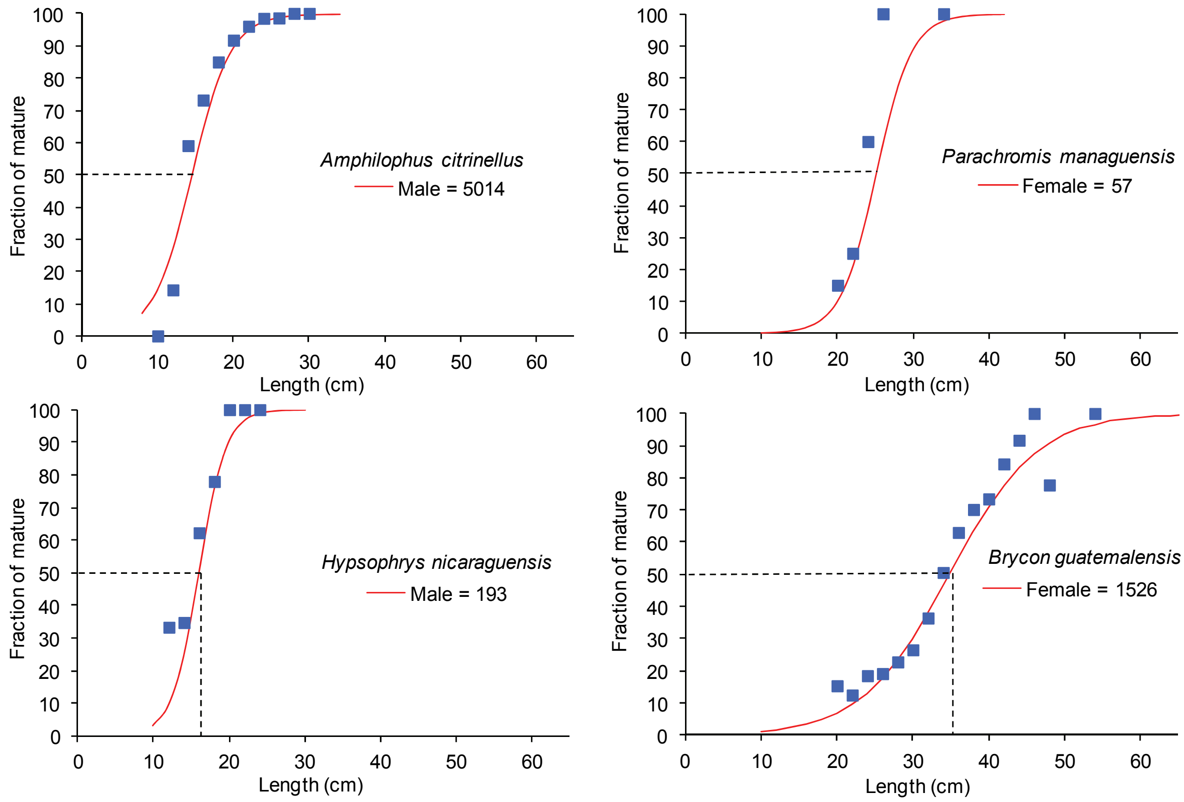


Figure 101. Maturity ogives of *A. citrinellus, H. nicaraguensis P. managuensis* and *B. guatemalensis.*

Table 40. Length-at-50% maturity (L_{50}) and optimum length (OL) estimated by net mesh size of four species captured in the Lake Nicaragua. * estimated in males; ** estimated in females.

	L_{50} (cm)		OL: Mesh size (mm)			
Species	Macroscopic	Microscopic	75	100	125	150
Amphilophus citrinellus	* 14.6		17.9	23.8	29.8	35.7
Hypsophrys nicaraguensis	* 16.1		15.9	21.2	26.5	
Parachromis managuensis	**25.2		22.8	30.3	37.9	
Brycon guatemalensis	**34.9	**27.3	26.7	35.6	44.4	53.3

For each species the macroscopically estimated L_{50} and the optimum length (OL) at each mesh size of the gill nets are presented in Table 40, and L_{50} are plotted in Figure 99. All L_{50} of cichlids felt in the area of the curve where these lengths had more than 80 % probability of being captured in the 75 mm mesh size. Instead, the L_{50} estimated for *B. guatemalensis* had 100 % probability of being captured in the 100 mm mesh size (Figure 99) since both L_{50} and OL were similar (Table 40). Considering the maturity ogives based on macroscopic determination, the higher proportions of immature fishes, within each mesh size, were captured in the smaller mesh size, i.e., 75 mm, except for *H nicaraguensis* which higher proportion of immature were captured in the 100 mm net (Table 41). In mesh size larger than 100 mm this proportion notably decreased, excepting for *B guatemalensis* that decreased steadily (Table 41).

On the other hand, considering the estimated maturity ogives obtained by histological procedures (only for *B. guatemalensis*, see section 4.2.3), the 75 mm net captures 28.1% of immature fish, while the proportion of immature captured by the 100 mm net drop to 4.5% (Table 41). The larger mesh size analyzed (125 and 150 mm) only capture mature fish. The L_{50} estimated for *B. guatemalensis* in 27.3 cm slightly above from the optimum length (OL=26.7 cm) of being caught estimated for the net of 75 mm mesh, therefore, the L_{50} estimated fall in the range of 24 to 30 cm at which the net has 80 % efficiency (Figure 99), confirming that this net is highly efficient in capturing specimen around the L_{50}.

Table 41. Proportion of immature fish captured within each mesh size net of each species, based on macroscopic and microscopic maturity ogives.

	Net mesh size (mm)			
Species	75	100	125	150
	From macroscopic ogives			
Amphilophus citrinellus	19.2	12.1	4.9	0.3
Hypsophrys nicaraguensis	53.3	62.6		
Parachromis managuensis	68.0	34.8	3.5	
Brycon guatemalensis	74.1	44.7	28.2	8.9
	From microscopic ogives			
Brycon guatemalensis	28.1	4.5	0.2	0.0

5.2.2. Selectivity and reproduction on female *B. guatemalensis*

The female size structure of *B. guatemalensis* examined (n = 1643) ranged between 13.2 and 55.5 cm of total length, with average length of 32.2 ± SD 5.34 cm. The females presented a bi-modal distribution with modal lengths of 28 and 37 cm, respectively (Table 42). Smaller individuals than 13 cm were not available to the gears and individuals larger than 45.0 cm were caught in low frequencies, whereas specimens between 25.0 and 40.0 cm were the most frequently caught.

Most of the specimens were caught in the smaller mesh size panel, 75 mm (Table 42), and the size range caught by each mesh size was quite similar, 27 cm, except for the 100 mm net, 30 cm. The observed female mean length increases with mesh size, with a decreasing rate (6.8, 4.9 and 1.7 cm) and the modal lengths shifted from 28.0 cm in the 75 mm to 37.0 cm in the 100 mm net, i.e. 9 cm, while the shift between the other nets was 3 and 4 cm respectively (Table 42).

The estimated parameters from the gillnet selectivity analysis are shown in Table 43. For each mesh size net, the optimum length for being catch (OL) increases with mesh size, while, the selection factor (SF) decreases. The SF and the OL obtained for each net (75, 100 and 125 mm), considering females only, were virtually the same than those obtained when considering males and females together (Table 43 and Table 38, respectively), reflecting not only the relation of mesh size and length, but a similar behaviour, in relation with net retention, of males and females.

The observed and estimated length parameters (Table 42 and Table 43) were compared with the optimum length (OL) from the selectivity modelling (Figure 102). While these values were similar at 75 and 100 mm mesh size, they differed in the larger mesh size, i.e., 125 and 150 mm, by 4.4 and almost 10 cm respectively. The selectivity curves for the different gillnet mesh sizes (Figure 103) shows the probability on capturing fish at different length classes. Although 75 mm mesh size captures more fish, the 100 mm net captures almost the whole size range of the population.

Table 42. Length parameters of the females caught and retained in each mesh size of the net.

		Mesh size (mm)			
Observed parameters	Total	75	100	125	150
Number of specimen caught (n)	1643	940	554	101	48
Observed female mean length (OM) in cm	--	28.8	35.6	40.3	42.0
Size range in cm	13-55	13-40	15-45	22-49	28-55
Observed female modal length (OMo) in cm	--	28.0	37.0	40.0	44.0

Table 43. Estimated parameters from the gillnet selectivity analysis of four mesh size of the net tested.

		Mesh size (mm)			
Estimated parameters	Total	75	100	125	150
Abundance (A)	2315	1326	714	159	116
Estimated female mean length (EM) in cm	--	29.9	36.5	40.2	45.3
Standard Deviation (SD)	--	3.17	4.09	2.95	1.74
Optimum length (OL) in cm	--	26.8	35.7	44.6	53.5
Selection factor (SF) for each net	--	9.64	9.35	8.34	--
Selection factor (SF) whole set of net	8.92				

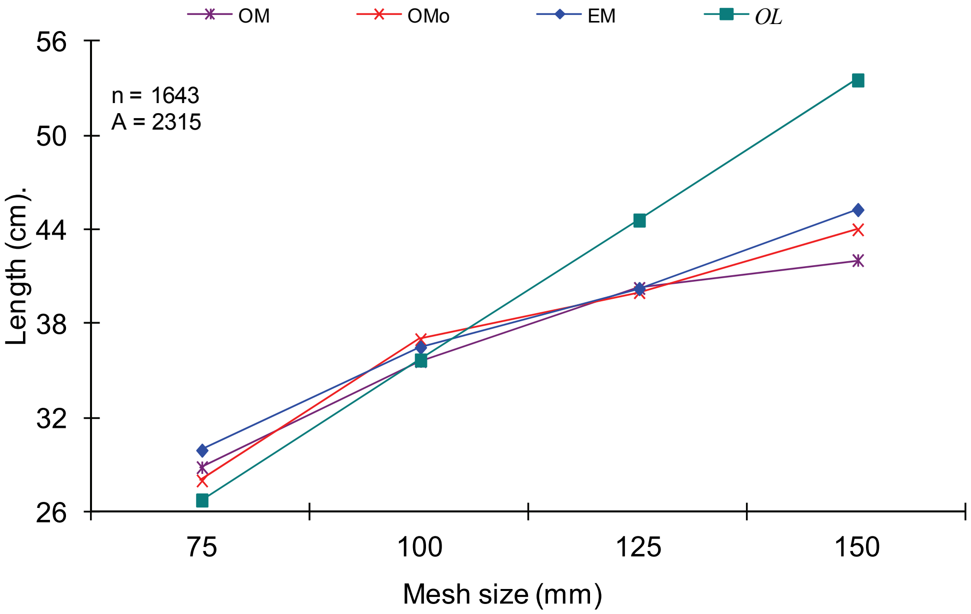


Figure 102. Pattern of the observed and the estimated length parameters with the mesh size of the net. OM- Observed female mean length; OMo- Observed female modal length; EM- Estimated female mean length; OL- Optimum length; n: is the total catch; A: Estimated abundance.

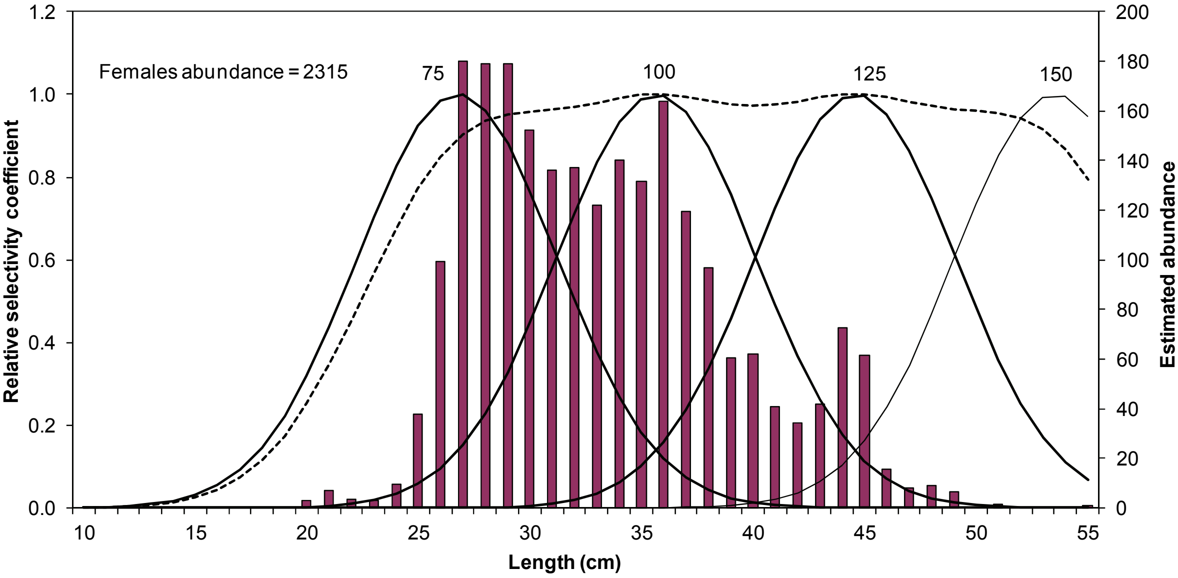


Figure 103. The relative selectivity curves for individual nets (mesh sizes tested: 75, 100, 125, and 150 mm stretch mesh) and the length frequency distribution pattern of *B. guatemalensis.*

5.2.3.2. Reproductive phases

The caught and retained specimen changes as a function of the mesh size of the net and body length of the fish, and both observed catch (Table 42) and the estimated abundance index (Table 43) clearly decreased with increasing mesh size, given the size selectivity pattern of the gillnet, reflecting the expected lower abundance of larger individuals in the populations. However, when the selectivity analysis is conducted by reproductive phase (I, D, SC, AS and R) a different pattern is obtained (Figure 104). Thus, as expected, most of the immature fish are retained by the 75 mm nets and very few by largest mesh sizes, as also estimated above. Among the mature phases (D, SC, AS and R) it was expected the catch to be similar within each net, as size of these phases do no differ (ANOVA: $F=0.287$, $p>0.05$) (Figure 105), but excepting the D and R phase that follow a similar trend of the immature, the females in SC and AS phases, i.e. in spawning condition, have highest probability on being catch by 100 mm net than other phases, thus 64% of the AS females are retained by this net, while only 26% of the females on regenerating phase are taken by this net (Figure 104). Moreover, regenerating females have similar probabilities on being caught by 75, 100 and 125 mm nets.

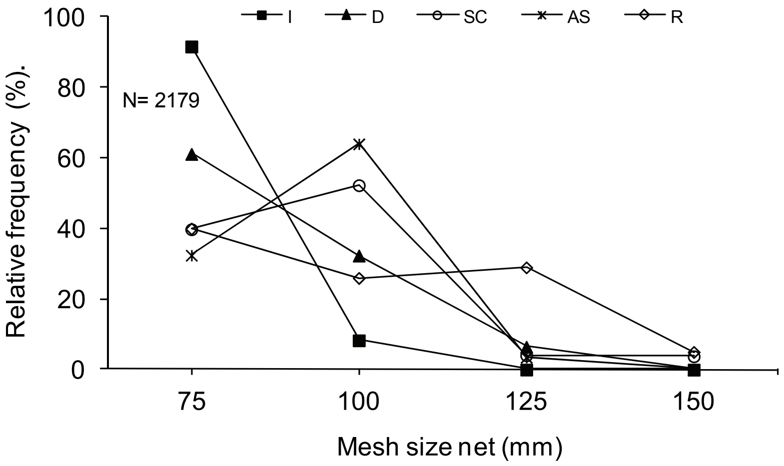


Figure 104. Relative frequencies of the reproductive phases of: Immature (I); Developing (D); Spawning capable (SC); Actively spawning (AS) and Regenerating (R) by mesh size of the net.

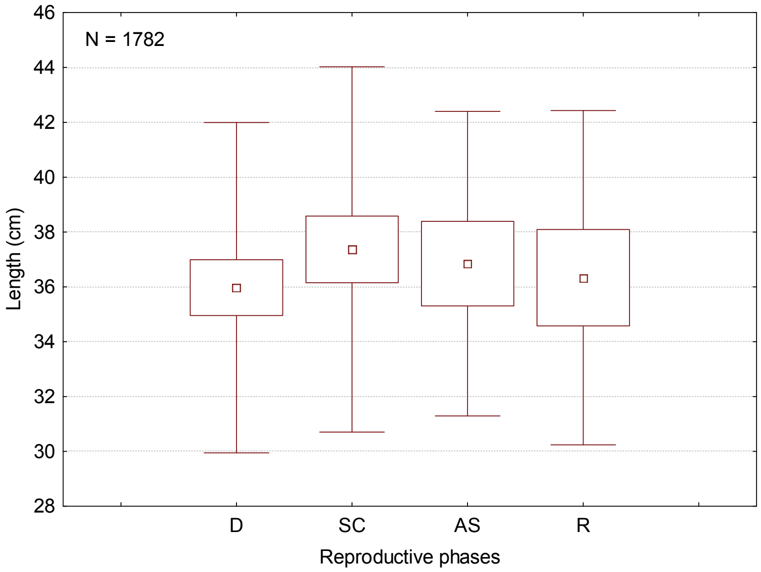


Figure 105. Mean-length variation of the reproductive phases of *B. guatemalensis* in whole mesh size tested. Mean (midpoint); Mean ± SE (box); Mean ± SD (whisker). Reproductive phases: Developing (D); Spawning capable (SC); Actively spawning (AS); and Regeneration (R).

The analysis of the annual reproductive cycle (section 4.2.2) showed that females of *B. guatemalensis* spawn during the whole rainy season and in lesser extent during the dry season. The average catches of mature females increased from dry to rainy season by 11.7% but not significantly (ANOVA: F= 0.116, p=0.735). The catches by mesh size neither shows significant variation (Figure 106). However, during the dry season 100% of the active spawning females (AS) were captured by 75 mm net (Figure 107), while SC females were taken almost equally by 75 and 100 mm nest, i.e., 52 and 48% respectively. However, this pattern change considerably during the rainy season, when most of the catches were taken, as now 52% of the SC females are captured by 100 mm net, and only 42% by 75 mm net. This difference is even more pronounced for AS females which are now taken by both 75 and 100 mm at 23 and 72 % respectively.

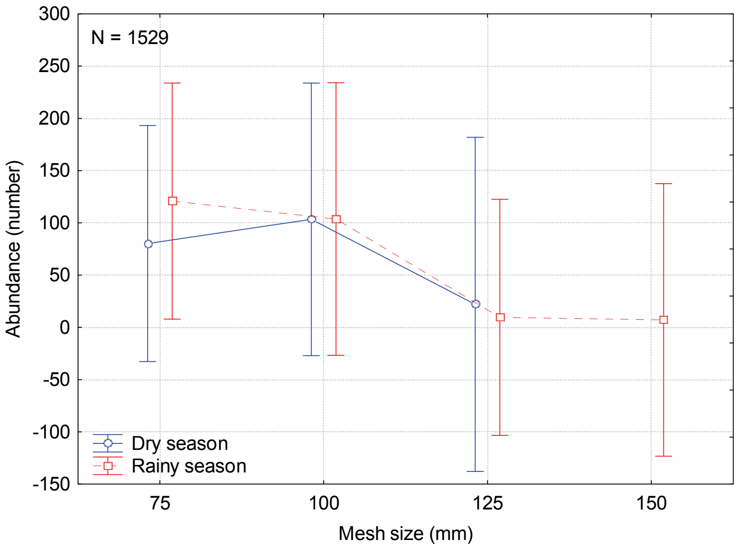


Figure 106. Seasonal variation of the female mean catches by mesh size net of *B. guatemalensis*. Mean ± CI: Vertical bars denote 0.95 confidence intervals.

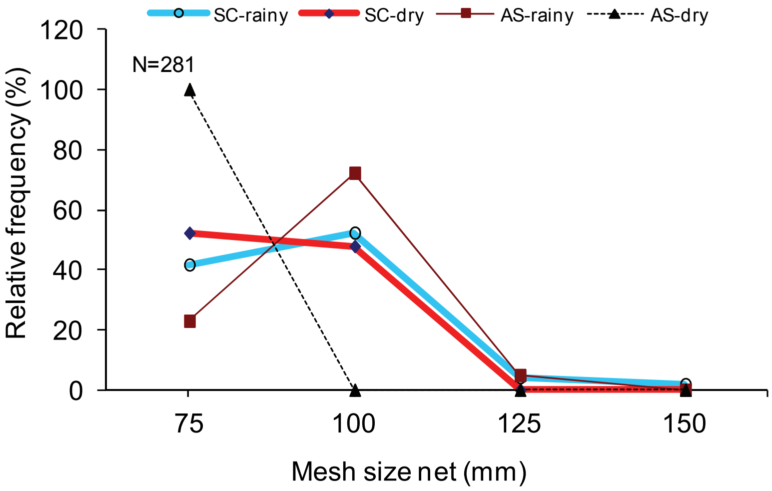


Figure 107. The presence-absence of females of *B. guatemalensis* proxy to spawn (SC) and actively spawning (AS) by mesh size nets (75, 100 and 125+150 mm). SC-rainy and AS-rainy: during rainy period; SC-dry and AS-dry: during dry period.

5.2.3.3. Size at reproductive phases

Catch for each reproductive phase was analyzed within each mesh size of the net (Figure 108):

75 mm mesh size. Mature females in all reproductive phases were caught and retained in this net; the mean length showed significant variations (ANOVA: F= 4.171, $p<0.05$) among the reproductive phases (Figure 108 A). Tukey HSD post hoc test evidenced that mean length was significantly higher only in SC phase in comparison with the others. In all phases the mean length was above the optimum length estimated for being caught in this mesh size net.

100 mm mesh size. The mean size of each reproductive phase differed significantly (ANOVA: F=24.420, $p<0.05$) and among all phases except between D and R (Tukey HSD test – post hoc test). The Figure 108 B shows the increasing trend in the mean size from D to AS phase, while females in R phase were smaller than those in D phase, but not significantly. In this net the spawning females (SC and AS phases) were the only phases whose mean length was clearly above the optimum length (35.7 cm).

125 and 150 mm mesh size. Due to the low number of individuals in the different reproductive phases captured in these larger mesh size nets, the catches of both nets were analyzed together The mean-length of each reproductive phase diverged significantly (ANOVA: F= 37.149, $p<0.01$), and the larger specimens caught were those in SC phase, i.e., specimens in the onset of spawning (Figure 108 C). All reproductive phases were below the optimum length of being caught in this net.

An overview of the female length among reproductive phases (D, SC, AS and R), across the different mesh size shows that i) the largest variations in mean-length occurred between D, SC and AS phases within each mesh size net, ii) the largest mean length were observed in SC and AS phase, iii) the mean-length of each reproductive phases increased with mesh-size as expected for gillnet selectivity; and iv) in the 75 and in 100 mm nets the mean length of the different reproductive phases were generally above the optimum length (OL), whereas in the larger than 125 mm mesh size the SC phase is the only one above the OL.

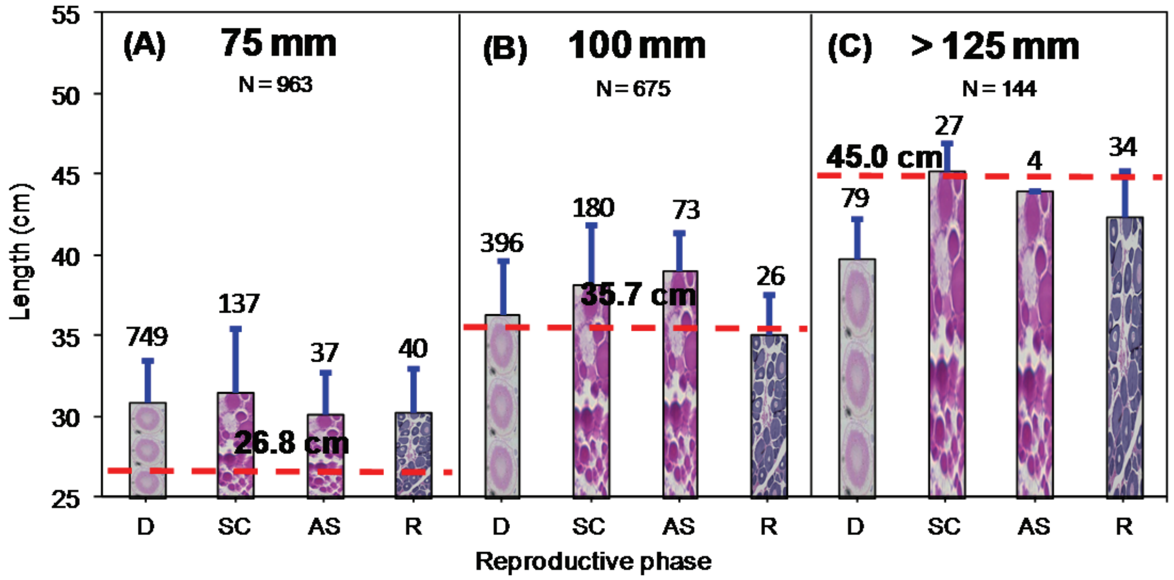


Figure 108. Mean length and standard deviation of each reproductive phase of *B. guatemalensis* by mesh-size of the net. D: Developing; SC: Spawning capable; As: Actively spawning; R: Regenerating. Red dashed lines: Optimum length (OL).

5.2.3.4. Potential egg production (EP)

In chapter 4 (section 4.2.4) it was shown that larger females of *B. guatemalensis* have higher potential annual fecundity, i.e., higher potential egg production (EP). The individual EP (fecundity) of the spawning females retained by net differed significantly (ANOVA: F = 3.67, $p<0.05$) between nets (Figure 109). The average egg production in 75 mm net was significantly lower than in the 100 (Post hoc test $p<0.05$) but not with the >125 mm nets (Post hoc test $p=0.91$). The total EP in each net, i.e., the sum of individual fecundities for all female sizes retained in each net, increased from one to three million from 75 to 100 mm net, i.e., a ratio of 2.8. EP notably decreased in the larger mesh size nets to a ratio of less than 0.5 of the 75 mm net, but down to 0.2 compared with 100 mm net. Although larger spawning females (from 44 to 51 cm), i.e., more productive, were retained in larger mesh size, and therefore is expected higher egg production in that net, the higher number of spawning females caught in 100 mm net produces this difference in productivity (Table 44).

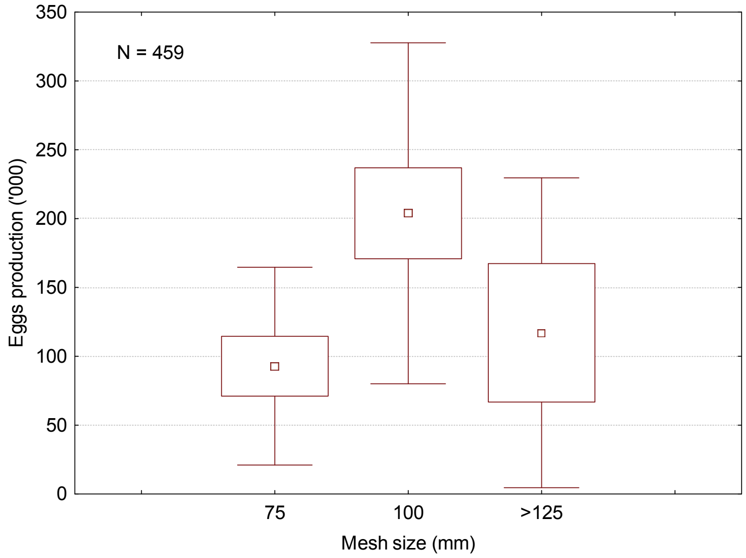


Figure 109. Average individual egg production (fecundity) of females of *B. guatemalensis* by each net mesh-size. Mean (midpoint); Mean±SE (box); Mean±SD (whisker).

Table 44. Estimated potential eggs production (EP) of the spawning females caught by mesh-size of the net.

Mesh size (mm)	N	Length-range (cm) of spawning females (SC & AS)	Total EP
75	175	25-36	1 020 709
100	253	31-45	2 854 166
>125	31	43-51	585 457
	459		

5.3. Discussion

Gillnet selectivity

In the present study all selectivity curves were formulated accordance to the "*principle of geometrical similarity"* (Baranov, 1948), that produce bell-shaped curves. Each curve cover up a relative wide but limited fish size range, confirming that gillnet are selective for a certain size range only (Sparre & Venema, 1998). However, the net selectivity largely differed among species. Out of the four mesh size tested, the more efficient net in term of catch abundance of smaller specimens was, as expected, the 75 mm, whereas in terms of catches of wider range of size-class, the 100 mm mesh size is more efficient, meaning that both induce high fishing mortality. However, except for *B. guatemalensis*, most of the fish were retained in the 75 mm net.

Considering that gillnet is a passive gear, selectivity depend on the probability that the fish encounters the net and on the probability that the fish is caught and retained by the net (Hamley, 1975). Gillnet selectivity largely depend on many technical factors intrinsically related to the fishing gear performance. Therefore, awareness of net construction and design should be account for. Hovgård & Lassen (2000) consider the major gear parameters for optimizing research with gillnet in order to choose as efficient a gear as possible are: colour of netting, dimensions of netting material, types of netting material, hanging ratio and design of net. All this aspects of net construction may affect the net performance and the interaction between the net and the fish. The characteristic of the gillnet type used in the present study are described in Chapter 2.

Net twine colour and thickness induce changes of fish visibility at different water turbidity level. These affect avoidance behaviour of fish and the probability of catching fish that swim into the net (Hamley, 1975). Experiments have shown that avoidance decreased with decreasing light intensity (Parrish, 1969), therefore, is recommend darker nets in good light or clear water, and lighter nets in turbid water. Visibility of nets can affect their selectivity, because the reactions of fish to nets colour can changes with growth and species. Beside, thinner twine can catch many times more fish, but too thin twine may be broken by large fish (Hamley, 1975). Gillnet selectivity differ between multifilament or monofilament nylon net because differences in elasticity and flexibility of the net twines. This affects the probability of holding fish that have swum into the net (Hamley, 1975).

Hanging ratio used in the present study was established in 0.5 (See chapter 2). Commercial nets typically have a hanging ratio between 0.25 and 0.65 (Hovgård & Lassen, 2000). For research purposes hanging ratio is an important parameter since it may affects gear selectivity, and usually it should vary from 0.4 to 0.6 (Engås, 1983). Experiments have shown different results by using different hanging ratio with different targeted species. For example, the decrease in hanging ratio has resulted in an increase of the number of smaller fish becoming entangled in the net which is the case of *Tilapia mosambica* and blue ling (Riedel, 1963; Engås, 1983), while the number of larger perch increased when the hanging ratio decreased (Mohr, 1965). No changes in length frequencies for roach *Rutilus rutilus* was observed when changing hanging ratio. Overall, in several studies higher catch are observed for the more loosely hung nets. In the species studied in the present work the effect of hanging ratio has not been evaluated.

Other factors affecting gear performance are the net interactions and saturation. For selectivity studies the full size range of the fish population need not be covered and fewer mesh-sizes are therefore necessary in the research gillnet series (Hovgård & Lassen, 2000). However, multimesh type of net series without separation between nets is not recommended because fish that are too large to be caught in a mesh size may be led to a more appropriate mesh-size by the net wall. This violates the fundamental assumption of indirect estimation that a fish of a particular size has an equal probability of encountering all different mesh-sizes (Hamley, 1975; Hovgård & Lassen, 2000). On the other hand, for gillnets the importance of gear saturation appears to be relatively weak (Hovgård & Lassen, 2000). Some studies have indicated a reduction in CPUE for longer setting times (Kennedy, 1951; Hovgård, 1996). Engås (1983) compared catches of blue ling (*Molva dypterygi*) in gillnets lifted at 1, 2 or 3 day intervals and found no differences in catch per day in two experiments whereas a third experiment showed increasing catch rates with increasing set time. In some others experiments have not found statistical differences between the catch per hour in the long and short settings (Hickford & Schiel, 1996).

In the gear selectivity curves the left slope represents smaller fish wedged in the meshes, while the right slope are largest fish mainly tangled by head parts (Hamley, 1975). However, in the present study only wedged fish were considered for gillnet selectivity analysis. This is evinced in the curve normality, since gillnet selectivity curves generally are more skewed to the right when many fish are tangled (Ishida *et al*, 1968). Overall size selection ranges observed in each mesh indicate heterogeneity of sizes in the lake. Selectivity was quite different among species partly reflecting growth pattern what explains the maximum size captured in each species, as some of them were virtually not captured by largest mesh sizes. Overall, the maximum size theoretically retained by the gears used was 50 cm, well above the maximum lengths recorded for *A. citrinellus* (41), *H. nicaraguensis* (25) and *P. managuensis* (42), but not *B. guatemalensis* (55.5). It indicates that the range of mesh sizes used in this study is suitable to study growth and population dynamics of large fish.

The absence of larger fish in the catches may indicate a migration pattern out of the lake, but very likely it indicates the expected maximum size of each species within the lake ecosystem. If fish ageing were possible then mortality curves can be estimated using this sampling methodology. On the other hand, the fact of the minimum size captured differed among species must be explained only due to fish shape and/or different behaviour of the life stages of each species. *A. citrinellus* and *H. nicaraguensis* are very similar in body shapes, having both dorsoventral compressed bodies (Klingenberg, Barluenga & Meyer, 2003). However, *P. managuensis* and *B. guatemalensis* are more rounded fish. To what extent this difference in fish shape has affected the catch rates of smaller fish should be further investigated using smaller mesh sizes. Nevertheless, the similar smaller fish sizes in both *A. citrinellus* and *H. nicaraguensis* may indicate similar home range and behaviour, like swimming, foraging or mating activity, and also that both share similar habitat. Instead, in *P. managuensis* and *B. guatemalensis*, although similar in body shape, the minimum size differed in the 75 and 100 mm net but not in the 125 mm. According to Ishida (1969) the condition of a fish affects is girth at abdomen more than a head and small changes in plumpness affects mostly the left slope. However, changes in body shape in smaller fishes not only differ at abdomen level but at the head. This apply even for smaller males of cichlid species as *A. citrinellus*, which develop a hump on their head during reproductive periods (Bussing, 2002) that favour its retention in gillnets. However, considering that most of the fish at these sizes were immature, the lower than expected catches of these sizes can be also related with fish not being available to the gear. Low availability, which affects catchability, could be related with a reduced swimming activity or more likely because smaller fish of these species occupy a habitat not covered by the sampling scheme, as the rocky and vegetation patches in the lake edges.

On the other hand, the higher abundance of males in each net is related with the sexual size dimorphism found in adults of these species as males are larger than females in order to maintain a hierarchical dominance on other males and to achieve best reproductive success as in *A. citrinellus*, (Oldfield, McCrary & Mckaye, 2006; Elmer, Lehtonen & Meyer, 2009), *H. nicaraguensis* (Bussing, 2002) and *P. managuensis* (Meral, 1973). Because cichlids assemblages are highly territorial fishes when begin the breeding season and exhibit biparental care, females-only care or may switch between these two strategies (Kolm *et al.*, 2006; Gonzalez-Voyer, Fitzpatrick & Kolm, 2008), during some periods one of the sex (male or female) might reduce or increase the probability of being caught by the fishing gear. Thus, the breeding season is protracted in *A. citrinellus* and *H. nicaraguensis*, occurring the whole year although with more intensity during rainy season (Hernández-Portocarrero & Saborido-Rey 2007). It can be hypothesized that females are less accessible to the gear than males during the breeding season, i.e., most of the year. In the case of *P managuensis*, a seasonal breeding season has been reported (Conkel, 1993) and in consequence males and females were caught in similar proportions.

Off the cichlids group, *B. guatemalensis* is the largest fish, and the major abundance range between 25 and 35 cm length, and different to the previous species, females were larger than males which explains partially the highest proportion of females in the catches. It may also be explained by a differential migratory behaviour searching for spawning grounds, or because changes in body shape due to female gravidity.

In summary, the survey design of our study with the use of four mesh size nets is suitable to understand population dynamics of large immature and mature fish of each species, but inappropriate for recruitment analysis. As discussed in Chapter 3 the gillnet catches obtained in this study reflect abundance of fish stock and cover up a wide size range of immature and adult population present in the lake.

Among the four species the cichlid *A. citrinellus* is the most abundant species in the eastern coastal area of the Lake Nicaragua representing 43 % of the total abundance, followed by *B. guatemalensis* (19 %), *H. nicaraguensis* (11 %) and *P. managuensis* (4 %). This pattern of abundance seems to have changed since 1982-1983 years, when *Dorosoma chavesi* was the most abundant (55 %) in the coastal area around the lake and in decreasing order followed by *A. citrinellus*, *H. nicaraguensis*, *B. guatemalensis* and *P. managuensis* with 12.5%, 6.4%, 1.8% and 0.2 % respectively (Orellana, 1986). However, abundance reported from the extreme southern side of the lake showed *B. guatemalensis* as the most important species in the catches (36 %), followed by *A. citrinellus* (27 %), *Atractosteus tropicus* (22 %) and *P. managuensis* (0.5 %) (Gadea, 2003) differing also in the order of importance with the present study in that particular zone.

Mean length caught and retained in the whole gear for *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* and *B. guatemalensis* varied from 18.4 to 23.5; 16.7 to 17; 23.2 to 31.4 and 29.1 to 41.8 cm respectively. In the study conducted in the coastal areas around the whole lake in 1982-1983 (Orellana, 1986)_cichlids were grouped in Mojarra category (including *A. citrinellus*, *H. nicaraguensis* and *A. longimanus*) and the mean catches-at-length yielded a mean length of 26.0 to 24.0 cm in the gillnets monofilament type 75 and 130 mm respectively. Similar trend was observed here for *B. guatemalensis*, i.e., 53.0 and 51.0 cm in both respective mesh sizes. These lengths were not in the size range of being caught with a high probability in the nets of similar size in the present study, i.e., 75, 100 and 125 mm tested. In fact in the present study those lengths for Mojarras have less than 40 % and as higher as 90 % probability of being caught in the 75 and 100 mm net respectively, while *B guatemalensis* were in the size range of 80 % probability of being caught and retained in the 150 mm net. The differences of catch-at-length between both studies suggest that *A. citrinellus* and *B. guatemalensis* population in the lake has declined its sizes. Furthermore, the study carried out along the San Juan River using gillnets with equal mesh size (75, 100, 125 and 150 mm stretch mesh with hanging ratio of 0.6) produced similar results than the present study, i.e., very low catches of smaller sizes of *B. guatemalensis* (PROCUENCA-SAN JUAN, 2004) confirming the net selectivity. In most of its catches, Brycon size ranged between 35 and 40 cm. The low number of *B. guatemalensis* specimens captured in the 125 mm net, with mean length of 42.0 cm contrast with the higher catches of similar mean length of 43.0 cm reported in this net by Gadea (2003), who considered this net the more efficient one. This is probably related with the relative restricted area where that study was conducted, i.e., southeast side, since in the present study, also higher abundance (see section 3.2.2.2) and larger fish were found (section 3.2.4) in that area.

The selectivity results indicate the size at which fish is more vulnerable to be caught. Those specimens with length close to the optimum length (OL) estimated for each net mesh sizes are the most vulnerable of being caught and retained. As the fish size departs from this optimum the probability of capture decreases (Hamley, 1975), i.e., less vulnerable. As mentioned in Chapter 2, the fishers in the lake use the same mesh sizes as used in our study and mostly the 75 and 100 mm. The catches-at-length pattern of cichlid species shows that these are highly vulnerable of being caught (above 90%) in the smallest mesh sizes, i.e., 75 and 100 mm, excepting *P. managuensis* which slightly reduce its probability of being caught in the 100 mm to a 80%. Thus a great proportion of the population of these species is vulnerable to these nets. In *B. guatemalensis* the larger sizes reduce the probability of being catch to a 75 % in the 75 mm, i.e., 25 % escapement, indicating an escapement portion of larger fish to that net. This is not the case of *B. guatemalensis*, where the population size range considerably exceeds the sizes captured by each net. Thus, the rate of escapement using one particular net by fishers is *a priori* high enough to reduce the vulnerability in this species. Thus, in the 75 mm net escapement of females larger than 34 cm occur in similar magnitude (86%) as in the whole population (male and female), i.e., have high probability of escapement; in larger mesh size (> 125 mm) the escapement portion of females larger than 49 cm is more than 50 %. On the contrary, smaller fishes are not captured by larger mesh sizes (>125 mm), and thus fish smaller than 39 cm has more than 50 % probability of escapement.

The most vulnerable part of the population of cichlids is males and females in *B. guatemalensis*, particularly during reproductive periods. The male-female proportions of each species obtained in the present study very likely are similar to those in the catches in a routine fishing operations performed by the fishers in the lake. The pattern of catches have great implication for species conservation and the sustainability of the fisheries, because the equilibrium in the sex ratio can be severely altered and consequently the potential reproductive ratio (PRR) of some species may be directly affected, e.g., parental care in cichlid groups where male play an important role, and the spawning stock biomass in *B. guatemalensis*.

Length at 50% maturity

Fish body size is a key component on life history determining the ecological processes of a species. Changes in size distributions may have many causes, but fishing is considered one of the most important factor because is always size-selective (Shin *et al*., 2005). In most fisheries larger fish in the stock, probably being the mature one, are the main target, and this is thought to modify the size structure and functioning of fish assemblages, with consequences for productivity and resilience of some stocks (Shin *et al*., 2005). The size distribution, i.e., length frequency distribution, of fish assemblages derived from surveys such as mean length in a population, mean length in a community, mean maximum length in a community, length at maturity, are used as size-based indictor (SBI) and may provide a relevant integration of the effects of fisheries on community structure and processes (Shin *et al*., 2005). SBIs are typically used to describe the response of communities or individual populations to exploitation (Garcia *et al*., 2003). Maturity ogives and the corresponding size at 50% maturity are commonly used in fisheries management in many ways, but mostly to estimate spawning stock biomass and to establish a minimum landing size (MLS), and often biological reference points (RP) or references direction of changes (RD) are also based on these estimations. Shifts in maturation severely determine the population dynamics (Saborido-Rey & Trippel, 2013). In data limited stocks L_{50} can be critical to establish size-based indicators (SBIs) as management procedure (Shin *et al*., 2005). As reference point (RP) for SBIs, length higher than mean length at maturity have being suggested to ensure that at least half the individuals of a cohort caught have had a chance to spawn at least once (Caddy & Mahon, 1995). This measure should be accompanied with mesh size regulation used for exploited stocks, since it objective are in line with the establishment of the RP. Jones (1984) indicates two important objectives of mesh size regulation. One of the objectives is to conserve the spawning stock, and by that a suitable choice of mesh size should reduce the rate of capture of juveniles, and make it more likely that an individual will survive to the size of first maturity and have an opportunity of spawning at least once. The second important objective is to increase the long-term sustainable yield, and by that to conceive of an optimum exploitation pattern, or harvesting strategy, which leads to the optimum yield per year class.

The estimated female L_{50} for *H. nicaraguensis*, *A. citrinellus* and *P. managuensis,* based on macroscopic determination, 16.1cm, 14.6 cm and 25.2 cm respectively, were too close to the optimum length (OL) of the 75 mm mesh size gillnet. Only in the case of *A. citrinellus* optimum length was above L_{50}. This indicates that this mesh size may be adequate for these species, although some vulnerability to recruitment overfishing will exits, especially in the case of *H. nicaraguensis* where the entire size range of the population is taken by this mesh size net. Different L_{50}, macroscopically determined, has being reported for *H. nicaraguensis* and *A. citrinellus*, i.e., 12.5 cm and 16.0 cm, respectively (Orellana, 1986). These differences may indicate temporal changes in maturity, but can be also the consequence of the uncertainty when using macroscopic maturity stage, as discussed below.

In the case of *B. guatemalensis* the estimated L_{50} was 34.9 cm, well above the OL obtained for 75 mm mesh size and only slightly below the 100 mm mesh OL. Clearly, and according to traditional fisheries management, the 75 mm net is inadequate because it may produce growth overfishing, but yet, some vulnerability to the 100 mm mesh size net exits in this species. However, the microscopic maturity ogives produced a L_{50} estimated in 27.3 cm, i.e., considerably smaller than the macroscopic and now closer to OL of the 75 mm mesh size. Fish on the size of 50% maturity has 100 % probability of being caught and retained in this net. In any case the L_{50} falls in the range of 24.0 to 30.0 cm at which the net has 80 % efficiency. However, the efficiency of this net for fish about 20 cm drops considerably, protecting the mature stock of the population, but with risk of growth overfishing. Therefore, when considering the four species together and from a traditional fisheries management perspective, the 75 mm mesh size gillnet may become hazardous and subsequently its use for fishing operation should not recommended and larger mesh size nets should be considered. Thus, the minimum landing size of the species should be larger than L_{50} estimated.

L_{50} is an important parameter to track maturation temporal shifts in a population and an important predictor of the risk of overexploitation (Reynolds *et al.*, 2005). Therefore, the accuracy of its estimation is critical for the conservation of exploited fish stocks (Hannah, Blume & Thompson, 2009). The few data on length at maturity of fish stock from the Lake Nicaragua used for establishment of minimum landing size have been based on macroscopic (visual) assessment of ovary condition. However, there is abundant evidence that histological evaluation of ovarian thin-sections is much more accurate (Lowerre-Barbieri *et al.*, 2011b, and reference therein). The current management measures should be revised based on more reliable biological information. Yet, ontogenic maturity should not be the only life history parameter that should be considered in fisheries management.

Considering the uncertainties in the different L_{50} macroscopically estimated for *A. citrinellus*, *H. nicaraguensis* and *P. managuensis*, the correspondent estimated mean length (from selectivity analysis) caught in the 75 mm mesh size, as closer sizes to L_{50}, is recommended as reference direction of changes (RD) for monitoring landing size in those species, i.e., 18.6, 16.7 and 23.1 cm, respectively. This RD can be used while a biological reference such as a more precise L_{50} estimation is obtained. For *B. guatemalensis*, the L_{50} microscopically determined (27.3 cm) can be used as RP due to the accurate of its estimation, and considering 20 % increase over the size at maturity, a 30 cm minimum landing size (MLS) is recommended. The recommended MLS for *B. guatemalensis* would have 40 % probability of being caught in the 100 mm mesh size net.

Reproductive behaviour

The traditional gear selectivity analysis focus on the fish size range caught and retained, and a direct comparison with the minimum landing size (MLS) fixed for a species in particular. This MLS is sometimes based on some biological information, as discussed above. However, this approach considers the physical characteristics of the fishing gear and the size of the fish only, but leaves aside the fish behaviour which also affects the fish catches (Arreguín-Sánchez, 1996). For example cichlid *A. citrinellus* is known to be territorial fish during breeding season (McKaye & Barlow, 1976), and among cichlidae family some species exhibit biparental care, female-only care, as well as some that may switch between these two strategies (Kolm *et al*., 2006; Gonzalez-Voyer *et al*., 2008). This indicates that during these periods one of the sexes, reduce considerably its spatial activity or home range, and very likely reducing also the probability of being caught by a passive fishing gear, as gillnets. It might produce a sex-dependent catchability, i.e., the interaction between the resource abundance and the fishing effort (Arreguín-Sánchez, 1996), and hence a higher fishing mortality in one sex if fishing mortality remains constant during these periods. Estimation of sex ratio, to be used for stock assessment for example, should consider fish behaviour to avoid bias, especially, but not only, if estimated from fishery data.

Reproductive activity of species analyzed here take place mostly during rainy season, both for cichlids (Hernández-Portocarrero & Saborido-Rey, 2007) and in *B. guatemalensis* (section 4.2.2), in the latest species with major intensity in July and August. The selectivity analysis conducted by reproductive phase showed the catch composition of *B. guatemalensis* in the different gillnets changes depending on female size but also in relation to the reproductive phase of the female. Thus, unexpectedly the 100 mm net resulted to be the more efficient net in removing the spawning females (SC and AS phase) from the mature stock, i.e., among all mesh size nets used, this is the one catching more spawning females, while females in developing and regressing are mostly, and expected, caught in 75 mm, even though catches in the 75 mm shows more uniformity in females size. The reason behind this may be related to the body shape of the females, well because they are gravid or because its condition, producing a higher retention in gillnets of that mesh size (McCombie & Berst, 1969). Both would affect its girth at abdomen more than in the head (Ishida, 1969).

Potential egg production (EP)

The reproductive studies on *B. guatemalensis* (see section 4.2.4) have demonstrated that its potential fecundity (Fp) increases allometrically with female length, with an allometric coefficient significantly larger than 3, i.e., larger females produce more eggs than the body biomass predicts. Moreover, larger females produce larger eggs too, which might be an indicative of better egg quality and highest survival rate (Saborido-Rey, Murua & Macchi, 2011 and references therein). In summary, larger females own larger reproductive potential and hence contributing unequally to future recruitment and the sustainability of the fishery (Saborido-Rey & Trippel, 2013 and references therein).

The maintenance of the spawning stock biomass (SSB) has been considered one of the key factors to produce sufficient recruitment to the fisheries, since the stock-recruitment relationship imply that spawners biomass influence the recruitment (Myers & Barrowman, 1996), under the assumptions that SSB is an index of egg production (Beverton & Holt, 1957). However, this assumption has been widely invalidated (Saborido-Rey & Trippel, 2013, and references therein) and the concept of stock reproductive potential (SRP, Trippel, 1999) has often replaced SSB. Several SRP indexes have been developed, but undoubtedly, total egg production (TEP) is a better estimate of a stock's reproductive output than the less sensitive

SSB (Marshall, 2009). There is recent and increasing evidence that variations over time in stock structure, sex ratio, fish condition, growth rate, maturation and fecundity produce large variability in TEP (Saborido-Rey & Trippel, 2013, and references therein). In determinate fecundity species, like *B. guatemalensis*, annual TEP can be estimated from the spawning stock size structure, i.e., female abundance at each size class, and the potential fecundity at size (Murua & Saborido-Rey, 2003).

The impact of fishing gear on the stock egg production has been seldom studied; and even more rarely in gillnets used in small-scale fisheries. In the present study it was shown that the 75 mm net catches a higher proportion of smaller spawning females, very likely recruit spawners, i.e., those that have matured in the year in course. These are less experienced females having an earlier spawning cessation (see section 4.2.3), but more importantly being less productive in terms of egg production and egg quality. However, our study demonstrates that the 100 mesh size net is more harmful in terms of egg production removal, since it causes the highest fishing mortality among the more productive spawning females stock. Additional benefits of the larger individuals in a population have been mentioned as the enhancement of the survival and reproductive success of the next generation, and that young fishes learn the route to spawning aggregation by following the more experienced adults (Birkeland & Dayton, 2005). The importance on conserving stock reproductive potential allowing larger fish to survive is crucial in fishery management and has been demonstrated essential in marine fishes (Berkeley *et al*., 2004a; Bobko & Berkeley, 2004; Birkeland & Dayton, 2005; Saborido-Rey & Trippel, 2013, and references therein). Our results are in line with these evidences as larger female *B. guatemalensis* has longer spawning season and higher reproductive potential.

The catchability coefficient is defined as the proportion of individuals in a fishing ground of a certain size removed by a gear with some efficiency (Gulland, 1983), thus considering the physical characteristics of the fishing gear in relation to the size of the fish alone. However, our findings suggest that this coefficient should also consider the fish reproductive performance. The spawning females seems less vulnerable to the smallest net, i.e., 75 mm due to differences between the optimum length (OL) and the mean length of each reproductive phase, whereas in the larger mesh size than 125 mm net, the low vulnerability of those females is due mainly to size selectivity. However, the 125 mm net produces a very low yield (catch rate) clearly inadequate for a profitable fishery. On the other hand, the 100 mm net efficiently protect juveniles and recruit spawners, avoiding growth overfishing, but it captures with great efficiency very productive females. These findings indicates that to increase the egg production of the females stock and to reduce the fishing mortality of young females, a compromise between the use of one or another mesh size should exits depending on the management strategy. It is advisable to use the 100 mm net during dry season protecting recruitment and females in the onset of the ontogenic maturation, but switching to 75 mm bet during the rainy season, especially in July and August when spawning activity of *B. guatemalensis* is higher, and hence protecting females with larger reproductive potential. This management measures would be in agreement with the biology of the species and may provide stock sustainability.

CHAPTER 6: Concluding Remarks

Abundance, distribution and movement patterns

The ichthyic population structure in the lake shows long-term changes since the 70´s reflecting very likely changes in exploitation pattern as well. By the 70´s, Guapotes (*Parachromis managuensis* and *Parachromis dovii*), Snook (*Centropomus parallelus*), Shark (*Carcharhinus leucas*) and Sawfish (*Pristis perotteti*) were the target of the fishery and hence highly exploited-, whereas Gaspar or Gar (*Atractosteus tropicus*), Mojarra (*Amphilophus citrinellus*, *Hypsophrys nicaraguensis*) and Machaca (*Brycon guatemalensis*) were less exploited because their low commercial importance (Davies & Pierce, 1972). By the 90´s, the overexploitation of the big fishes, and in particular Shark and Sawfish, and the symptoms of overexploitation of Snook and Gar forced changes in the fish exploitation and commercialization patterns. Currently all the species listed above, excepting Shark and Sawfish, are the main target of the fishery. In addition, fishing effort pattern showed important changes also. Although the total number of fishers remained similar, the time spent in fishing activity increased, increasing therefore the fishing effort. Thus, the number of fishers operating in the lake did not substantially changed from 1972 when 600 fishers were registered (Davies, & Pierce, 1972) to 2002 when 762 were registered (ADPESCA/AECI 2002), neither the fishing techniques. However, by 1972 fishing was a part-time activity because fishers often shifted seasonally from agriculture to fishing; in recent times they permanently dedicate to the fishing activity, increasing the annual total number of fishing hours. This change in fish exploitation pattern is thought to have induced a pressure on fish stocks in the lake that led to overexploitation and to a lack of recovery of the resources.

The research surveys carried out in the lake allowed to detect those long-term changes in the fish population structure, but when conducted on monthly basis, as done in this study, they also detect short-term changes as spatial and vertical changes between "shallow benthic" habitat (coastal zones: from 3.7 to 9.1 m depth) dominated by *Dorosoma chavesi*, and "deep benthic" habitat (central zone of the lakes: from 12.8 to 16.5 m depth) dominated by *Rhamdia spp* (Koenig *et al.*, 1976; Orellana, 1986), between zones of the southeast quadrant (Gadea, 2003) and along the San Juan River (PROCUENCA-SAN JUAN, 2004). In the present study spatio-temporal changes in population structure have been shown both horizontally, i.e., along the “coastal area” and vertically, i.e., between depths. Short-term migrations seems to be connected with the fish life history, moving across different habitats during their life span according to their habitat affinity and by environmental factors, in particular the rainfall that affects the water level, the flooding areas and hence the existence of different habitats suitable for feeding or reproduction. These movements can be described as follows: **a**. Movements within shallowness areas or “coastal areas” of the lake, that occur along its larger axis between rocky and /or muddy areas, which is exhibited by some cichlid (Mojarras) species as *Amphilophus sp*; **b**. Movement between the shallow waters and open water (central zone of the lake or deeper zones) observed in Moga, *H. nicaraguensis*; **c**. Movements from the rivers to the lake, both shallow and open waters, and viceversa, which are characteristic of species with migratory habits as Machaca, *B. guatemalensis*; and **d**. Movements that imply fish migration in and out of the lake toward the Caribbean Sea, during which fish cross four different habitats as mentioned, the Caribbean Sea, the San Juan River, the lake shallower areas and finally the open water in the lake. This last movement type is characteristics of those fishes with marine affinity, among others Sabalete, *Dorosoma chavesi*; Guavina, *Gobiomorus dormitor*; Snook (Robalo), *Centropomus parallelus*; and Roncador, *Pomadasys croco*.

Freshwater fish exhibit home range or homing affinities, daily or seasonal movement pattern or longer-distance migrations, reflecting the autecology of the species in the search for optimal environmental conditions (Matthews, 1998). The different movement patterns described in the species inhabitant the lake are manifested in their spatiotemporal variations of the abundance and size distribution. The Cichlids covered in this study, *A. citrinellus, H. nicaraguensis* and *P. managuensis*, and the Characid *B. guatemalensis* (Characidae family) are widely distributed in the eastern part of the Lake Nicaragua. The more deterministic factors influencing the spatial distribution of cichlids species was depth and latitude, i.e., macro-zones. These species were more abundant in shallower waters of the southern and northern zones. While season and depth were the main factors influencing abundance of *B. guatemalensis*, which largest abundances were found in the southeast and northwest side, during both dry and rainy seasons, but highest abundances occurred in rainy season at shallower waters, and lower abundance in the central zones. Seasonality strongly modulates the migratory behaviour of *B. guatemalensis* from rivers to the lake environment and vice versa. During rainy season it is allocated near the river drainage of both outermost zones, i.e., southeast and northwest, while in dry season its major abundance are found upstream in the tributary San Juan (PROCUENCA-SAN JUAN 2004). Although depth is a significant factor influencing the distribution pattern of the four species, its importance vary with the hydro-periods fluctuations (Fernandes, Machado & Penha, 2010) that in lakes occur moderately (Welcomme *et al*., 2010). The greater the depth of the water body, the greater the hydro-period and, therefore, the greater the time available for processes of extinction or colonization of the species in the assemblage (MacArthur & Wilson, 1967).

There was a clear spatial size distribution in all studied species. Larger fishes are found in the southeast and to a lesser extent in the central zone of the lake, whereas in the northwest area the individuals were smaller. In spite of fishes are unevenly distributed, in size, the number of fishers is similar among areas (CETMAR, 2005). On the other hand, larger fish are found in the deeper waters studied (3-5 m), while smaller sizes are found in shallowest water, excepting for *P. managuensis* which larger size has preferences for shallower water (1-3 m). This overall pattern of smaller size fish inhabiting in shallower waters is in line with previous studies covering the entire lake (Orellana, 1986), which indicates that recruitment not only occur in the lake, but very likely linked to the shore. Considering that the area surveyed overlapped with the traditional fishing ground and the fishing gear used is the same as those used by fishers, very likely the size composition of landings should be similar with the size distribution found in this study. Thus the size composition in the landings should range between 13 and 18 cm in *H. nicaraguensis*; 18 and 23 cm in *A. citrinellus*; 21 and 27 cm in *P. managuensis* and 26 and 38 cm in *B. guatemalensis*. Differences in fish abundances and sizes along the eastern side of the lake reflect the presence of different ecosystems and the rivers influence, since higher abundances and larger fish are found in areas of river drainages. Very likely the reason for this is the high nutrient load of these areas (PROCUENCA-SAN JUAN, 2004). However, fish reproductive behaviour also determines the distribution and abundance patterns in this part of the lake. Although cichlids apparently do not undergo major reproductive migration, they move to colonize rocky areas along the shore, disperse in the whole area or even move into tributary rivers (Lowe-McConnell, 1999). On the contrary *B. guatemalensis* display strong migratory behaviour from the lake into tributary rivers and vice versa (Drewe *et al*. 2003; Horn, 1997; McLarney *et al*. 2010). This is confirmed in our study, that shows also a connection between the migratory behaviour and reproduction which occur mainly during rainy season.

The Lake Nicaragua is a very dynamic ecosystem influenced by strong winds during dry season and by high precipitation and river discharge during rainy season. The Papagayo wind shrieks over the lake from October to March (NASA SeaWIFS 2000-2001) affecting the entire water column of the eastern side due to the shallowness of this area These factors cause periods of different water stability and consequently induce periods of presence-absence of particular species in the shallower area. This probably affect the behaviour of the species, e.g., instability in cichlids might induce sheltering until weather conditions improves, which is reflected in a lower abundance; excepting in *P. managuensis* which average abundance is higher; on the contrary, in *B. guatemalensis* it may induce an erratic migration pattern that is reflected in the monthly pattern of abundance. On the other hand, from April to October the strong wind effects over the lake disappear and rainy season start (in May). It produces a rise of lakes water level and consequently depth increase, as well a nutrient enrichment from rivers runoff (PROCUENCA-SAN JUAN, 2004). In this new situation, changes in species distribution may take place for feeding and/or reproduction. For example, feeding is known to induce temporarily changes in *H. nicaraguensis*, from rocky affinity, to searching for food in open waters (Conkel, 1993) and the lower abundance in the study area may reflect this behavior. In the case of *B. guatemalensis* the gently and sustained increase of abundance during rainy periods may reflect massive migrating pattern through shallow areas.

All of the above shows the ecological importance of the shallowness areas, along the shoreline of the lake. They are the key habitat for shelter, reproduction and breeding of territorial fishes, and the main path for potamodromous fish that migrate from tributary rivers to deeper water of the lakes and for diadromous fish that migrate between the coastal Caribbean Sea and the lake. Therefore, this corridor should be considered as buffer or transitional zone for sustainability of fish assemblages.

Implications in fisheries and lake management

Fishing mortality over immature fish seems to be very limited in the lake given the gillnet selectivity estimated in our study. However, environmental modifications and in particular alteration of the shoreline, constitutes a clear threat to the whole population, but in particular to the juvenile stock and recruits that take advantage of the shallower waters. Thus, in order to promote a sustainable fishery and given the characteristics of the Lake Nicaragua fishery and environment, management actions should not be based alone on the classic fishery management. Regulating catch and effort, temporal and/or spatial closures, fish size limitations, gear restrictions and other measures are still important but yet not sufficient. It is desirable to restock vulnerable and valuable native species to improve recruitment or to maintain productive species. Also it is desirable the removal of unwanted species such as recent reported invasive pez Diablo of the Loriicaridae family which is know responsible for high ecologic impact in freshwater environments (Marenco, 2010). But overall the protection of the habitats, especially the shoreline and including the water quality, is essential to maintain healthy fish populations, and hence an integrated management approach should be taken.

Changes in the water quality is the major driver of lake ecology and shifts in water transparency and dissolved oxygen regimes (Welcomme *et al*., 2010), and processes of eutrophication is one of the most important management problem facing conservationist today (Maitland & Morgan, 1997). The trophic state of the Lake Nicaragua has changed from early eutrophic (waters rich in mineral and organic nutrients that promote a proliferation of plant life) or mesotrophic (narrow range of nutrients, principally phosphate and nitrate) (Patrick, 1954; Hutchinson, Patrick & Deevey, 1956) to oligo-mesotrophic (from low to intermediate primary productivity) (PNUMA-OEA, 1997). However, it has been reported a eutrophic condition and high productivity level of the Lake, indicating a deterioration of water quality (PROCUENCA-SAN JUAN, 2004). Eutrophication is likely to be the main cause of the extinction of fish in many lakes, e.g., the vendace, *Coregonus albula*, in the Castle and Mill Lochs in Scotland and the melt, *Osmerus eperlanus*, in Rostherne Mere in England (Maitland & Lyle, 1991). In the Lake Nicaragua important quantity of dead fishes has been observed from time to time in the shallowness areas due to unknown causes.

The deforestation of the surrounding slopes followed by the runoff increases the presence of sediments in the water lake, reported as one of the major conservation problems in lakes (Maitland & Morgan, 1997). On one hand it increases sedimentation problems, which have been reported in the Lake Nicaragua (PROCUENCA-SAN JUAN, 2004). It may destroy habitats where fish spawn and breeding take place (Welcomme *et al*., 2010). Both *A. citrinellus* and *B. guatemalensis* lay eggs in sandy bottoms (McKaye, 1977; Greenfield &

Thomerson, 1997; Bussing W., 2002). On the other hand sediments increases water turbidity that alters behaviour of fishes and influence vulnerability to fishing gear. Moderate levels of turbidity apparently decrease the likelihood that fish will perceive the gear presence (Kirkland, 1965) but also reduce the reactive distances, altering foraging behaviour, and decreasing association with substrates (Noggle 1978; Gradall & Swenson 1982; Barrett *et al.*, 1992). This seems to be the case of *B. guatemalensis*, a rapid swimmer that swim constantly and sustained because it migratory behaviour (Horn, 1997) that needs enough visibility for swimming activity. Most cichlids are stenotopic (Eccles, 1986), i.e., able to adapt only to a narrow range of environmental conditions. Therefore, cichlids are probably less adapted to habitat with low water transparency since these fish are visually oriented and often associated with transparent water (Lowe-McConnell, 1999; Rodriguez & Lewis, 1997). The low visibility has being adverted in haplochromine cichlids in which the decrease of water clarity seems to affect foraging, social interactions (Fryer & Iles, 1972), to hamper mate recognition or even frustrate breeding (Seehausen *et al.*, 1998), and also may decrease prey selectivity which result in an increased interspecific competition, that have negative impact on species coexistence (Seehausen *et al.*, 2003).

In the fishing ground the males and females abundance change according to the intrinsic behaviour pattern showed by each sex within each species. The differential behaviour is related to the habitat preferences, reproductive biology and reproductive strategy in responses to the fluctuating environment. However, species vulnerability to the fishing gear also changes because sexual size dimorphism and changes in body shape during reproductive periods. Cichlids are highly territorial fishes during breeding season and exhibit biparental care, females-only care or may switch between these two strategies (Kolm *et al.*, 2006; Gonzalez-Voyer *et al.*, 2008). However, we hypothesized that females are less accessible to the gear than males during the breeding season, i.e., most of the year, probably because maternal care predominate over paternal care. In the case of *P managuensis*, stronger breeding seasonality has been reported (Conkel, 1993) and in consequence males and females were caught in similar proportions when the whole year is considered. Males vulnerability also is thought to obey of being larger than females in order to maintain a hierarchical dominance on other males and to achieve best reproductive success as in *A. citrinellus*, (Oldfield, McCrary & Mckaye, 2006; Elmer, Lehtonen & Meyer, 2009), *H. nicaraguensis* (Bussing, 2002) and *P. managuensis* (Meral, 1973). Moreover, sex differential changes in body shape may affect also catchability, as some cichlid males, even the smaller ones, develop a hump on their head during reproductive periods, as in *A. citrinellus* (Bussing, 2002), that favour its retention in gillnets, increasing its vulnerability. In *B. guatemalensis* differences in size, being females larger than males, differential migratory behaviour between sexes, which is more conspicuous in females, and female changes in body shape due to the ovary development, may explain the higher catchability of females, especially during rainy season. In consequence, the sex ratio estimated from fishery and even from fishery-independent surveys should be used with caution for both, stock assessment and management. It may reflect catchability, i.e., the interaction between stock structure, the distribution of fishing effort and the gear selectivity (Arreguín-Sánchez, 1996).

More importantly, the sex ratios obtained in the present study are very likely similar to those in the fishery, as we used a similar gear. The pattern of catches have great implication for species conservation and the sustainability of the fisheries, because the equilibrium in the sex ratio can be severely altered and consequently the potential reproductive ratio of the species may be directly affected, e.g., parental care in cichlid groups where male play an important role, or the spawning stock biomass. Thus, the decreasing trend in *A. citrinellus* catch ratios between earlier studies (Martínez, 1976), posterior results (Orellana, 1986; Gadea, 2003) and the present study, it might be a symptom of a unbalance sex ratio. Therefore, fisheries management should consider these findings when establishing measures and regulations to avoid the depletion of a stock by a simple overfishing of one sex, by reducing fishing mortality of the more vulnerable sex for each species.

Considering that fishing is the main factor affecting population size structure and functioning of fish assemblages, it is of relevant the establishment of size-based indicator (SBIs), typically used to describe the response of communities or individual populations to exploitation (Garcia *et al.*, 2003), among these, mean length, mean maximum length and length at maturity (L_{50}) (Shin *et al.*, 2005). L_{50} is an important parameter to track maturation temporal shifts in a population and an important predictor of the risk of overexploitation (Reynolds *et al.*, 2005), because shifts in maturation severely determine the population dynamics (Saborido-Rey & Trippel, 2013). However, this study has shown the uncertainties in the L_{50} estimation in cichlids species, and in *B. guatemalensis* was demonstrated that macroscopic observations tend to overestimate L_{50}, and there is a need for improving the estimation of maturity ogives using microscopic methods. Therefore, as reference direction of changes (RD) for monitoring size exploitation pattern in cichlids (*A. citrinellus*, *H. nicaraguensis*, *P. managuensis*), we recommended the respective mean length obtained in this study, whereas for *B. guatemalensis* we recommended a minimum landing sizes (MLS) based on the L_{50} microscopically estimated (see chapter 5 for details).

In fishery biology, analysis of life history traits related to reproduction has mainly focused on females, in part because offspring production is limited to a greater degree by egg production (Helfman *et al*, 1997) and because females provide nourishment to the developing embryos and thus at least during the very early life stages the maternal role is more important than the paternal role in influencing progeny production (Murua &Saborido-Rey, 2003). But fishes exhibit great diversity of reproductive strategies and associated traits (Helfman *et al.*, 1997; Pitcher & Hart, 1982; Wootton, 1984; Murua & Saborido-Rey, 2003). The knowledge of those strategies and reproductive patterns, at least from the commercial important species, may lead to the adoption of management actions based on biological sound scientific information. Little is known on the reproductive ecology of the lake species, and in particularly on aspects like fecundity type, ovarian development organization, spawning season and frequency, potential fecundity, influence of the environmental fluctuation. Therefore, the implication of those biological aspects on fisheries management is not possible. In our study we have tried to elucidate such implications on focusing, comprehensively, on the reproductive ecology of *B. guatemalensis*.

B. guatemalensis shows a seasonal breeding activity that occurs during rainy season, with main peak in July-August. This peak coincides with the massive presence in the lake from May to August of eggs and larvae of an insect of the chironomidae family which is a major food source of small fishes and particularly for those living in muddy zones (enlace, 2001). Feeding occur when eggs of the insect, which initially are placed on the water surface, sink to the bottom where becomes larvae. In spite of the seasonality its spawning season is protracted because spawning asynchrony at population level. Spawning activity is considerably dependent on female size, i.e., smaller females have an earlier spawning cessation, while larger females have a more extended spawning season. Gillnet selectivity in *B. guatemalensis* was related with fish size, as expected. However, during the reproductive season the proportion of fishes captured in each gillnet differed unexpectedly among reproductive phases. Of particular importance are the selectivity pattern of fishes in spawning phases, since high fishing mortality (catches) on these affect the egg production and the subsequent recruitment. The fact that females in spawning capable and actively spawning are more vulnerable to the 100 mesh size, may have an important impact on the spawning stock biomass. The identification of the more vulnerable females group being fished out may lead to more effective management action, in particular regulating mesh size and avoiding over-exploitation of the spawning stock biomass.

The reproductive potential is a measure of the capacity of a population to produce viable eggs and larvae, and can considered as the main outcome of a reproductive strategy (Murua & Saborido-Rey, 2003). The conservation of a given spawning stock biomass (SSB) has been considered one of the key factors to produce sufficient recruitment to the fisheries, since the stock-recruitment relationship imply that spawners biomass influence the recruitment (Myers & Barrowman, 1996), under the assumptions that SSB is an index of egg production (Beverton & Holt, 1957). However, this assumption has been widely invalidated (Saborido-Rey & Trippel, 2013 and references therein) and the concept of stock reproductive potential (SRP, Trippel, 1999) has often replaced SSB. Several SRP indexes have been developed, but undoubtedly total egg production (TEP) is a better estimate of a stock's reproductive output than the less sensitive SSB (Marshall, 2009). There is recent and increasing evidence that variations over time in stock structure, sex ratio, fish condition, growth rate, maturation and fecundity produce large variability in TEP (Saborido-Rey & Trippel, 2013 and references therein). TEP is very much depending on fecundity, spawning duration and spawning frequency, all of these increasing with age and size (Fitzhugh *et al.*, 2012). Our findings demonstrated that *B. guatemalensis* egg production is related to spawning duration and fecundity which in turn are related to female condition and length. Moreover, egg quality of larger females is higher and it decays as spawning progress, associated to the declining condition factor of females and also to changes in the environmental conditions, as rainy season close to the end, which might induce oocyte maturation at smaller sizes. Thus, stock structure, and not only biomass, is the key component to understand reproductive potential and recruitment.

From fisheries sustainability point of view, the estimated egg production actually represents the loss egg production when those females are removed from the fishing ground.

Through this study is demonstrated that 75 mm net remove a higher proportion of smaller spawning females, very likely recruit spawners. These are less experienced females having an earlier spawning cessation, but more importantly being less productive in terms of egg production and egg quality. On the contrary the 100 mesh size net is more harmful in terms of egg production removal, since it causes the highest fishing mortality among the more productive females. Benefits of maintaining larger individuals in a population have been mentioned as the enhancement of the offspring survival and reproductive success, and that young fishes learn the route to spawning aggregation by following the more experienced adults (Birkeland & Dayton, 2005). Classically, fisheries management is oriented to protect juveniles and recruit spawners, avoiding growth overfishing. To reduce fishing mortality of young females it is recommended the use of the 100 mm net, which will protect recruitment and females in the onset of the ontogenic maturation. However, reducing fishing mortality over the more productive females, and consequently to minimizing the loss of eggs production, would imply using in the fishery the 75 mm net. Coping with this paradox is possible if the 100 mm net is used during the dry season, and the 75 mm during the rainy season, especially in July and August when spawning activity of *B. guatemalensis* is higher, and hence protecting females with larger reproductive potential. These management measures would be in agreement with the biology of the species and may provide stock sustainability. Obviously, these types of management measures are based on a single species, which have a particular reproductive strategy, i.e., determinate fecundity and total spawner. However, fisheries in the Lake Nicaragua are multi-specific, and many species are target or by-catch of the fishery. Undoubtedly, the reproductive strategy must differ among them and specific biological studies are required to achieve a balanced management in the lake.

Of course, alternative management measures can be taken depending on the management goals. Thus, if protecting spawning females becomes critical, for stock rebuilding for instance, the uses of 100 mm mesh size during whole year and a closing season in July and August can be approached. Also it is interesting to consider the vertical spatial use of each species, i.e., the benthopelagic and/or demersal behaviour, as a regulation of the gear height may improve the gear selectivity. Our findings show that the species cluster in the net in different positions and management actions can be taken to reduce by-catch. Reducing the gear height might allow to perform a better fishing operation targeting only the species of interest, avoiding fish discards and leave space in the water column for the freely movements of non commercially but biologically important species. Nevertheless, the implementation of these scientific recommendations does not lack difficulties. Fishery in the lake has been always claimed being for subsistence and with relatively low income for fishers. The use of two distinct fishing gears during the year may affect fishers' income. On the other hand, the implementation of a close season implies stopping fishing, with important implications in the community economy. Beyond that, institutions responsible for monitoring, control and surveillance may find difficulties in the application of the management measures due to the usual high fisher resistance and low institutional capacity. Under these circumstances co-management may contribute to develop alternative management approaches more easily to be adopted and in consequence promoting resources sustainability. Co-management should be viewed not as a single strategy to solve all problems of fisheries and coastal resources management, but rather as a process of resource management – maturing, adjusting and adapting to changing conditions over time. Thus, the co-management process is inherently adaptive, relying on systematic learning and the progressive accumulation of knowledge for improved resource management (Pomeroy & Rivera-Guieb, 2006). Co-management experiences have been successful, at a certain level, in some estuarine water bodies in Nicaragua, in the sense of community participation on management actions. Therefore, we believe that this co-management performance can be taken over for fishery in the lake to promote sustainability of the fishery.

CHAPTER 7: Conclusions

Population ecology. Abundance and distribution patterns

1. The fishes studied are widely distributed in the eastern side of the Lake Nicaragua and the fish distribution and abundance are not influenced by water turbidity but this may affect fish catchability because of the differences in fish behavioural response to different level of water transparency.

2. Intra-annual variations of fish abundances are strongly influenced by spatiotemporal effects, both horizontal (macro-zones), vertical (depth) and by environmental factors, i.e., the seasonality of precipitation.

3. Although seasonality has been shown to affect the distribution and abundance pattern of three cichlids, its influence was negligible in *A. ctitrinellus* but certainly important in *H. nicaraguensis* and in less extent in *P. managuensis*. The more deterministic factors influencing the spatial distribution of the cichlids *A. citrinellus*, *H. nicaraguensis* and *P. managuensis* was depth and macro-zones, being more abundant in shallow water and in the southeast zone.

4. Season (dry and rainy) and depth are the main factors influencing abundance of *B. guatemalensis*. Largest abundances were found in the southeast and northwest side, during both seasons, but highest abundances occurred in rainy season at shallower waters, and lower abundance in the central zone.

5. All species studied shows similar spatial size distribution pattern. Larger fishes are found in the southeast and to a lesser extent in the central zone of the lake, whereas in the northwest area the individuals are smaller. Besides, larger fish are found in the deeper waters studied (3 and 5 depth strata), excepting for *P. managuensis* which larger size has preferences for shallower water (1 to 3 depth strata).

6. The selectivity of the gear used during the surveys prevents us to discern where the juveniles of each species inhabit. That because size of *A. citrinellus*, *H. nicaraguensis*,

P. managuensis and *B. guatemalensis* smaller than 14.0, 11.0, 17.0 and 20.0 cm, respectively, were not captured during the surveys.

Reproductive strategy of *Brycon guatemalensis*

7. The *Brycon guatemalensis* oocyte final maturation ends with the migration of the germinal vesicle to the animal pole, without oocyte hydration. However, oocytes increase 1.6-fold in volume during final maturation. Eggs of *B. guatemalensis* are released surrounded by mucus, produced within the ovary, that is visually observed when enter in contact with water.

8. The reproductive season of *B. guatemalensis* occurs mainly during rainy season which trigger the spawning season. Spawning completely cesses in dry season. It exhibits a protracted spawning season lasting 8 months (from July to February), with the higher activity between July and November. But highest spawning event occurring in July and August.

9. Duration and timing of the spawning season are female size-dependent. Smaller females have an earlier spawning cessation (early spawners), coupled to the finalization of the rainy season (November), while larger females have a more extended spawning season (later spawners), till February.

10. The gonadosomatic index (GSI) and the female condition (K) relate fairly well with the reproductive cycle. At the onset of the spawning both GSI and K reflect gonad maturation and energy utilization for reproduction. The decoupling pattern of both along the spawning season and the influence of fish size indicates female population asynchrony at spawning activity, i.e., smaller females have an earlier spawning cessation, while larger have a more extended spawning season.

11. The length at 50% maturity (L_{50}) of *B. guatemalensis*, using microscopic (histological) ogives, was estimated in 27.3 cm. This evinced the macroscopic overestimation of L_{50} in 7.6 cm and the imprecise that macroscopic methods can be. These results have a great implication for assessment and management of the stock in the Lake Nicaragua, since in

the current management measures, minimum landing size and mesh size of the net can be better established based on more reliable biological information.

12. The ovary dynamic of *B. guatemalensis* adjust to the “group-synchronous” type ovary organization. The species shows determinate fecundity and probably spawn only one batch in each breeding season, i.e., is a total spawner.

13. Spawning asynchronous among female population was also evinced through the individual distribution pattern of the oocytes development stages. The protracted spawning season can be consequence of different reproductive behaviour among different size classes, both in term of reproducing timing, condition, egg production and egg quality. Females spawning late in the season decrease eggs size as spawning season progress, and the frequency of larger oocytes becomes lower.

14. Larger females show higher reproductive potential, i.e., produce more eggs and these are larger. The potential annual fecundity of *B. guatemalensis* fluctuates between 700 to 35,500 eggs and the average egg production of the stock, in the area of study, was 11,013 ± 6697 eggs. The low incidence of atresia in Brycon might indicate high reproductive success, since the high incidence of atresia has been linked to a reproductive failure.

Reproduction in fisheries management

15. The net of 75 mm mesh-size is the more efficient catching smaller specimens, as expected, whereas in terms of catches of wider range of size-class, the 100 mm mesh size is more efficient, meaning that both induce high fishing mortality.

16. Differences in selectivity among species partly reflect growth pattern explained by maximum size captured in each species, as some of them were virtually not captured by largest mesh sizes. The theoretically retained maximum size by the gears used was well above the maximum lengths recorded for cichlids species, but not for *B. guatemalensis*, indicating that the range of mesh sizes used in this study is suitable to study growth and population dynamics of large fish. On the other hand, the fact of the minimum size

captured differed among species must be explained only due to fish shape and/or different behaviour of the life stages of each species.

17. Cichlid species shows high vulnerability of being caught (above 90%) in the smallest mesh sizes, i.e., 75 and 100 mm, excepting *P. managuensis* which slightly reduce its probability of being caught in the 100 mm to a 80%. Thus, a great proportion of the population of these species is vulnerable to these mesh sizes. In *B. guatemalensis* the larger sizes reduce the probability of being catch to a 75 % in the 75 mm, i.e., 25 % escapement.

18. The most vulnerable part of the population of cichlids species are males and females in *B. guatemalensis*, particularly during reproductive periods. The male-female proportions of each species very likely are similar to those in the catches in a routine fishing operations performed by the fishers in the lakes. Therefore, care should be taking because the equilibrium in the sex ratio can be severely altered and consequently the potential reproductive ratio of some species may be directly affected, e.g., parental care in cichlid groups where male play an important role, and the spawning stock biomass in *B. guatemalensis*.

19. *B. guatemalensis* on the size of 50% maturity (microscopic estimation), has 100 % probability of being caught and retained in the 75 mm net, and L_{50} falls in the range of 24.0 to 30.0 cm at which the net has 80 % efficiency. However, the efficiency of this net for fish about 20 cm drops considerably, protecting the largest part of the mature stock of the population, but with risk of growth overfishing. Therefore, its use in fishery activities should not recommended and larger mesh size should be considered.

20. For *A. citrinellus*, *H. nicaraguensis* and *P. managuensis*, the correspondent estimated mean length (from selectivity analysis) caught in the 75 mm mesh size, as closer sizes to L_{50}, is recommended as reference direction of changes for monitoring landing size in those species, i.e., 18.6, 16.7 and 23.1 cm, respectively.

21. For *B. guatemalensis*, the L_{50} microscopically determined (27.3 cm) can be used as RP due to the accurate of its estimation, and considering 20 % increase over the size at

maturity, a 30 cm minimum landing size (MLS) is recommended. The recommended MLS for *B. guatemalensis* would have 40 % probability of being caught in the 100 mm mesh size net.

22. The catch composition of *B. guatemalensis* in the different gillnets changes depending on female size but also in relation to the reproductive phase of the female. The 100 mm net is the more efficient net in removing the spawning females (SC and AS phase) from the mature stock, while females in developing and regenerating are mostly caught in 75 mm, even though catches in the 75 mm shows more uniformity in females size.

23. The impact of gillnet, used in small-scale fisheries, on the stock egg production has been rarely studied. The 75 mm net catches a higher proportion of smaller spawning females, very likely recruit spawners, which have an earlier spawning cessation and are less productive in terms of egg production and egg quality. However, our study demonstrates that the 100 mesh size net is more harmful in terms of egg production removal, since it causes the highest fishing mortality among the more productive spawning females stock.

24. To increase the egg production of the females stock and to reduce the fishing mortality of young females it is advisable to use the 100 mm net during dry season protecting recruitment and females in the onset of the ontogenic maturation, but switching to 75 mm bet during the rainy season, especially in July and August when spawning activity of *B. guatemalensis* is higher, and hence protecting females with larger reproductive potential.

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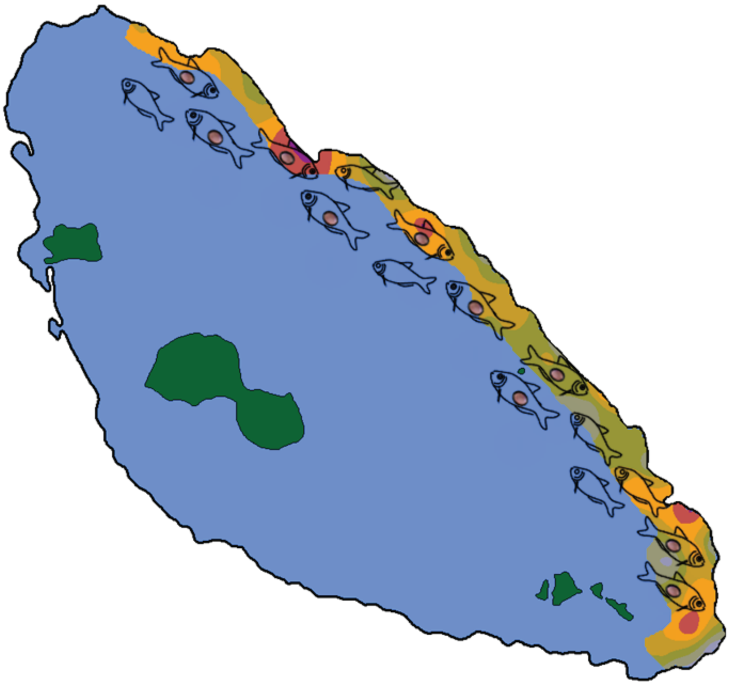
Appendix I: RESUMEN

Universida de Vigo

Departamento de Ecoloxía e Bioloxía Animal

Memoria de Tesis Doctoral
para optar al título de Doctor por la Universidad de Vigo

Ecología pesquera de los peces de agua dulce en el Lago de Nicaragua. Reproducción y manejo de *Brycon guatemalensis*



Presentada por:

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Vigo, España 2013

Introducción

Los cuerpos de agua dulce son sistemas muy dinámicos, pero a la vez muy vulnerables frente al impacto de las actividades humanas. Sorprendentemente, estos ecosistemas responden positivamente a las medidas de manejo (Maitland & Morgan, 1997). Los habitas dulce acuícolas han sido divididos en humedales y aguas abiertas. Estos son muy variables en características y varían en lenticos (lagos) y loticos (ríos) (Maitland & Morgan, 1997). Los lagos son sistemas cerrados con un cuerpo de agua definido y ecología relativamente más estable que los ríos (Welcomme *et al*., 2010). En los lagos de áreas tropicales la temperatura no varía mucho, y la profundidad es uno del parámetro más importante que influye en el ecosistema (Maitland & Morgan, 1997). La transparencia del agua depende de la profundidad de la zona fótica la cual puede ser alterada por la cantidad de sedimentos que entra en el ecosistema. En los lagos se han observado cambios ecológicos debido a la introducción de especies exóticas, causando la extinción de especies nativas por depredación u otros mecanismos (Cowx, 1998a; 1999).

Las pesquerías en cuerpos de aguas continentales (CAC) se han incrementado de 9.8 millones de toneladas en el 2006 a 11.5 millones de toneladas en 2011 (FAO, 2012). A pesar del incremento de la producción se sabe de que el grado de utilización de los recursos pesqueros varía de un lago a otro de acuerdo a dos tipos de pesquerías: demersal/ costero y pelágico/aguas abiertas. Esto contribuye a la percepción de que las pesquerías en algunos CAC no son sostenibles debido a que las capturas están descendiendo, especies están desapareciendo y muchos otros síntomas de sobrepesca son reportados (Welcomme *et al*., 2010). Las pesquerías son generalmente caracterizadas por ser pesquerías de pequeña escala practicadas de manera artesanal que tienen una gran importancia como fuente de alimento y empleo para el desarrollo de las comunidades rurales.

El Lago de Nicaragua es el más grande de Centro América con una superficie de 8000 km^2, es el noveno lago más grande de las Américas y el diecinueveavo más grande en el mundo. Este ha sido reconocido como un importante cuerpo de agua con una importante fuente de recursos vivos para el sector pesquero (Davies & Pierce, 1972), pero sus dimensiones lo convierten en un CAC muy atractivo para el desarrollo de la acuicultura. Sin embargo, contrasta con el hecho que algunas especies están sobreexplotadas y otras en riesgo de sobreexplotación si no se toman medidas de manejo (Thorson, 1982; Adams *et al*., 2006).

En el Lago de Nicaragua las precipitaciones oscilan entre 700 y 2500 mm y una marcada estación seca (PENUMA-OEA, 1997). Las aguas del lago atraviesan por ocho diferentes ecosistemas terrestres (Montenegro-Guillén, 2003). La ausencia de estratificación física-química y clorofila a, indica que es un lago polimíctico, y el cálculo del índice trófico de Carlson indica que es un lago eutrófico con tendencia a disminuir la calidad de sus aguas (PROCUENCA-SAN JUAN, 2004). Los cambios en la calidad de las aguas son lo que más afectan la ecología de los lagos, afectando su transparencia, el régimen de oxígeno disuelto y la residencia de los organismos (Welcomme *et al*., 2010). En la zona tropical donde está localizado el Lago de Nicaragua predominan dos estaciones bien definidas, la estación lluviosa de Mayo a Octubre y la estaciona seca de Noviembre a Abril. Además el lago es afectado por los vientos Alisios que soplan de este a oeste durante los meses de Enero a Mayo que no permiten una estratificación térmica del lago.

El subsistema del lago recibe contribuciones de numerosos ríos siendo los más importantes los localizados en parte este del lago tales como Malacatoga, Tecolostote, Mayales, Acoyapa, Oyate, Comastro y Tule. La salida natural del lago es el Río San Juan el cual drena sus aguas al Mar Caribe. El nivel del agua del lago oscila entre 3 y 4 metros cada año y el nivel más bajo y más alto ocurre en Abril y Octubre, respectivamente. Las temperaturas de superficie de las aguas del lago varían entre los 25º y 28º C sin haber estratificación térmica.

Los estudios sobre la distribución taxonómica de los peces continentales en Centro América han permitido reconocer la existencia de cuatro provincias, entre ellas la Provincia de San Juan (Bussing, 1976), a la cual fueron asignados los peces de agua dulce de Nicaragua. La mayor diversidad de peces se encuentra en el Río San Juan (46 especies), 32 de ellas se encuentran en Lago de Nicaragua. Nueve especies con afinidad marina que entran al lago han sido reportadas.

Las áreas de reproducción de las especies más estudiadas como los ciclidos son las zonas rocosas (McKaye, 1977; Olfield, McCrary & McKaye, 2006), mientras que las depresiones arenosas son habitas adecuados para el desove de otros ciclidos como *Hypsophrys* (Conkel, 1993). El reclutamiento de especies migratorias como *Brycon guatemalensis*, que exhiben migración potádroma ha sido identificado a lo largo del río San Juan (PROCUENCA-SAN JUAN, 2004) mientras las zonas de desove ocurren río arriba hacia el lago (Horn, 1997) y en los ríos tributarios (McLarney *et al*., 2010).

El patrón de explotación de los peces en el lago de Nicaragua ha variado pasando de explotar grandes peces como el Pez Sierra y Tiburón Toro para consumo domestico y exportación (Thorson, 1982) a pescar peces más pequeños como Robalos, Gaspar, Guapote, (*Parachromis spp.*) y una variedad de Mojarras (*Amphilophus ssp.*). Los datos históricos de desembarque de 30 años hasta 1987 fueron menores 300 toneladas lo que se debe probablemente a que estos datos provienen de los principales mercados de comercialización del producto. Las estadísticas han mejorado desde 1993, y de 1994 a 2006 se reflejaron estadísticas de desembarque no registrado equivalente al 100 % de lo registrado (ADPESCA, 2006). Sin embargo, no permiten obtener una clara estimación de la composición por especie de las capturas.

La actividad pesquera en el Lago de Nicaragua es desarrollada principalmente por pescadores artesanales. Esta actividad ha variado de ser ejercida de manera temporal a permanente (Davies & Pierce, 1972). La pesca se caracteriza por el uso principalmente de redes de enmalle o agalleras (gillnet) bajo la modalidad de pesca pasiva. Sin embargo, estas son utilizadas bajo otras modalidades como la modalidad de “Chinchorro playero” y “pimponeo”. Otra forma de pesca es el uso de líneas de mano (línea y anzuelo).

La pesquería en el Lago de Nicaragua enfrenta la misma complejidad de cualquier otra pesquería a aguas continentales, debido principalmente a la naturaleza multiespecífica de su explotación, i.e., muchas especies, con diferentes tallas y formas son capturadas con el mismo tipo de red. Las medidas regulatorias de la pesquería en el Lago de Nicaragua están en la línea de: i) recuperación de los recursos sobreexplotados como Tiburón Toro y Pez Sierra (Thorson, 1982; McDavitt, 2002; Adams *et al*., 2006); ii) prevención de sobreexplotación de otras especies como Gaspar, Robalo, Roncador (Camacho & Gadea, 2005); iii) la sostenibilidad de los recursos comercialmente explotados tales como Mojarras, Guapotes, Machaca, Guavina y Bagres (Gadea, 2003; Hernández-Portocarrero & Saborido-Rey, 2007).

Las regulaciones adoptadas para las pesquerías del lago van desde la prohibición del uso de redes de arrastre, de palangres y uso de redes agalleras cerca de la boca o dentro de los ríos. Sin embargo, medidas de referencia biológica para el manejo de los recursos pesqueros aún no se han establecido, ya que la mayoría de las medidas están basada en la evaluación de la distribución y abundancia de las capturas de las especies importantes comercialmente, sobre estudios de selectividad de la red y en la determinación macroscópica de dos parámetros biológicos como longitud de madurez y estados de madurez gonadal (Davies & Pierce, 1972; INFONAC, 1974; Martínez, 1976; Ketúnin *et al.*, 1983; Orellana, 1986; Gadea, 2003, Hernández-Portocarrero & Saborido-Rey, 2007).

Actualmente hay un vacío de conocimiento sobre otros parámetros biológicos importantes como la dinámica del comportamiento reproductivo de la población a nivel inter e intra específico, el ciclo reproductivo, área de desove, producción de huevos y características maternales que afectan el producto final de la reproducción. Esto previene la implementación de acciones de manejo dirigidas a la conservación del potencial reproductivo (Saborido-Rey & Trippel, 2013), tales como épocas y/o zonas de veda, y mínima y máxima talla de desembarque. En este estudio además de proveer información acerca del actual estado de distribución y abundancia de regulaciones de *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis*, y *Brycon guatemalensis*, es suministrada información de la estrategia reproductiva de *B. guatemalensis* y propuesta algunas medidas de manejo alternativo basado en características biológicas.

El objetivo del presente estudio es desarrollar una herramienta de manejo apropiado en el Lago de Nicaragua basado en conocimiento biológico y ecológico de las especies explotadas. Para alcanzar los objetivos del estudio es analizado: a) la distribución y abundancia relativa de las principales especies a una escala temporal y espacial en función de los factores ambientales basado en las exploraciones pesqueras mensuales realizadas en el algo (Chapter 3); b) la estrategia reproductiva aplicando procedimientos histológicos, enfocado en la biología reproductiva y potencial reproductivo del stock utilizando como caso de estudio Brycon guatemalensis (Chapter 4); c) el impacto del arte de pesca sobre el potencial reproductivo del stock (SRP), determinando la parte de la población más sensible y relevante, en términos de productividad para delinear el manejo del stock de peces en el Lago de Nicaragua (Chapter 5).

Materiales y Métodos

Area de estudio

El área de estudio localizada en la parte este del Lago de Nicaragua abarcó un total de 1000 km^2, desde la orilla del lago hasta el estrato de profundidad de 5 m y limitada por el banco de pesca identificado como Yolillal al suroeste de San Carlos y el Río San Juan, y el Río Estrella al noroeste de Puerto Díaz (Figura 1). El área de estudio y el rango de profundidad se corresponden con los sitios de pesca donde se desarrolla la pesquería de pequeña escala durante todo el año.

El muestreo mensual estratificado fue realizado entre Febrero de 2005 a Enero de 2006. Nueve estratos fueron definidos de acuerdo a la latitud y profundidad. Las áreas de exploraciones fueron divididas en tres macro zonas: Sureste, Central y Noroeste. Tres estratos de profundidad fueron definidos: entre la orilla del lago y 1.5 m, 1.5 y 3.0 m y entre 3.0 y 5.0 m de profundidad. Se realizaron un total de 47 estaciones definidas en 16 transeptos ortogonales a la orilla del lago con tres estaciones en cada transepto (Figura 1).

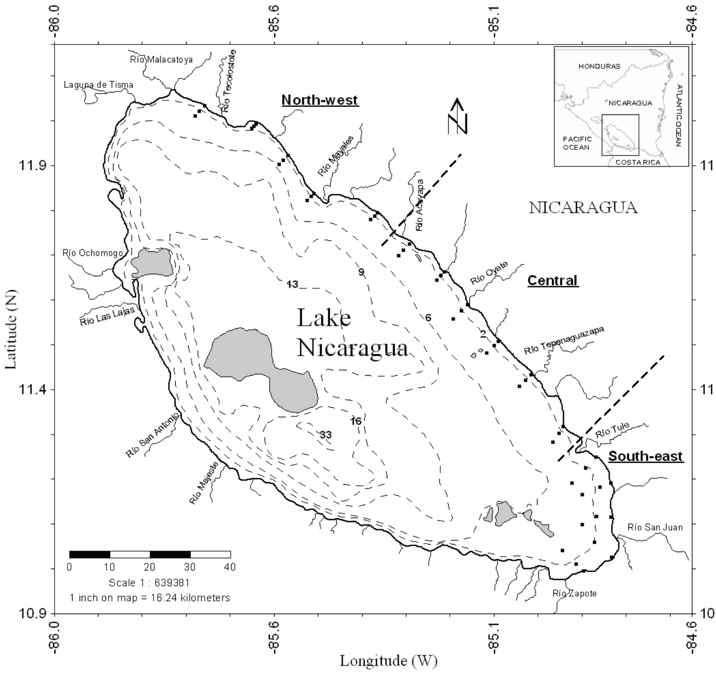


Figura 1. Localización geográfica de las campañas de pesca mensuales (●) en la parte este del Lago de Nicaragua: Febrero 2005 a Enero del 2006. Línea punteada: Perfiles de profundidad en metros.

Para la captura de los peces se utilizaron tres redes enmalle (agalleras) monofilamento de 200 metros de largo, cada una compuesta de 50 m, con luz de malla de 75, 100, 125 y 150 mm de malla estirada. La altura de la red se correspondieron con el estrato de profundidad, i.e., 1.5, 3.0 y 5.0 metros.

La captura fue registrada en número de individuos. Los peces enmallados fueron separados por luz de malla de la red, a los que se tomaron datos biomorfométricos adicionales como altura del cuerpo entre el opérculo y la aleta dorsal.

A los especímenes colectados se les tomó datos de talla, peso entero y eviscerado, se determinó el sexo (macho y hembra) y se colectaron ovarios de *Brycon guatemalensis* que fueron pesados en condición fresca. En total 371 ovarios fueron colectados y fijados en formalina al 4 %.

Distribución y abundancia

Captura Por Unidad de Esfuerzo (CPUE): En el presente estudio la CPUE es expresada como la proporción entre la captura (en número de especímenes) y el esfuerzo (en horas multiplicado por el área de la red). La CPUE fue modelado en función de la escala espaciotemporal y de los factores ambientales. Debido a la ocurrencia de "cero" capturas en algunas estaciones de pesca, el método "ad hoc" (Robson, 1966) fue utilizado para al cálculo de la CPUE de *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* y *B. guatemalensis*, al que fue sumado un valor constante antes de ser transformado:

$$\mathrm{Ln}\,(\mathrm{CPUE}\ n/h * m^2 + 1)$$

Estudios reproductivos

Desarrollo del ovocito: Mediante procedimientos histológicos fueron analizados los ovarios de 371 hembras de *B. guatemalensis* en los que se determinó el estado de desarrollo de los ovocitos en base a la terminología de clasificación (Wallace & Selman, 1981; West, 1990; Tyler & Sumpter, 1996; Saborido-Rey & Junquera, 1998; Murua & Saborido-Rey, 2003) siguiente: crecimiento primario (PG), alvéolos corticales (CA), vitelogénesis inicial

(VIT1), vitelogénesis avanzada (VIT2) y vesícula germinal migratoria (GVM), además se identificaron las estructuras: folículos post-ovulatorios (POF) y huevos en atresia.

Ciclo reproductivo: Las gónadas fueron clasificadas en fases reproductivas siguiendo la terminología propuesta por Brown-Peterson *et al.*, (2011), incluyendo en este estudio la sub-fase puesta activa (AS) como una fase reproductiva. Así seis fases fueron consideradas para la clasificación reproductiva: Inmaduros (I), Desarrollo (D), Capacidad de desove (SC), Puesta activa (AS), Regresión (Rgs) y Recuperación (Rgn) basadas en la presencia de los diferentes estados de desarrollo de los ovocitos como PG, AC, VIT1, VIT2, GVM ovocitos en atresia y en la presencia de POF.

Fracción desovante (Sf): La fracción desovante (Sf) definida como la fracción de hembras maduras que desovan por día (Alheit, 1985) fue calculada en base a la prevalencia de estados de desove o fases determinadas a partir del muestreo de gónadas al azar:

$$\mathrm{Sf} = \frac{\mathrm{SC} + \mathrm{AS}}{\mathrm{D} + \mathrm{SC} + \mathrm{AS} + \mathrm{Rgn}}$$

Índices somáticos: El índice gonadosomático (GSI) y el factor de condición (K) fue estimado en 240 y 305 especímenes, respectivamente, de acuerdo a:

$$GSI = \frac{GW}{W_g} * 100 \qquad K = \frac{W}{L^b} * 100$$

Madurez: La ojiva de madurez de hembras de *B. guatemalensis* fue determinada utilizando los resultados de la observación macroscópica de 1526 ovarios examinados, y los resultados de las observaciones histológica (microscópica) de las 371 ovarios. La madurez fue analizada en función de la longitud del pez ajustada a una ecuación logística:

$$\hat{P} = \frac{e^{a+bL}}{1 + e^{a+bL}}; \qquad \text{y su transformación logarítmica:} \qquad \ln \frac{\hat{P}}{1 - \hat{P}} = a + bL$$

Donde “P” es la proporción de individuos maduros, “a” y “b” los coeficientes estimados de la ecuación logística y “L” la talla. La L_{50} es definida como –a/b.

Fecundidad: La fecundidad fue estimada por medio del método gravimétrico. El método se basa en la relación entre el peso del ovario y la densidad de ovocitos en el ovario, y se puede estimar la fecundidad parcial, total y potencial (Hunter & Golberg, 1980; Hunter, Macewicz & Kimbrell, 1989). El número y diámetro de los ovocitos contenido en la submuestra del ovario fue estimado por medio de la ayuda de un sistema de análisis de imagen siguiendo la metodología de Domínguez-Petit (2007) y Alonso-Fernández (2011). El número de ovocitos en desarrollo (NDO), referido al total de ovocitos con vitelo en el ovario (Murua & Motos, 2006; Domínguez-Petit, 2007) y el número relativo de ovocitos en desarrollo (RNDO), referido al NDO dividido por el peso eviscerado de las hembras, fue evaluado para determinar el tipo de fecundidad de *B. guatemalensis*. La fecundidad potencial anual (F_p) de *B. guatemalensis* fue estimada en un número total de ovocitos igual o mayores que 1000 µm que corresponde a la cohorte de ovocitos en estados desarrollo más avanzado (VIT2 y GVM).

Estudios de selectividad

Para los estudios de selectividad del arte de pesca (red de enmalle o agallera) se seleccionaron cuatro especies (Tabla 1), pero un énfasis especial fue puesto en la relación entre la selectividad y las fases reproductivas de hembras de *B. guatemalensis*.

Tabla 1. Especies y número de especímenes considerados en los análisis de selectividad de la red agallera. Redes con luz de malla de 75, 100, 125 y 150 mm malla estirada.

		Espécimen para estudios de selectividad		
Familia	Especies	♂	♀	Total
Cichlidae	*Amphilophus citrinellus*	4258	2487	6745
	Hypsophrys nicaraguensis	1556	97	1653
	Parachromis managuensis	393	331	724
Characidae	*Brycon guatemalensis*	1284	1643	2927
	Total			12049

El estudio de selectividad de las redes con luz de malla de 75, 100, 125 y 150 mm, fue especialmente dirigido a las hembras de la especie en los diferentes estados reproductivos. Tomando como referencia la abundancia resultado de los cálculos de selectividad en base a 1643 hembras de *B. guatemalensis* y la proporción de hembras en los diferentes estados reproductivos, determinados histológicamente en 371 hembras, se estimó el número de hembras en la población utilizando la siguiente ecuación:

$$NR_{lmr} = \frac{A_{ml}HR_{lmr}}{\sum HR_{lmr}}$$

Donde NR$_{lm}$ = número total de peces de talla *l* por luz de malla *m* en la diferentes fases reproductivas.

El impacto de cada luz de malla en el stock de inmaduros y maduros fue evaluado utilizando la ojiva de maduración macroscópica estimada para *H. nicaraguensis*, *A. citrinellus*, *P. managuensis* y *B. guatemalensis* previamente estimada (Hernández-Portocarrero & Saborido-Rey, 2007) y la ojiva microscópica estimada para *B. guatemalensis*. Adicionalmente, basados en los estudios histológicos, fue evaluado impacto de la selectividad en el stock de hembras de *B. guatemalensis* en las fases reproductivas de los individuos maduros.

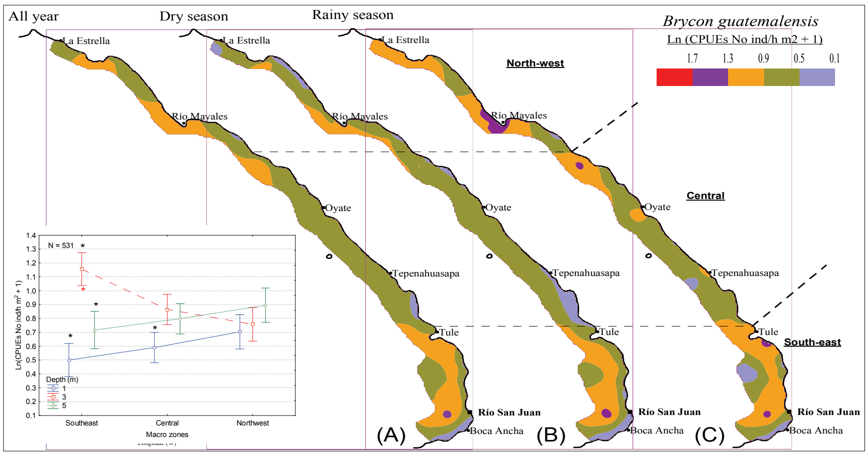
Además, el impacto de las redes en la producción de huevos fue evaluado estimando el potencial de huevos producidos por las hembras capturadas en cada luz de malla de la red, utilizando la ecuación potencial obtenida de la relación de la fecundidad potencial y la longitud de las hembras de *B. guatemalensis*:

$$EP_m = \sum_{l=1}^{n} HR_{lm} * 0.0626l^{3.3094}$$

Donde EPm es la producción potencial de huevos por luz de malla de la red: HRlm es el número de hembras de talla *l* y luz de malla *m*.

Resultados y Discusión

Ecología Poblacional. Patrones de Abundancia y Distribución



La captura por unidad de esfuerzo (CPUE) es la fuente primaria de información para las pesquerías comerciales y recreativas más valoradas y vulnerables (Maunder & Punt 2004), y es el dato más común utilizado para la evaluación de un stock (Maunder & Hoyle, 2006). En pesquería independientes de las pescas comerciales, i.e., resultados de investigaciones pesqueras rigurosas, la CPUE se asume proporcional a la abundancia de los recursos estudiados (Harley, Myers & Dunn, 2001; Bishop, 2006) y las variaciones en la abundancia reflejan la vulnerabilidad de los recursos al arte de pesca utilizado y estrategia de pesca, además, a la biología del recurso, comportamiento y respuesta a los factores ambientales (Arreguín-Sánchez, 1996).

En este estudio es analizado el patrón de variabilidad de la CPUE expresada como Ln(CPUE No ind/h m^2+1) de tres especies pertenecientes a la familia Ciclidae *Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* y una especie de la familia Characidae *Brycon guatemalensis*. El índice de abundancia es examinado en función de la escala temporal como son los meses del año, de la escala espacial como las macro zonas (noroeste, central y sureste), el estrato de profundidad (1, 3 y 5 metros) y en función de los factores ambientales como la estación lluviosa y la turbidez del agua. En la línea de los objetivos de esta tesis, especie interés es puesto en cómo es modulado el índice de abundancia relativo (CPUE) y la distribución de tallas de *Brycon guatemalensis* por los cambios espaciotemporales y ambientales. Por lo tanto, la discusión de este capítulo es enfocada principalmente en esta especie que a su vez es considerada es caso de estudio de toda la tesis.

Resultados y discusión

La relación de la captura y el esfuerzo de pesca (horas) en las cuatro especies consideradas en este estudios es asintótica, lo que indica la forma de operación del arte de pesca. Inicialmente las capturas son bien bajas y a medida que se incrementa el esfuerzo de pesca se incrementan también las capturas hasta alcanzar el nivel máximo, que en estas especies se alcanza entre 6 y 7 horas de pesca (Figura 2). Cuando se alcanza este nivel máximo, aunque se aumente las horas de pesca las capturas no aumentan significativamente y los rendimientos comienzan a disminuir, lo que se interpretado como una disminución del poder de pesca de la red debido a la acumulación de peces en la red (Kennedy, 1951; Beverton & Holt 1957). La simple observación durante los muestreos indica que la red se satura a diferentes niveles en relación a las especies capturadas lo que podría tener una gran implicación para efectos de manejo en pesquerías multiespecificas como las del Lago de Nicaragua debido a que las redes para la pesca de este recurso no necesitan cubrir toda la columna de agua, por consiguiente esto permitiría que especies que exhiben diferentes comportamiento natatorio no quedaran atrapadas en de manera incidental en la misma red. Esto además supondría una reducción de los costos de operación pesquera al reducir la altura de la red.

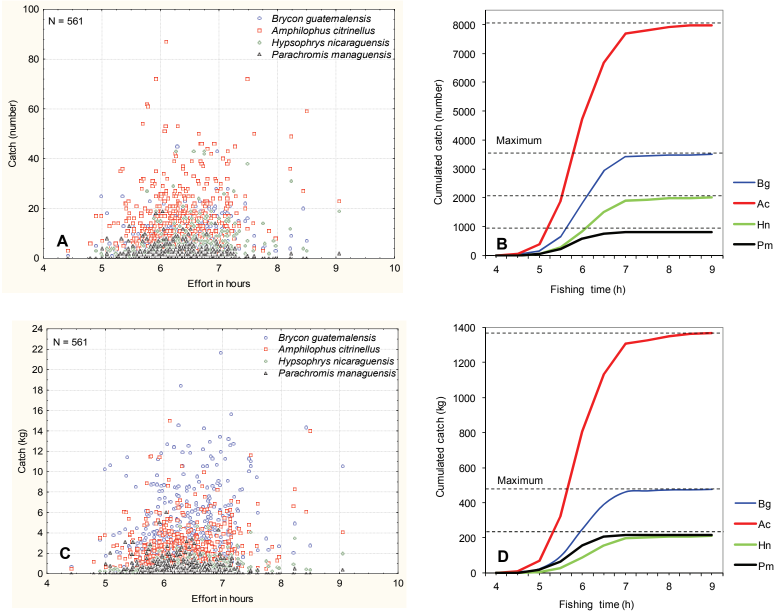


Figura 2. Patrón de capturas y esfuerzo durante el estudio realizado. Bg: *Brycon guatemalensis*; Ac: *Amphilophus citrinellus*; Hn: *Hypsophrys nicaraguensis*; Pm: *Parachromis managuensis*: Línea discontinua: Capturas máximas. Lago de Nicaragua 2005-2006.

Las redes de enmalle (gillnet) han sido ampliamente utilizadas para investigaciones pesqueras (Hansen, Schorfhaar & Selgeby, 1998) y la CPUE es usada en investigaciones aplicadas como un índice de abundancia de los peces, basado en diseños de muestreo utilizando varias mallas (European Union, 2000; Sondergaard *et al*., 2005; Diekmann *et al*., 2005). Pero la eficiencia de este tipo de arte depende grandemente de factores técnicos y biológicos, incluyendo luz de malla, longitud de la red, tiempo de calado, saturación de la red, abundancia de los peces, morfología, comportamiento y actividad del pez (Beverton & Holt 1957; Hamley, 1975; Olin *et al*., 2004; Rotherham *et al*., 2006). A pesar de que el arte está muy influenciado por los factores indicados, técnicas hydroacústicas para estimar biomasa de peces en lagos estratificados han mostrado una fuerte correspondencia con las CPUE obtenidas con gillnet (Emmrich *et al*., 2012). Por lo que probablemente la CPUE estimada en el presente estudio puede ser considerada como un buen índice de abundancia de los peces del Lago de Nicaragua.

La variación de la abundancia interanual es hipotéticamente está fuertemente influencia por el efecto espaciotemporal, tanto horizontal (macro zonas) y vertical (profundidad), y por los factores ambientales como la estacionalidad de la precipitación. Cada uno de estos factores de manera independiente determina significativamente la abundancia en el área de estudio, pero también las interacciones entre estos factores indican la complejidad de la distribución de los peces y los movimientos estacionales.

Las cuatro especies estudiadas se distribuyen ampliamente en la parte este del Lago de Nicaragua (Figura 3). Los factores más determinantes que influyeron en la distribución espacial de los ciclidos fueron la profundidad y las macro zonas (Figura 4). Estas especies fueron más abundantes en aguas someras. La profundidad influye en la composición de los grupos de peces en los lagos (Rodriguez & Lewis, 1997), debido a la variación del periodo en que los humedales son inundados o hidro periodo. (Fernandes, Machado & Penha 2010). La distribución y abundancia de los ciclidos puede estar relacionada con la afinidad de estos con las áreas rocosas (Olfields, 2006) que en el lago están localizadas cerca de la orilla.

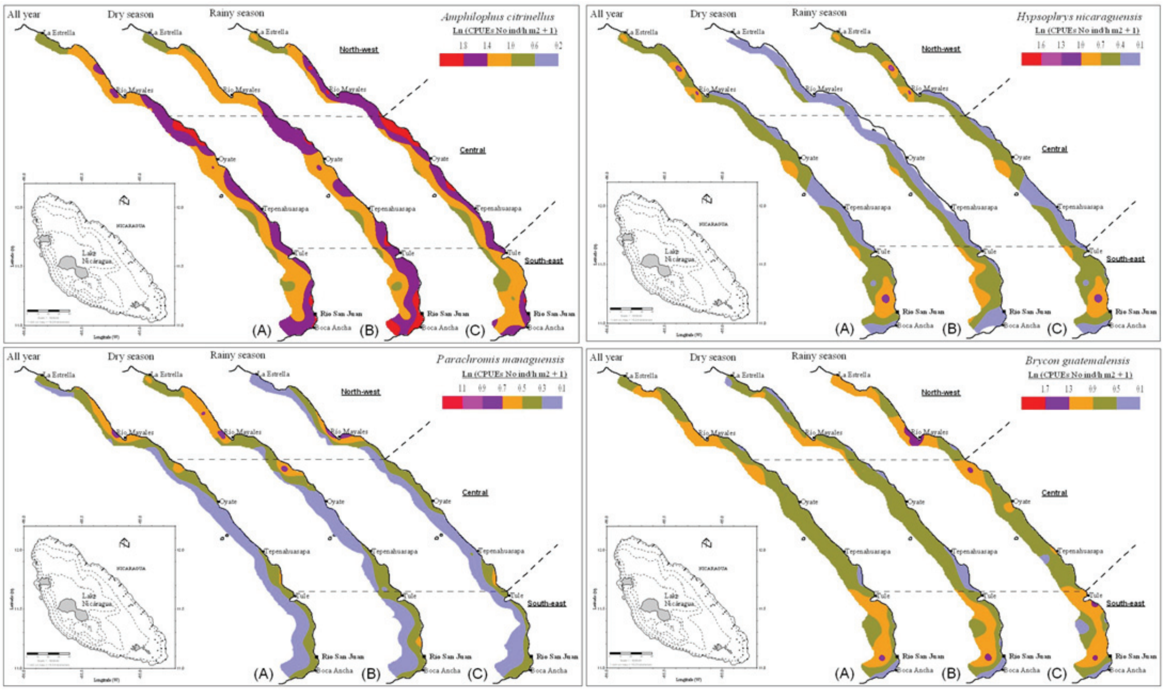


Figura 3. Indice de distribución y abundancia [Ln(CPUE No ind/h m^2 + 1)] de cuatro especies en la parte este del Lago de Nicaragua.

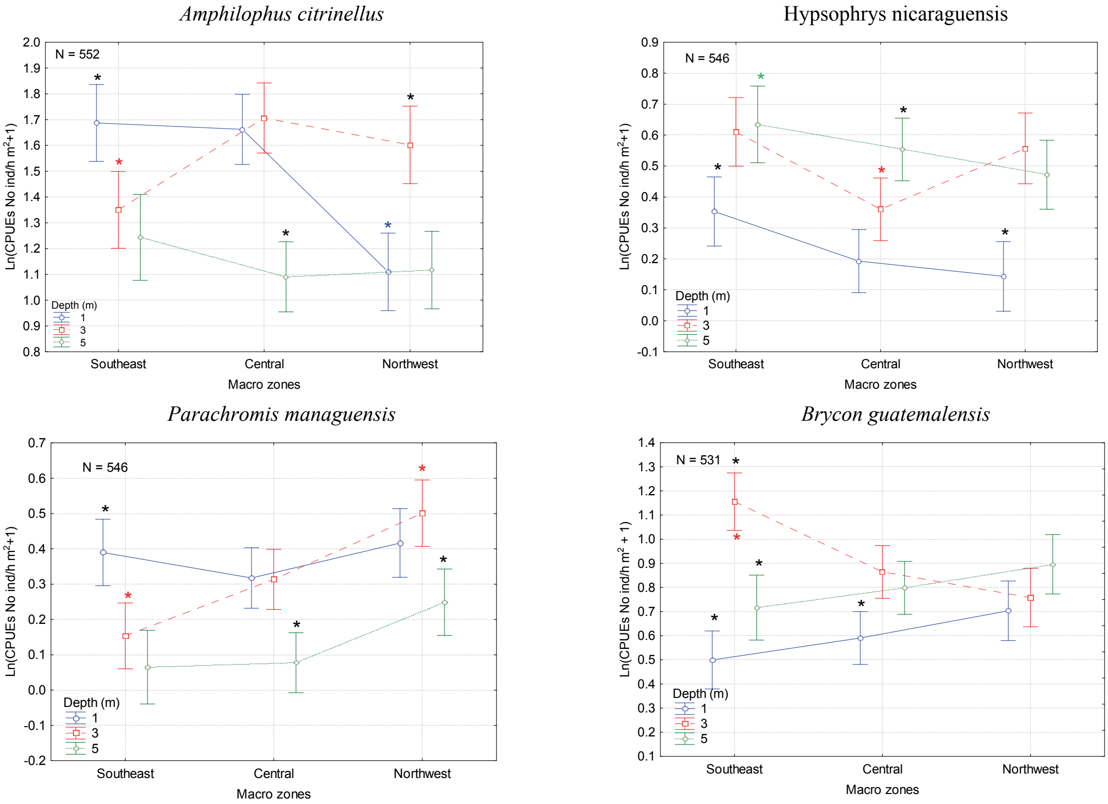


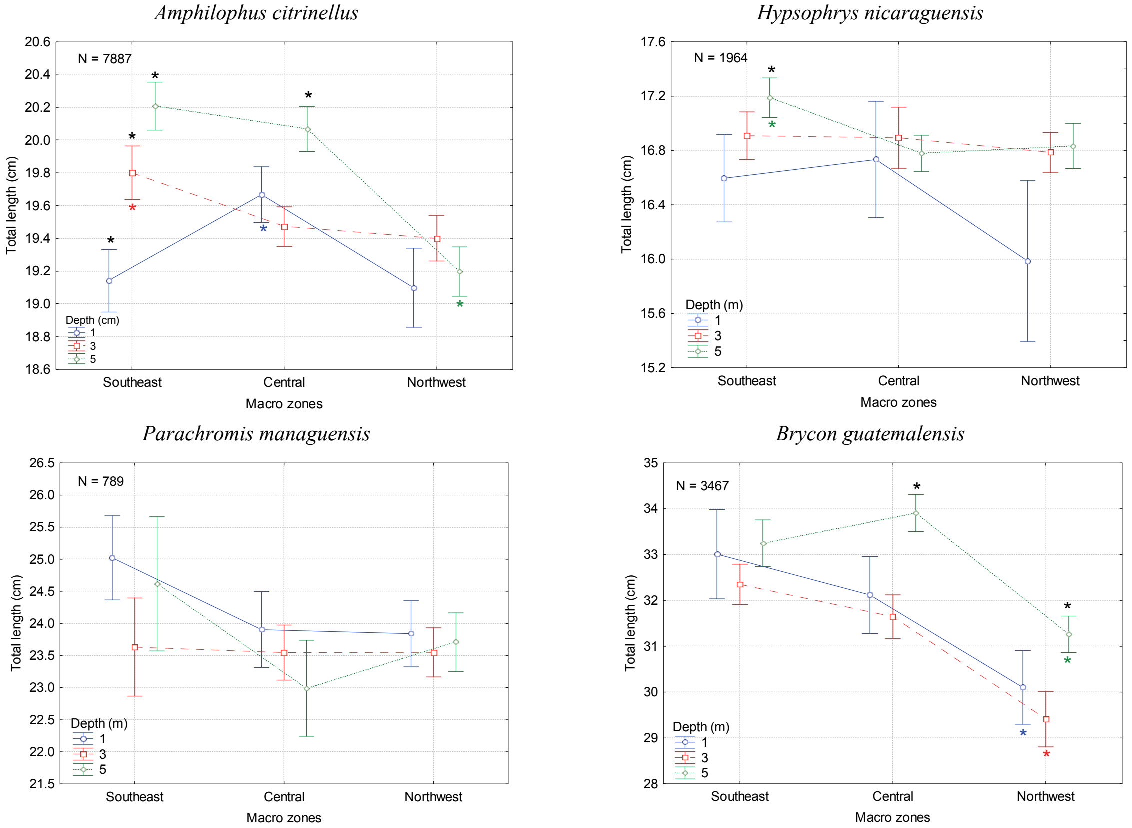
Figura 4. Variación espacial de la CPUE [Ln(CPUE No ind/h m2 + 1)] de cuatro especies. Media ± CI: Barras verticales denotan 0.95 intervalo de confidencia. * azul, rojo y verde muestran diferencias significativas entre el estrato de profundidad dentro de la macro zonas. * gris denota diferencias significativas entre macro zonas dentro del mismo estrato de profundidad.

La estación del año y la profundidad son los principales factores que afectan la abundancia de *B. guatemalensis*. Las mayores abundancias fueron encontradas en el sureste y noroeste durante ambas estaciones (seca y lluviosa) pero las mayores abundancias ocurrieron en la estación lluviosa en aguas someras y las más bajas en la zona central del área de estudio. La estación parece modular fuertemente el comportamiento migratorio de esta especie de los ríos al lago y viceversa. El aumento de la abundancia durante la estación lluviosa es más evidente cerca de la zona de drenaje de los ríos. Los ríos son reconocidos como importantes habitas para potadromous (migración dentro de ambientes acuáticos de agua dulce) especies como *Brycon guatemalensis* la cual habita en el lago y exhibe comportamiento migratorio hacia ríos tributarios (Drewe *et al*., 2003) para desovar (McLarney *et al*., 2010)

El patrón de distribución espacial de las tallas es muy evidente en todas las especies estudiadas. Los peces de mayor talla son encontrados en el sureste y en menos concentración en la zona central del área de estudio, mientras en el noroeste los especímenes son más pequeños (Figura 5). Este patrón podría estar relacionado a la influencia del Río San Juan (RSJ). El RSJ desde el punto de vista ecológico es el río más importante en la región debido a su extensión y diversidad de habitas, así como por su gran biodiversidad, lo que provee de las condiciones óptimas para el crecimiento y reproducción de muchas especies (Bussing, 2002; Villa, 1982).

La selectividad del arte de pesca utilizado durante el estudio no permite conocer el habita de los juveniles ya que tallas de *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* y *B. guatemalensis* menores de 14.0, 11.0, 17.0 y 20.0 cm, respectivamente, no fueron capturadas por la red. En el presente estudio las mayores tallas fueron encontradas en estratos más profundos (3 y 5 m). En aguas someras el mayor porcentaje de los especímenes tenían tallas por debajo de la longitud media estimada para cada especie (*A. citrinellus*, *H. nicaraguensis*, *P. managuensis* y *B. guatemalensis*), i.e., 64%, 41%, 70%, 50%, en la estación seca y 66%, 57%, 83%, y 59%, en la estación lluviosa, respectivamente (Figura 6).

La talla máxima reportada de *B. guatemalensis* fue de 61.7 cm capturada en la zona sureste cerca del RSJ (Gadea, 2003). Esta talla es similar a la talla máxima (59 cm) registrada por IGFA (2001). En el presente estudio la talla máxima encontrada fue 55.5 cm, capturada en la zona sureste y central de la zona de estudio.


Amphilophus citrinellus

Hypsophrys nicaraguensis

Parachromis managuensis

Brycon guatemalensis

Figura 5. Variación espacial de la longitud media de las cuatro especies estudiadas, entre la macro zona y la profundidad. Barras verticales denotan 0.95 intervalo de confidencia. * azul, rojo y verde denota diferencias significativas entre estrato de profundidad dentro de macro zonas. * gris denota diferencias significativas entre macro zonas y dentro del estrato de profundidad.

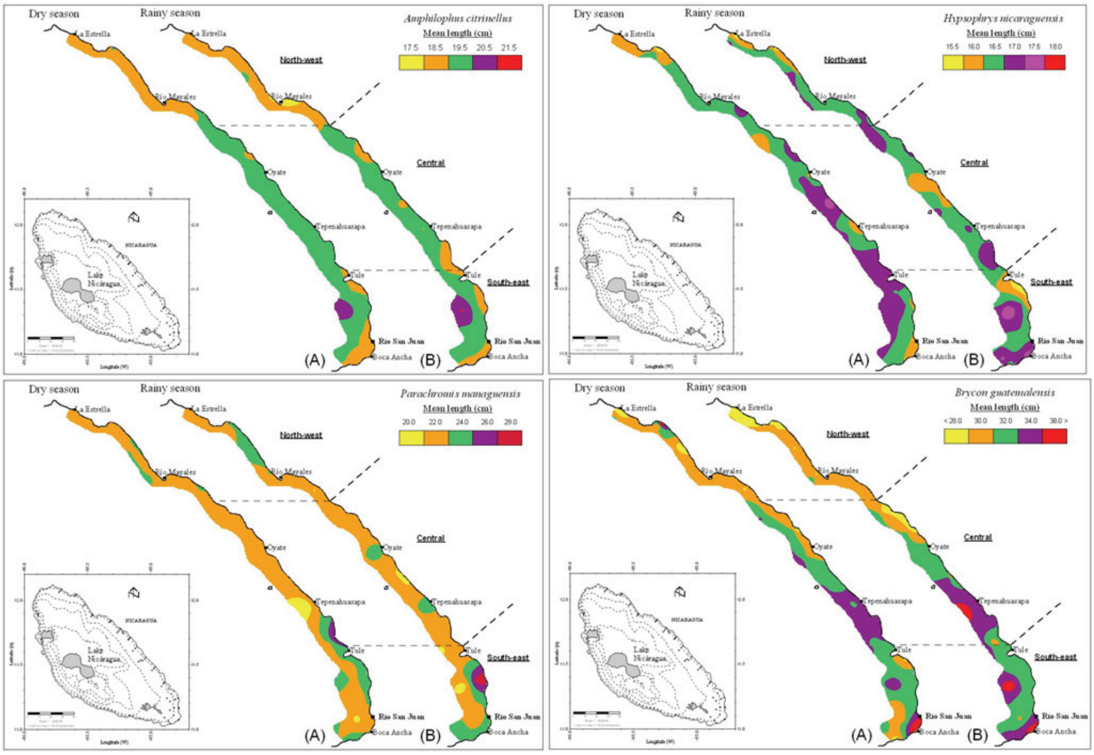
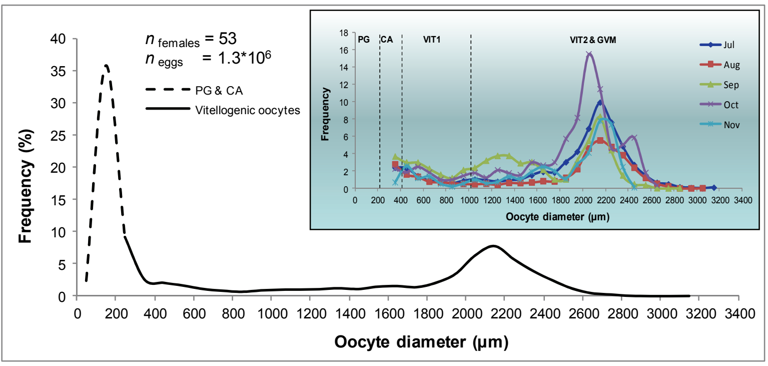


Figura 6. Distribución de la longitud media de cuatro especies estudiadas en la parte este del Lago de Nicaragua.

Estrategia Reproductiva de *Brycon guatemalensis*



La estrategia reproductiva de los peces es la combinación de rasgos reproductivos característicos del mismo grupo de genes, algunos rasgos pueden ser muy plásticos exhibiendo un amplio rango de expresiones fenotípicas como respuesta a los cambios ambientales (Wootton, 1990). En ambientes tropicales de agua dulce se encuentra una gran diversidad de especies de la familia Characidae, en la que se incluye *Brycon guatemalensis*, con una gran diversidad de comportamientos y estrategias reproductivas, que varía de especies que desovan en tierra y hacen nidos de espuma (Kramer, 1978a), especies que producen huevos muy adhesivos, débilmente o no adhesivos (Rizzo *et al.*, 1998; 2002) a peces que desovan en ambiente meramente acuáticos en plantas sumergidas (Brederc & Rosen, 1966) o quienes excavan nidos en fondos arenosos (Bussing W., 2002).

Resultados y discusión

En *Brycon guatemalensis*, a diferencia de muchos otros peces teleósteos, no ocurre la hidratación de huevos que indicaría la pronta liberación de los ovocitos, y la evidencia de que los ovocitos han alcanzado la madurez completa y están listos para ser liberados al medio externo es la presencia del núcleo migratorio o vesícula germinal migratoria (GVM). Esta característica se ajusta a lo observado en laboratorio que los huevos al ser liberados se precipitan al fondo, se vuelven pegajosos y se aglomeran ((Molina, 2006) y son depositado en nidos excavados en fondos arenosos de Greenfield & Thomerson (1997); Bussing W. (2002). La hidratación de los huevos se caracteriza por el rápido incremento del volumen (Wallace & Selman, 1985). Comparativamente, los huevos bentofilicos marinos aumentan su volumen de 1.3 a 3.0, mientras en huevos betofilicos de especies de agua dulce aumentan su volumen de 1.0 a 1.8. (Craik & Harvey, 1984; Cerdá, Fabra & Raldúa, 2007). A pesar de la ausencia de hidratación en los huevos de *B. guatemalensis* estos aumentan 1.6 veces su volumen durante la maduración final. Este incremento está dentro del rango de incremento de otros peces teleósteos de agua dulce pero por debajo del promedio. Los ovocitos de esta especie son liberados envueltos en un mucus, producido dentro del ovario, que se observa al entrar en contacto con el agua. Esta característica permite ubicar los huevos de *B. guatemalensis* en la categoría de huevos adhesivos ya que este mucus hace que los huevos se mantenga unidos y se forme una especie de masa de huevos.

El periodo de reproducción de las hembras de *Brycon guatemalensis* es relativamente largo hasta de ocho meses (de Julio a Febrero) (Figura 7), con mayor actividad reproductiva entre Julio y Noviembre. Sin embargo la fracción desovante (Sf) es mucho mayor en Julio y Agosto. Este periodo reproductivo está estrechamente vinculado a la estación lluviosa del año. En otras especies de esta misma familia, que habitan en otra latitudes, el comportamiento reproductivo es bien diverso el que varía en el tiempo de desove, de 1 a 2 días en *Bryconamericus emperador*, 2 meses *Brycon petrosus* y 4 meses en *Hyphessobrycon panamensis*; hasta especies de desove continuo *Roeboides* y *Gephyrocharax* (Kramer, 1978a).

Los valores más altos del índice gonadosomático (GSI) se observaron de Julio a Diciembre sin un pico definido. Los valores más bajos se observaron durante los meses del período seco indicando la finalización del desove lo que es confirmado por la atresia generalizada en Diciembre y Enero, pero tanto el GIS como la varianza fluctúan durante el periodo de desove, lo que es asociado a la presencia de diferentes fases reproductivas y diferentes tallas de peces dentro del stock de desovantes. La influencia de la talla de los peces en el desarrollo de las gónadas se ha observado en *Engraulis mordax* en que los peces más pequeños tienen un bajo GSI que los peces de mayor tamaño y esto afecto el desarrollo del ovario (Hunter & Golber, 1980). El cambio en la actividad de desove en *B. guatemalensis* en la cual hembras más pequeñas finalizan el desove más temprano que las hembras de mayor tamaño podría explicar las variaciones observadas en el GSI. El GSI de *B. guatemalensis* es más bajo (1 a 4 %) en comparación a otras especies de agua dulce de la misma familia (Characidae) como *Oligosarcus jenynsii* (1 a 8%) y *Oligosarcus robustus* (1 a 10%) (Nunes, Pellanda & Hartz, 2004), lo que podría indicar que *B. guatemalensis* invierte, relativamente, menos energía en la reproducción.

Las variaciones de K a lo largo del año reflejan tanto un periodo de intensa alimentación (Enero a Abril-período seco) y un periodo (Mayo a Diciembre) en que la condición de los peces fluctúa grandemente pero decrece significativamente en Mayo. La disminución de K en Mayo es la primera evidencia de utilización de energía que podría ser relacionada al inicio de la maduración debido a que las variaciones de K primeramente reflejan estados de madurez sexual (Williams, 2000). La disminución de K en los meses siguientes es atribuida a la acumulación de vitelo (vitelogénesis). La tendencia decreciente de K hasta Septiembre seguido de una recuperación en Octubre soporta la idea de que la actividad de desove está relacionada con la estructura de las tallas de las hembras en desove. El patrón de K en *B. guatemalensis* es muy similar al presentado por otros miembros de la familia Characidae como *Astyanax altiparanae* y *Aphyocharax nasutus* (Lizama & Ambrocio, 2002). La influencia de la talla de las hembras en K no fue claramente establecida pero de manera indirecta se observó una relación con los estados de madurez. El desacoplamiento observado entre GSI y K (Figura 8) a lo largo del periodo de desove y la influencia de la talla de las hembras soporta la idea de que la actividad de desove está relacionada con la estructura de las tallas de las hembras en desove.

La longitud a la que el 50 % de la población alcanza la madurez (L_{50}) estimada macroscópicamente fue de 34.6 cm es similar a la estimada por Froese & Binohlan (2000) en 34.6 cm. Sin embargo esto valores están muy por encima del valor de L_{50} estimada mediante procedimientos histológicos 27.3 cm (Figura 9). El métodos de clasificación macroscópica de las gónadas produce muchas incertidumbres y los errores de interpretación deben ser evaluados debido a que los límites entre los estados de desarrollo gonadal son estimados muy subjetivamente (Williams, 2007).

Los estudios de fecundidad realizados en *B. guatemalensis* indican que la especies tiene una fecundidad determinada y que la dinámica del desarrollo ovario es del tipo sincrónico por grupos descrito por Wallace & Selman (1981). Además, la tendencia decreciente del número de ovocitos presentes en el ovario durante la época de desove (NDO y RNDO) (Figura 10) indica que no hay reclutamiento de ovocitos a la cohorte más avanzada durante el desove confirmando la fecundidad determinada de la especie. La cohorte de avanzada o “leading cohort” (ovocitos > 1000 µm), i.e., ovocitos en VIT2 y/o GVM, dominan la frecuencia de ovocitos en hembras con capacidad de desove, aunque una segunda cohorte de ovocitos VIT1 estaba presentes (Figura 11). Debido a que los ovocitos en la cohorte de avanzada entran en GVM al mismo tiempo, probablemente indica que *B. guatemalensis* realiza un solo desova durante el periodo de desove, i.e., es un desovador total (Murua & Saborido-Rey, 2003). Si un segundo desove ocurriera, el número de huevos debe ser muy pequeño.

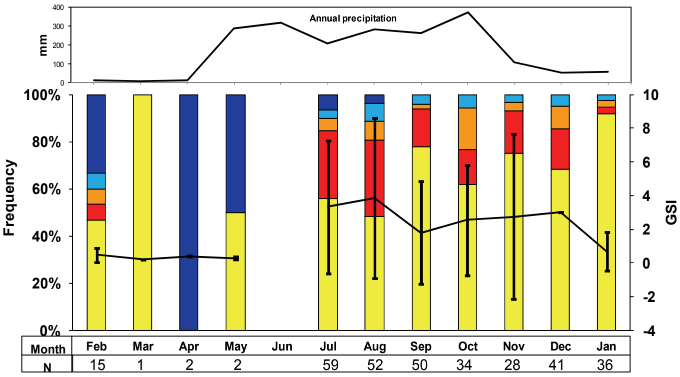


Figura 7. Frecuencia de las fases reproductivas de hembras maduras de *B. guatemalensis*. Desarrollo (amarillo); Capacidad de desove (rojo); Desove activo (anaranjado); Regressing (azul cielo); Recuperación (azul). Variación de GSI (línea gris) y desviación estándar (barras verticales). En el panel superior: Precipitación anual (mm).

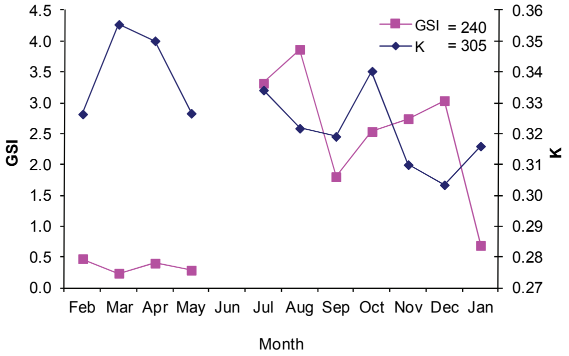


Figura 8. Patrón mensual de GSI y K en hembras de *B. guatemalensis*.

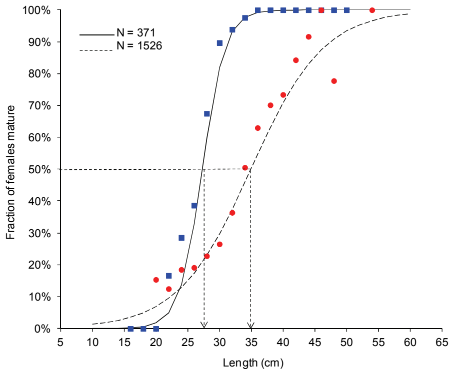


Figura 9. Ojivas de madurez para *B. guatemalensis*. Macroscópica (línea discontinua) y proporción de hembras (círculos rojos sólidos); Microscópica basada en procedimientos de histológica (línea sólida) y proporción de hembras (cuadros azules). Flechas indican la L_{50}.

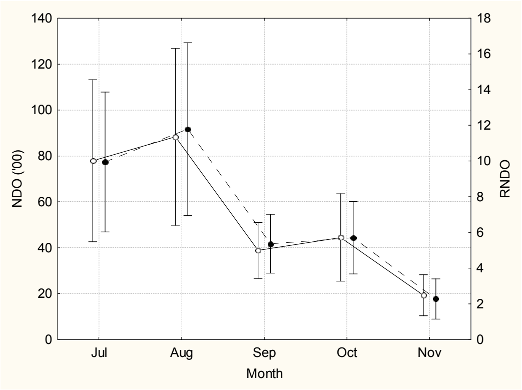


Figura 10. Variación mensual del numero de ovocitos en desarrollo (NDO: línea continua) y el número relativo de ovocitos en desarrollo (RNDO: línea discontinua). Barras denotan 0.95 intervalo de confidencia.

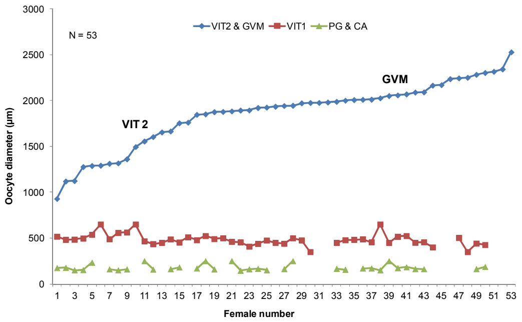


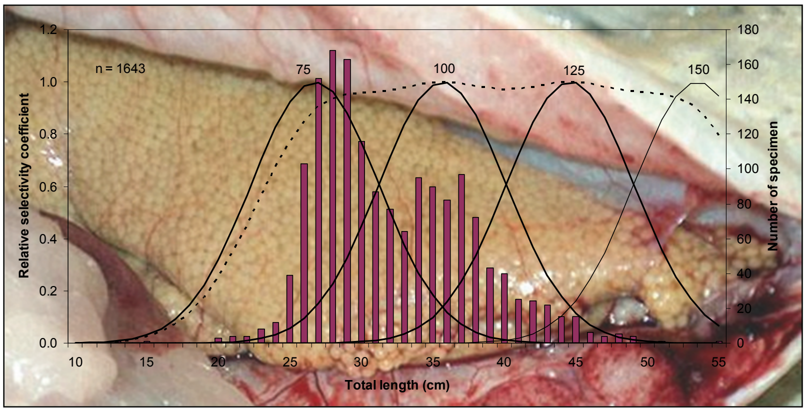
Figura 11. Progresión del diámetro de los ovocitos en tres cohortes de ovocitos identificadas en ovarios en estado de vitelogénesis avanzada en *B guatemalensis* durante el periodo de desove.

Considerando el tipo de fecundidad determinada se estimó la fecundidad potencial anual (Fp) de *Brycon guatemalensis* a partir de los ovocitos en la cohorte de avanzada con diámetro mayor a 1000 µm, es decir ovocitos completamente maduros listos para ser liberados. La Fp muestra una alta dependencia de la talla (r^2=0.71). La Fp varía exponencialmente entre 700 y 35,500 huevos (Media 11,013 ± 6,697) mucho más alta que la fecundidad de otras especies de la familia Characidae como *Bryconamericus iheringii* con Fp de 370 a 1600 (933.71 ± 303.10) y *Bryconamericus stramineus* Fp de 98 a 1100 (371.3 ± 244.6) (Lampert, Azevedo & Bernhardt, 2004; 2007) pero similar a *Salminus hilarii* (familia Characidae) con similar rango de talla que *B. guatemalensis*.

En *B. guatemalensis* se encontró una buena relación de la Fp con la talla y el peso lo que indica que ambos parámetros son indicadores confiables para evidenciar la capacidad de producción de huevos de la especie, pero el alto coeficiente alométrico (> de 3.0) indica que hembra de mayor tamaño producen mayor cantidad de huevos que lo esperado de acuerdo al peso. En otras especies de la misma familia se ha encontrado una mejor correlación con el peso que con la talla, por ejemplo en *Bryconamericus iheringii*, pero el peso puede ser alterado por factores externos como la disponibilidad de alimento o estrés ambiental (Bagenal, 1967).

La fecundidad potencial anual de *B. guatemalensis* podría ser estimada la curva de calibración obtenida de la relación del diámetro del ovocito (OD) con el número de ovocitos por gramo de peso del ovario (NG) debido que ambas observaciones se ajustan bien y fueron altamente correlacionados. Este tipo de correlación llamado "*the auto-diametric fecundity method*" fue desarrollado por Thorsen & Kjesbu (2001) para estimar la fecundidad potencial de Atlantic cod, y ha sido aplicado con buenos resultados en otras especies, especialmente esas con ovario del tipo sincrónico por grupo y fecundidad determinada en latitudes de aguas muy frías (Lambert, 2008; Alonso-Fernández *et al*., 2009; Witthames *et al*., 2009; Thorsen *et al*., 2010).

Estudios Reproductivos en el Manejo de las Pesquerías



El establecimiento de la talla mínima de desembarque es una medida de manejo muy común para prevenir la sobreexplotación de un recurso, particularmente para el manejo de los recursos explotados por las pesquerías de pequeña escala (artesanales). Esta regulación de la talla mínima va acompañada de una regulación sobre la luz de malla a utilizar para el desarrollo de la pesquería, la que resulta de la combinación de estudios de selectividad del arte de pesca y la determinación de la L50% de madurez. De esta manera se protege al stock de inmaduros lo que se considera suficiente para asegurar la sostenibilidad de la pesca ya que de esta manera se permite que el stock alcance la madurez y desove al menos una vez. De los individuos maduros la biomasa de desovantes (SSB) es una de las medidas más comunes para medir el estado del stock (Cerviño *et al*., 2012). Sin embargo, es cada vez más evidente que es esfuerzo por proteger el SSB no es suficiente para evitar la sobreexplotación (Saborido-Rey & Trippel, 2013) y es esencial incluir el potencial reproductivo del stock en las evaluaciones (Morgan *et al*., 2012)

Resultados y discusión

En el presente estudio las curvas de selectividad fueron formuladas de acuerdo al “principio de similitud geométrica” (Baranov, 1948) que produce curves en forma de campana. Cada curva cubre un rango relativamente ancho y limitado de la talla de los peces, confirmando que la red (gillnet) es selectiva para determinado rango de talla (Spare & Venema, 1998). Sin embargo, esta selectividad defiere entre especies. De las cuatro mallas utilizadas la más eficiente en capturar mayor abundancia fue, a como se esperaba, la red de 75 mm, mientras la más eficiente en capturar un rango de tallas más amplio fue la de 100 mm, lo que indica que ambas inducen altas mortalidades por pesca. Sin embargo, en el caso de *Brycon guatemalensis*, la mayoría de los peces fueron retenidos en la malla de 75 mm.

La selectividad de las redes estudiadas fue muy diferente entre las especies lo que indica parcialmente patrones de crecimiento que explica las tallas máximas capturadas de cada especie. En general la máxima talla, teoréticamente retenida por las redes fue de 50 cm, la que estuvo por encima de la longitud máxima registrada de encontradas *A. citrinellus* (41), *H. nicaraguensis* (25) y *P. managuensis* (42), pero no de *B. guatemalensis* (55.5). Esto indica que el rango de luz de malla utilizado en el estudio es adecuado para estudios de crecimiento y dinámica poblacional de los peces de mayor tamaño.

La ausencia de peces de gran tamaño puede indicar patrones de migración fuera del lago, pero muy probablemente indica la talla máxima de cada especie que se encuentra dentro del lago. Por otro lado, el hecho que sean capturadas tallas muy pequeñas de cada especie puede ser explicado solamente debido a la forma del cuerpo y/o diferente comportamiento durante cada estado de desarrollo de las especies. La mayor abundancia de machos de *A. citrinellus*, *H, nicaraguensis* y *P. managuensis* (Figura 12) en cada red está relacionado con el dimorfismo sexual de las tallas encontrados en los adultos, ya que los machos son más grandes que las hembras. Además, el comportamiento territorial de los ciclidos al inicio de la época reproductiva que puede inducir el cuido de ambos sexos, solo de las hembras o cambiar de uno a otro (Kolm *et al*., 2006; Gonzalez-Voyer, Fitzpatrick & Kolm, 2008), puede disminuir o aumentar la probabilidad de que uno de los sexos (machos o hembras) sea capturado por el arte de pesca. En *B. guatemalensis*, diferente a las especies anteriores, las hembras alcanzan mayores tallas que los machos lo que explica parcialmente la mayor proporción de hembras en las redes. Pero puede ser explicado también por el comportamiento migratorio diferenciado de las hembras en búsqueda de zonas de desove o debido a cambios en la forma de su cuerpo cuando están grávidas. En resumen, el diseño del estudio con el uso de las cuatro redes (75, 100, 125 y 150 mm de luz de malla) es adecuado para comprender la dinámica de los peces inmaduros de gran tamaño y maduros de cada especie, pero inapropiado para análisis de reclutamiento.

Las tallas medias capturadas y retenidas en todas las redes de *A. citrinellus*, *H, nicaraguensis* y *P. managuensis* y *B. guatemalensis*. Variaron de 18.4 a 23.5; 16.7 a 17.0; 23.2 a 31.4 y 29.1 a 41.8 cm, respectivamente. La diferencia de estas tallas medias con las tallas capturadas en otros estudios en el lago (Orellana, 1986) indican quelas poblaciones de *A. citrinellus* y *B. guatemalensis* en el lago han disminuido sus tallas. Por otro lado, las tallas capturadas de *B. guatemalensis* en los estudios realizados en el río San Juan (PORCUENCA-SAN JUAN, 2004) confirman la selectividad de las redes utilizadas.

Las tallas más vulnerables a ser capturadas y retenidas por las redes de 75, 100, 125 y 150 mm son esas cercanas a la talla optima de captura (OL) estimada para cada red, ya que la OL teóricamente es la talla a la que los peces quedan más firmemente retenidos en la red y mientras más se aleja la talla de los peces a la OL menos probabilidad tienen de ser capturados (Hamley, 1975). El patrón de tallas en las capturas de los ciclidos muestran que el 90 % de estas tallas son altamente vulnerables a la luz de malla de 75 y 100 mm, exceptuado *P. managuensis* que reduce ligeramente (80 %) la posibilidad de ser capturada en la red de 100 mm. En *B. guatemalensis* las mayores tallas reducen la probabilidad de ser capturadas en la de 75 mm en un 75 %, indicando que un 25 % de los peces grandes escapan a esta red. Pero particularmente las hembras mayores de 34 cm tienen una probabilidad similar en magnitud (86%) de escapar de esta red de 75 mm que toda la población de machos y hembras; las hembras mayores de 49 cm tienen una probabilidad de escapar del 50 % en redes mayores de 125 mm. Por el contrario, peces pequeños menores de 39 cm tienen una probabilidad mayor del 50% de escapara en las redes de mayor luz de malla (> 125 mm).

La L_{50} estimada para *H. nicaraguensis*, *A. citrinellus* y *P. managuensis,* basada en la determinación macroscópica, 16.1cm, 14.6 cm and 25.2 cm, respectivamente, es muy cercana a la longitud óptima (OL) de captura de la red de 75 mm (Figura 13). Solamente en el caso de *A. citrinellus* la OL estuvo por encima de la L_{50}. Esto indica que la luz de malla de esta red puede ser adecuada para esta especie, aunque puede existir una sobrepesca de los reclutas, especialmente en *H. nicaraguensis* donde el rango de esta población es capturado en esta red. En el caso de *B. guatemalensis* la L_{50} estimada fue de 34.9 cm, muy por encima de la OL obtenida en la red de luz de malla de 75 mm y ligeramente por encima de la OL de la red de 100 mm. Sin embargo, la ojiva microscópica produjo una L_{50} estimada de 27.3 cm, la cual es muy próxima a la OL en la red de 75 mm, i.e., la talla a la que el 50 % de los individuos son maduros tienen una probabilidad del 100 % de ser capturadas es esa red. Sin embargo la eficiencia de esta red para peces cerca de 20 cm cae considerablemente protegiendo el stock de maduros de la población, pero con riesgo de sobrepesca por crecimiento. Por tanto, cuando se consideran juntas las cuatro especies y desde la perspectiva tradicional del manejo pesquero, la red de 75 mm puede ser muy dañina y como consecuencia su uso para la desarrollar la actividad pesquera no es recomendad y debería considerarse redes de mayor luz de malla.

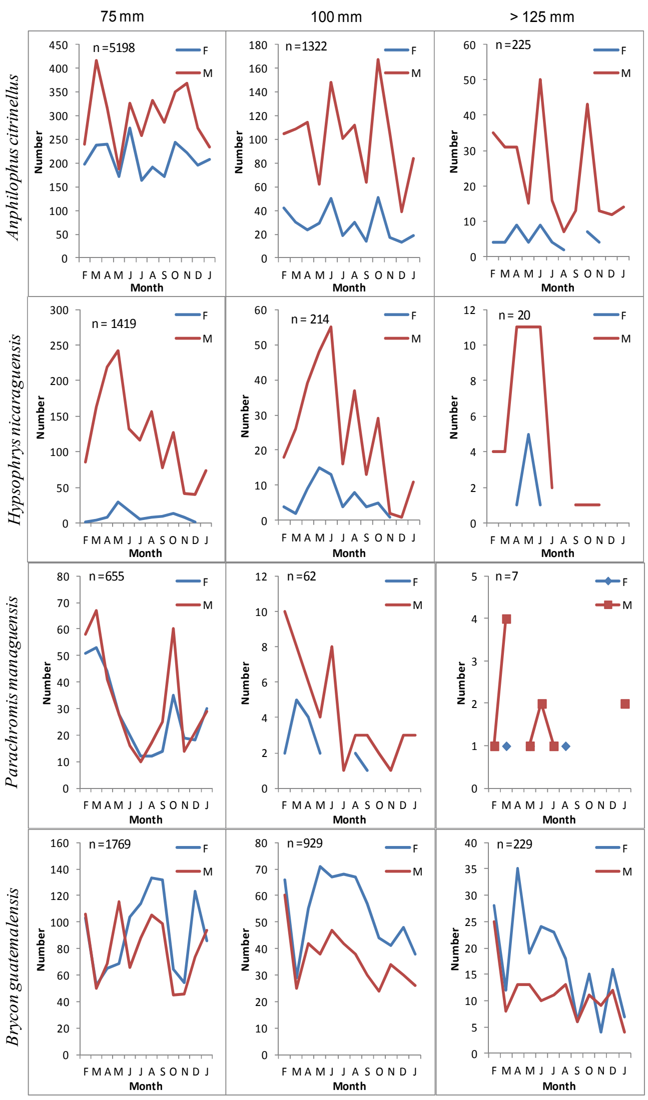
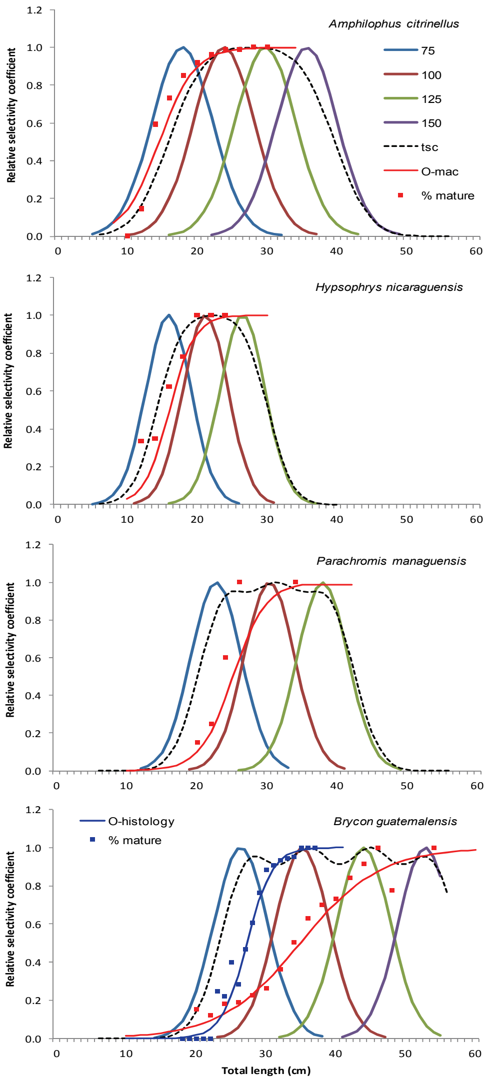


Figura 12. Patrón mensual de capturas, mostrando la captura en número de individuos machos y hembras, por especie y luz de malla de la red.



Figuara 13. Curvas de selectividad relativa de cuatro luz de mallas examinadas 75, 100, 125 y 150 mm de malla estirada, la curva de selectividad completa (línea grueza discontínua), O-mac (ojiva macroscópica) y O-histology (ojiva microscópica) para cada especie.

Los estudios de selectividad realizados en las fases reproductivas de *B. guatemalensis* muestran que la composición de la tallas cambia en las diferentes redes dependiendo de la talla de las hembras y de la fase reproductiva por la que atraviesan, i.e., en desarrollo (D), con capacidad de desove (SC), puesta o desove activo (AS) y en recuperación (R). Así, inesperadamente la red de 100 mm resultó ser la más eficiente en remover las hembras en fases de desove (SC y AS) del stock de hembras maduras. Mientras hembras en fase de D y R son más capturadas en la red de 75 mm. Esto puede ser relacionado con la forma del cuerpo de las hembras, bien debido a su gravidez o su condición, produciendo una alta retención en las redes (McCombie & Bert, 1969).

La fecundidad potencial de *B. guatemalensis* se incrementa exponencialmente con la talla, además las hembras de mayor tamaño producen huevos más grandes y probablemente de mejor calidad. Hembras de mayor tamaño tienen un mayor potencial reproductivo de manera que contribuyen de manera distinta al reclutamiento y la sostenibilidad de las pesquerías (Saborido-Rey & Trippel, 2013). El impacto de la red de 75 mm sobre la producción de huevos del stock de hembras en desove es menor que el impacto de la de 100 mm debido a que causa mayor mortalidad por pesca de las hembras más productivas.

Los resultados obtenidos de *B guatemalensis* indican para incrementar la producción de huevos del stock de hembras y reducir la mortalidad por pesca de las hembras jóvenes, es recomendable el uso de la red de luz de malla de 100 mm durante la época seca protegiendo así a los reclutas y hembras que inician la maduración, pero cambiando a la red de 75 mm durante la época lluviosa, especialmente en Julio y Agosto cuando la actividad del desove es mayor y de esa manera proteger a las hembras con mayor potencial reproductivo.

Conclusiones

1. Los peces estudiados (*Amphilophus citrinellus*, *Hypsophrys nicaraguensis*, *Parachromis managuensis* y *Brycon guatemalensis*) se distribuyen ampliamente en la parte este del Lago de Nicaragua y su abundancia y distribución no está influenciada por la turbidez del agua, pero la turbidez puede afectar la capturabilidad debido a las diferencias en el comportamiento reproductivo de los peces o diferentes niveles de transparencia del agua.

2. La variación intra-anual de la abundancia de estos peces está fuertemente influenciada por los efectos espaciotemporales, tanto horizontales (macro-zonas) como verticales (profundidad) y por factores ambientales, i.e., estacionalidad de la precipitación.

3. Aunque la estación del año ha mostrado que afecta el patrón de distribución y abundancia, su influencia es mínima en *A. citrinellus* pero ciertamente importante en *H. nicaraguensis* y en menos medida en *P. managuensis*. El factor más determinante que influencia la distribución espacial de los cíclidos *A. citrinellus*, *H. nicaraguensis* y *P. managuensis* fueron la profundidad y las macro-zonas, siendo más abundantes en aguas someras y en la zona sureste del área de estudio.

4. La estación (seca y lluviosa) y la profundidad son los principales factores que afectan la abundancia de *B. guatemalensis*. Las mayores abundancias se encontraron en la parte sureste y noroeste durante las dos estaciones del año, pero las mayores abundancias ocurrieron en la época lluviosa en aguas someras y las más bajas en la zona central.

5. Todas las especies estudiadas mostraron un patrón de distribución similar. Los peces más grandes se encontraron al sureste, peces de menor tamaño en la zona central y los más pequeños al noroeste. Además, los peces más grandes se encontraron en aguas más profundas (estratos 3 y 5 metros), exceptuando *P. managuensis* cuyas tallas más grandes tienen preferencia por aguas someras (estratos 1 y 3 m).

6. La selectividad del arte de pesca utilizado no permitió identificar las zonas de distribución de los individuos juveniles debido a que tallas menores de 14.0, 11.0, 17.0 y

20.0 cm en *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* y *B. guatemalensis*, respectivamente, no fueron capturas durante las exploraciones.

7. Los ovocitos de *B. guatemalensis* completan su madurez con la migración del núcleo o vesícula germinal migratoria hacia el polo animal sin alcanzar la hidratación. Sin embargo, el ovocito aumenta su volumen en 1.6 veces al final de la maduración. Los huevos de esta especie son liberados al medio rodeados de un mucus que es producido dentro del ovario, este se observa visualmente cuando los huevos entran en contacto con el agua.

8. La estación reproductiva de *B. guatemalensis* ocurre principalmente en la estación lluviosa del año con la cual inicia el periodo de desove. La especie presenta un periodo de desove prolongado que dura 8 meses (de Julio a Febrero), pero el desove es más intenso de Julio a Noviembre. El evento de desove más importante ocurre en Julio y Agosto.

9. El momento y la duración del desove depende de la talla de las hembras. Las hembras más pequeñas finalizan el desove más temprano (desovadores tempranos), coincidiendo con la finalización de la estación lluviosa (Noviembre), mientras las hembras más grandes tienen un periodo de desove más largo (desovadores tardíos), hasta Febrero.

10. El índice gonado-somático (GSI) y de condición (K) de las hembras muestran una buena relación con el periodo reproductivo. Al inicio del desove ambos reflejan la maduración de la gónada y la utilización de energía para la reproducción. El desacoplamiento observado a lo largo del periodo de desove y la influencia de la talla indica que hay una desincronización dentro de la población de las hembras durante el desove, i.e., las hembras más pequeñas terminan de desovar antes que las hembras más grandes.

11. La longitud a la que el 50% de las hembras de *B. guatemalensis* alcanza la maduración (L_{50}), utilizando la ojiva microscópica (histológica), fue determinada en 27.3 cm. Esta estimación evidencia una sobre-estimación de 7.6 cm de la L_{50} determinada macroscópicamente y lo imprecisa de esta estimación. Este resultado tiene una gran implicación para la evaluación y manejo del stock en el Lago de Nicaragua ya que las

medidas de manejo como talla mínima de desembarque y luz de malla de la red pueden ser establecidas basadas en información biológica más confiable.

12. La dinámica del ovario de *B. guatemalensis* se ajusta al tipo de ovario de desarrollo "sincrónico por grupo". La especie muestra una fecundidad determinada y probablemente realiza una sola puesta durante el periodo de desove, i.e., es un desovador total.

13. El patrón de distribución individual de los estados de desarrollo del ovocito evidencia una desincronización en el desove de las hembras. El periodo de desove prolongado puede ser consecuencia de diferencias en el comportamiento reproductivo de las diferentes clases de tallas, en términos de tiempo de la reproducción, condición, producción de huevos y calidad del huevo. Los huevos de las hembras que desovan más tarde tienden a ser más pequeños a medida que avanza el periodo de desove, así también la frecuencia de huevos grandes disminuye.

14. Las hembras más grandes muestran un mayor potencial reproductivo, i.e., producen más huevos y estos son más grandes. La fecundidad potencial anual de *B. guatemalensis* fluctúa entre 700 a 35,500 huevos y la producción promedio del stock de hembras en el área de estudio fue de 11,013 ± 6697 huevos. La baja incidencia de atresia en *B. guatemalensis* podría indicar alto éxito reproductivo, ya que la alta incidencia de atresia ha sido vinculada a un fallo reproductivo.

15. La red de luz de malla de 75 mm es más eficiente en la captura de individuos pequeños, en cambio la malla de 100 mm es más eficiente para la captura de individuos con un rango de talla más amplio, lo que indica que ambas redes inducen alta mortalidad por pesca.

16. Diferencias en la selectividad entre las especies refleja parcialmente patrones de crecimiento lo que se explica por la talla mínima capturada de cada especie, ya que algunas tallas no fueron capturadas en redes de mayor diámetro de luz de malla. La talla máxima teórica retenida por el arte de pesca utilizado estuvo por encima la talla máxima registrada en especies de cíclidos, pero no para *B. guatemalensis*, esto indica que el rango de la luz de malla utilizada en este estudio es adecuado para estudiar el crecimiento y la

dinámica poblacional de los peces de mayor tamaño. Por otro lado, el hecho que las tallas más pequeñas capturadas difieren entre las especias debe ser explicado solamente por la forma del cuerpo del pez y/o a diferencias en el comportamiento reproductivo durante el ciclo de vida de cada especie.

17. Los cíclidos muestran una alta vulnerabilidad (>90%) de ser capturados en redes con luz de malla de 75 y 100 mm, exceptuando *P. managuensis* la cual reduce ligeramente la probabilidad de ser capturado en la malla de 100 mm a un 80%. De manera que una gran proporción de estas especies es vulnerable a estas mallas. En *B. guatemalensis* las tallas más grandes reducen la probabilidad a un 75 % de ser capturados en la malla de 75 m, i.e., tienen una probabilidad de escape del 25 %.

18. En cíclidos los más vulnerables son los machos y en *B. guatemalensis* las hembras, especialmente durante los periodos reproductivos. La proporción de machos y hembras obtenida de cada especie probablemente sea similar a la obtenida en las capturas en las operaciones de pesca rutinarias de los pescadores en el lago. Por lo tanto, se debería tener cuidado porque la proporción por sexo puede ser alterada severamente y consecuentemente el potencial reproductivo de algunas especies puede ser directamente afectado, por ejemplo, el cuidado parental en el grupo de los cíclidos donde el macho juega un papel muy importante y en la biomasa del stock desovante en *B. guatemalensis*.

19. Hembras de *B. guatemalensis* sobre la talla del 50% de maduración (estimación microscópica), tienen el 100 % de probabilidad de ser capturadas y retenidas en la red de 75 mm de luz de malla, y la L_{50} cae en el rango de 24.0 a 30.0 cm a la que la red tiene una eficiencia de captura del 80 %. Sin embargo, la eficiencia de esta red para la captura de peces de cerca de 20 cm cae considerablemente protegiendo la mayor parte del stock maduro de la población, pero con riesgo de sobrepesca. Por lo que el uso de la malla de 75 mm no es recomendable para la actividad pesquera y redes de mayor luz de malla debería considerarse.

20. Para las especies *A. citrinellus*, *H. nicaraguensis*, *P. managuensis* las correspondientes longitudes medias (resultado del análisis de selectividad) capturadas en la red de 75 mm,

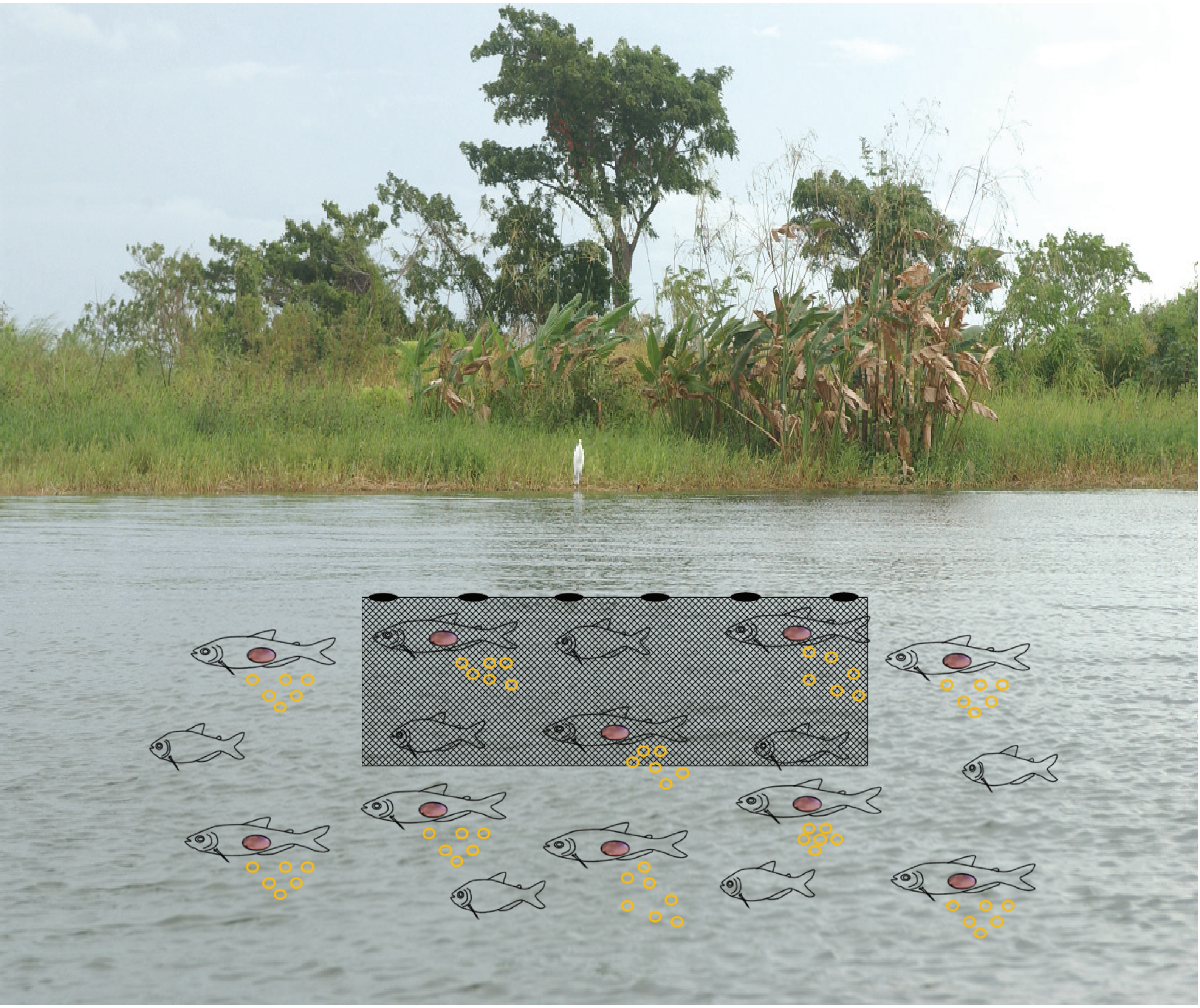
18.6, 16.7, y 23.1 cm respectivamente, se recomiendan como referencia para monitorear las tallas en los desembarques en esas especies.

21. Para *B. guatemalensis* la L_{50} determinada microscópicamente en 27.3 cm puede ser usada como referencia debido a la precisión de su estimación. Considerando un incremento del 20 % sobre la talla de madurez se recomienda una talla mínima de desembarque (MLS) de 30 cm. Esta talla tendría una probabilidad de 40 % de ser capturada en la red con luz de malla de 100 mm.

22. La composición de las capturas de *B. guatemalensis* en las diferentes luz de malla de la red cambia dependiendo de la talla y de la fase reproductiva por la que atraviesa. La red de 100 mm es la más efectiva en remover las hembras en puesta de la población de hembras maduras, i.e., con la capacidad de desovar –SC y en puesta activa –AS, mientras que las hembras en fase de desarrollo (D) y en recuperación (R) son más capturadas en la red de 75 mm, aunque si bien las capturas en esta red muestran mayor uniformidad en las tallas.

23. El impacto de la redes (75, 100, 125 y 150 mm) utilizadas en la pesquería de pequeña escala en el lago sobre la producción de huevos del stock de hembras ha sido poco estudiada. La red de 75 mm captura la mayor proporción de hembras en puesta de talla pequeña, probablemente ponedoras reclutas, las cuales finalizan el periodo de puesta antes que las grandes y además son menos productivas en términos de producción de huevos y calidad del huevo. Sin embargo, este estudio demuestra que la red de 100 mm afecta más la producción de huevos, puesto que causa mayor mortalidad por pesca entre las hembras más productivas del stock de hembras en puesta.

24. Para incrementar la producción de huevos del stock de hembras y reducir la mortalidad por pesca de hembras jóvenes es aconsejable el uso de la red con luz de malla de 100 mm durante la estación seca protegiendo el reclutamiento y a las hembras que inician la maduración, pero cambiando su uso por la red de 75 mm durante la estación lluviosa, especialmente en Julio y Agosto cuando el desove de *B. guatemalensis* es mayor; de esta manera proteger a las hembras con mayor potencial reproductivo.



Tesis Doctoral

2013