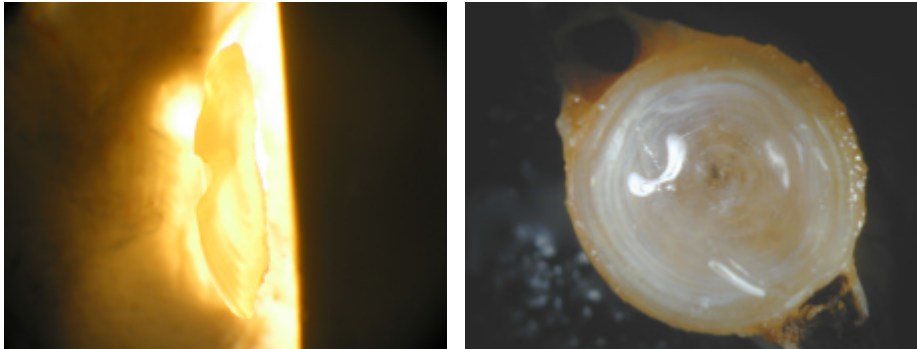


Age determination in the snapper *Lutjanus guttatus* (Pisces, Lutjanidae) and investigation of fishery management strategies in the Pacific Coast of Guatemala



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A thesis submitted in partial fulfillment of the requirements for the degree
of Master Science in International Fisheries Management

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 Photos: H. Andrade. Below: Catch composition of shrimp trawler. Photo: Manuel Ixquiac

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ABSTRACT

The rose-spotted snapper, *Lutjanus guttatus*, seems to be sequentially exploited by the shrimp trawler and the artisanal fleet along the Pacific Coast of Guatemala. The growth parameters of the snapper were estimated in the present study with basis on material collected in two fishing harbours. Other biological and fishery information was compiled to simulate stock dynamics with a yield-per-recruit model. This single-species model allowed the evaluation of possible outcomes of fleet interactions, in terms of relative yield, spawning stock development and profit.

A large emphasis was put in the evaluation of skeletal structures, otoliths and vertebrae, to determine age. Vertebrae seem to be the best structure for ageing, as they revealed better ring definition, and resulted in more adequate growth patterns and plausible Von Bertalanffy growth parameters. The VBGF (total length-at-age) obtained with vertebrae was $L_t = 66.4(1 - \exp(-0.13(t - 0.03)))$.

The age of first-capture (T_c) for the trawl and the artisanal fleets were estimated to be about 1 and 3 years, respectively. The age-dependent mortality was suggested to follow unimodal curves for the two fleets, owing to the patterns of selectivity of the gear and availability of the fish. The yield-per-recruit scenarios showed that for the suggested biological and fishery parameters, the highest yield of snapper is not being attained. Further, the model suggests that with the present fishing pattern high rates of fishing mortality could deplete the spawning stock. Implementation of size-selective practices that minimise the trawlers' by-catch of *L. guttatus*, and an increase of the artisanal T_c (to above the maturation age, T_m , about 4.5 years) are likely to result in increased yield, total profit, and prevent recruitment overfishing.

INTRODUCTION

The coastal fisheries of Guatemala are characterised by large numbers of commercial species and diverse fleets and fishing gears. An important commercial fish species is the rose spotted snapper *Lutjanus guttatus* (Fig. 1). This is captured by both the shrimp trawlers, as a by-catch, and by the small scale or artisanal fleet (used indifferently in the present work) as a target species to be sold in the national and international market (Figure 2).

The shrimp fleet utilises twin trawlers and mainly catch snapper as a by-catch. In his analysis of this by-catch, Ixquiac (1998) found that *L. guttatus* is the 12th most captured specie in volume, with an average individual weight of 65 gr. At this size fish do not have commercial value and are dumped to the sea. The depth at which this specie is captured with bottom trawls varies between 40-50 meters. The vessels are normally more than 30 GTR, vary in length between 15 and 24 m, and are powered by 250- 470 HP engines (www.fao.org). The hull of the vessels is made out of fibreglass, iron or steel. These vessels have fish finding equipment, freezers and storage rooms with the capacity to transport from 200 to 1000 gallons of Diesel. Trawlers are normally operated by a crew of 6 persons (DITEPESCA 1997, UNEPA 1998 *in* Ixquiac 1998), and can operate for relatively long periods at sea. The twin bottom trawl are set on both sides of the vessels, and range from 20 to 60 meters in length with a mesh size of 2 inches. Turtles exclusion devices (TED) are compulsory, and all vessels use the “super shooter” model. This is a rigid type of exclusion device (Ixquiac 1998).

Along the Pacific Coast of Guatemala, 3,982 artisanal vessels are found, and these are operated by 7652 fishermen. Most of these boats have a length between 3.6 and 10 m, are made of wood and fibreglass, and lack advanced technology such as fish detecting equipment (PRADEPESCA/UE/UNIPESCA/MAGA, MDN (www.fao.org)). The boats over 7 m normally have a main engine of 75 HP and auxiliary engine of 45 HP. These vessels normally target sharks, dolphin fish, and snappers (www.fao.org). Pérez-Cifuentes *et al* (1999) states that the vessels that target snappers are small boats made of fibreglass, with a length around 25 feet and a tonnage of 2 tons. The fishing gear

employed are hooks and lines, and gillnets with a mesh size of 7.5 cm. Artisanal landings are made in any place along the coast, and the production statistics are therefore not reliable.

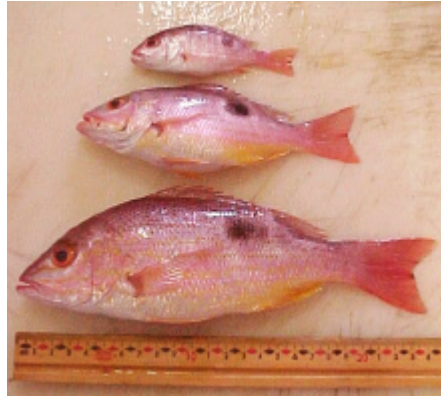


Figure 1. *Lutjanus guttatus*. Sample of sizes caught by the trawler in the present study. Photo: Rodolfo Liutti.



Figure 2. Typical vessels of the artisanal fleet (left), and shrimp trawlers (right). Photos: Manuel Ixquiac.

Relatively little information can be found about the biology of *Lutjanus guttatus* in the literature. The distribution of the species in the eastern Pacific Ocean is reported to stretch from México to Peru (Allen 1985). Works performed in Guatemala and other countries have focused mainly on the determination of the reproductive period, size at maturity and feeding habits. *L. guttatus* lives in coastal reefs, down to a depth of 30 m (Fischer *et al* 1995). Allen (1985) reports this species is an inshore reef dweller normally found over hard bottoms. Generally, it lives alone or in small groups

but occasionally can form big schools. The juveniles live in estuaries and mouths of rivers (Fischer *et al* 1995) and they adapt well to artificial reefs (Guzmán *et al* 1988). In Guatemala, research cruises have captured this species along the whole Pacific Coast (Digesa 1961; Salaverria 1989; Menendez *et al* 1993; Salaverria *et al* 1993 in Ixquiac 1998).

L. guttatus has a wide diet that has been described for some areas. In the Gulf of Costa Rica, the feeding spectrum ranges from fish (Engraulidae, Centropomidae and Ophychthidae), crustaceans (Penaeidae), echinoderms and polichaets to molluscs. Dietary composition varies also according to the size of the predator. Specimens below 20 cm total length feed principally on shrimps. Past this size, the consumption goes towards fishes, molluscs, stomatopods, polichetes, echinoderms, crabs and crustaceans. After 52 cm, squids dominate in the diet (Rojas 1996-1997a). Saucedo-Lozano & Chiapa-Carrara (2000) report similar results for juveniles caught along the Coast of Jalisco, México. They identified *Trachysalambria brevisuturæ* as the most common shrimp prey and *Eucinostomus gracilis* as the most frequent fish prey, with large seasonal variations.

The maximum total length of *Lutjanus guttatus* has been reported to be 50 cm (Allen 1985) and 80 cm (Fischer *et al.* 1995). Several field studies conducted in different areas of México and Central America report maximum lengths of capture varying from 60 cm in Costa Rica (Rojas 1996-1997a), 58.2 cm in the Coast of Guerrero, México (Arellano-Martínez *et al* 2001), and 53 cm in Guatemala (Pérez-Cifuentes *et al* 1999). According to Grimes (1987) lutjanids are fast-growers and spawn in batches over an extended period of time, depending in the availability of food for larvae. If food is abundant during a season, the reproduction will be seasonal. If it is scarce, the spawning will be continuous and in small batches. In Guatemala the spawning season of *L. guttatus* seems to extend throughout the year, with peaks on August, October and January (Pérez-Cifuentes *et al* 1999). In Gulf of Nicoya, Costa Rica, it extends from April and October in the (Rojas 1996-1997b), while it takes place from July to November and February to April in Guerrero Coast, México (Arellano-Martínez *et al* 2001). The size at first maturity in Costa Rica has been reported to be reached at lengths that range from 32.0 to 32.9 cm for males, and 33.0 to 33.9 cm for females.

For Guatemala, Pérez-Cifuentes *et al* (1999) reported maturation sizes to be at 31 cm and 33 cm for males and females, respectively.

Rojo-Vázquez & Ramírez-Rodríguez (1997) presented *L. guttatus* as one of the four dominant fish specie caught in gillnets (11.5% in number and 9.3% in weight) in Bahía de Navidad, Jalisco, México. Madrid-Sánchez & Ruiz, (1997) and Madrid-Sanchez (1997) reported *L. guttatus* to be one of the five most frequent species caught with gillnets in the fishing locations of Michoacán State, in the Mexican Pacific. Studies directed towards the importance of this species have not been conducted in Guatemala, but it is exploited for the national and international markets.

Problem statement

The fishery for *L. guttatus* is a typical case of fleet interaction that calls for management measures to ensure adequate yields, returns and opportunities. Unfortunately, managing fleet interactions also requires access to complex information, such as catch rates and micro-economic data, which are very scarce for the coastal fisheries of Guatemala. In the present work an attempt was made to perform scenario modelling of the interacting fisheries. A biological model combined with some sparse economic information, as well as strong assumptions regarding fishing mortality imposed by the two fleets, was utilised.

The first step in the analysis was to acquire and collate biological information on growth, mortality and reproduction of *L. guttatus* and other lutjanids. Larger emphasis was placed in the determination of growth patterns from skeletal structures of the fish. Pertinent questions were: what are the most adequate hard structures to study? Do the different structures reveal similar growth patterns? Have fish collected by the trawl fleet and artisanal fleet in different fishing grounds the same growth patterns (a possible reflection of stock identity)? What is the time of deposition of growth rings for fish that leave in a seemingly constant (tropical) environment?

The second step in the analysis was to develop a model for scenario simulation of the fleet interactions. A model of the yield per recruit family (Beverton & Holt 1957) that took into consideration the biological information was developed. These models are

not very demanding in fishery data, but still allow investigation of management strategies. Different scenarios were simulated, including one for a theoretically optimal fishery. Other scenarios included competing fleets with fishing mortality and economic characteristics similar to those observed in Guatemala. Although a great deal of uncertainty is attached to the results attempts were made to compare relative trends in yield and profits.

MATERIALS AND METHODS

The present study of *L. guttatus* was carried out in the Pacific Coast of Guatemala in July-August 2002. Samples were taken from a commercial trawler doing a study on shrimp and by-catch selection, and from the catches of artisanal fishermen. In the selectivity study, two trawling nets were used to collect shrimps in different areas of the Pacific Coast (Ixquiac & Salaverria 2002). The fish collected from the artisanal fleet were purchased directly from the fishermen or from market places in two of the most important landing harbours of the Pacific: Puerto de San Jose and Puerto Quetzal (Fig. 3). Mainly immature fish are collected with the trawler, whereas the artisanal fleet catches bigger fish. The information about the artisanal fleet and the fishing gear employed has been taken from Pérez-Cifuentes *et al* (1999).



Figure 3. Map of Guatemala (www.cia.org). Sampling sites of artisanal catches (encircled).

The sample was composed of 146 fishes. A wide range of fish sizes was selectively gathered to have a sample that represented the whole size spectrum (Brothers 1987). Structured sampling diminishes biases in the estimation of growth rates (Gallucci *et al* 1996). The fish were weighted using a digital balance with a precision of ± 0.1 g and

measured (total length TL). The sex was determined by macroscopic evaluation of the gonads (Rojas 1996-1997b). The data were stored and analysed in Microsoft EXCEL with the addition of the Statplus V2.0 statistic software (Berk & Carey 2000).

Fish scales were taken from the same location above the lateral line in each individual, and cleaned with Potassium hydroxide (5%) and acetic acid (40%) (SEP 1986) prior to fixation in microscope slides. Pictures of some of the scales were taken for later analysis. Vertebrae were collected from the 10th to the 20th position, washed in water, dried and stored in plastic bags for transport. Pictures were taken at constant magnification following procedures used for whole otoliths.

The two saggitae otoliths were taken after cutting the head off with surgery scissors. Otoliths were cleaned in water, dried and stored individually in marked plastic bags for transportation. For the analysis, the left otolith was always used unless missing or destroyed. In that case, the right otolith was used. Otoliths were soaked in glycerol at 87% to improve light penetration. Pictures of whole otoliths were then with a digital camera connected to a binocular magnifier. An auxiliary light was pointed towards the interior surface of the otolith. To avoid size selective bias, a set of pictures was taken with the same magnification for each otolith. The magnification chosen was that which fitted the largest otolith.

It was necessary to mark and count the rings repeated times. The total length of the fish was known and used as an auxiliary variable, since there were suspicions of the presence of false rings. To establish the first year zone in whole otoliths, marks were drawn three times. The criterion to choose the first annual ring was based on: 1) Results achieved after the evaluation of the first set of pictures (e.g. a 12 cm fish TL could not be 4 years old). 2) Secondary analysis of the biggest otoliths that showed a more consistence formation of the first year ring. Diffusive lines seemed only to disappear as the fish grew older and it was difficult to set the first ring for small otoliths. 3) Discussion of results with experienced age readers. The criterion for first ring thus defined was applied to the whole set of otoliths. Afterwards, the decision to assume the following rings as cyclic events was taken.

Sections of otoliths were prepared as an attempt to improve the otolith readings (as done in other Lutjanidae by e.g. Newman *et al* 2000a). To obtain the sections, the otoliths were cut through across the centrum and then polished using 2 kinds of wet sandpaper: 600p and 1200p. Pictures were taken using a direct light on the side of the otolith while a shade was created in the anterior part (facing the microscope). Thus, the otolith was illuminated in both parts revealing ring formations that could be recorded by the camera.

The digital pictures of the hard-part structures were transferred for analysis in the Computer Assisted Visualisation and Otolith Reading Program (CAVOR). With this program, rings were marked and distances between rings measured. Excel was used afterwards to analyse the data. To express the growth, the Von Bertalanffy growth function (VBGF) was used:

$$L_t = L_{\infty} (1 - e^{(-K(t-t_0)})}$$

where L_t is the length at age t , L_{∞} is the theoretical maximum length that the specie will reach if lived indefinitely, K is a growth coefficient that measures the rate at which maximum size is reached and t_0 is the theoretical age at zero length (King 1995).

The VBGF was fitted to the observed age-at-length data using the minimum least square criterion. Each individual fish was a sample. The VBGF was applied to the data obtained for the two skeletal structures and sexes. The type “A” curve fit method proposed by Kimura (1980) was used to calculate the growth parameters. Consequently, a bootstrap analysis (Kimura 2000) was run by taking 30 random samples with replacement in each of the 1000 iterations. Distributions of the output parameters and bias corrected 95% confidence percentiles were constructed as proposed by Haddon (2001). The different length-at-age VBFG were compared for coincidence by means of analysis of the residual sum of squares (ARRS). This technique does not compare the parameters separately but tests whether the curves are statistically coincident (Chen *et al* 1992 in Haddon 2001). This test was used by e.g.

Newman *et al* (2000b) to compare growth curves for *L. carponotatus* and *L. vitta* separated by sexes.

Growth models were fitted for both sexes separately, including immature (non-sexed) fish ($n=15$) in both groups. Rings were assumed to be deposited in annual events. The age was assumed to be number of zones + 0.8. October, one of the peak spawning months (Arellano-Martínez *et al* 2001, Pérez-Cifuentes *et al* 1999, Rojas 1996-1997b) was defined as birth date. Many 0+ year-old fish were found approaching the mean length of the first year of age. October corresponds to 10 months of a year, and this equals 0.8 years.

Back-calculations of length-at-age based on vertebrae were performed using the Fraser-Lee method. This is an adequate approach when the intercept of the regression between vertebra radius and fish total length is different from zero (Murphy *et al* 1996). Back-calculations were used to compare length-at-age of big fish captured by the artisanal fleet with smaller fish captured by the trawlers. The possibility of having fishes from different stocks was evaluated because the samples were taken in different times and areas with different gear. Back-calculated (mean) length-at-age of fish older than 3.8 years captured by the artisanal fleet were compared with the observed length-at-age for fish from the trawl catches (aged less than 3.8 years). Comparison was done using a paired t-test.

The age at maturity T_m was calculated using the available information for females from a database obtained in a previous survey. In that work gonads were collected during an 11-month sampling period (Pérez-Cifuentes *et al* 1999). The values of length-at-maturity were re-calculated using 3 cm intervals for the TL. Mature fish were defined as the fish that had reached maturity stage IV i.e. had well-developed ovaries or were spawning (as defined in the maturation key proposed by Rojas 1996-1997b). The weighed mean was calculated for each interval, and the mean length-at-maturity was converted to age using the Von Bertalanffy equation for pooled sexes. A probability table was constructed (King 1995), and age was plotted against the adjusted probability of maturation. An S-shaped curve was fitted to the data using the least square criterion.

The curve was described by the following equation:

$$M_i = \frac{1}{1 + e^{R_m \cdot (T_m - i)}}$$

where M_i is the proportion of fish mature at age i , T_m the (50%) maturation age and R_m the steepness parameter. The values of T_m and R_m were calculated using the Solver tool in EXCEL.

The natural mortality was obtained using the empirical equation presented by Ralston (1987) for lutjanids and groupers:

$$M = 0.0189 + 2.06K ;$$

where M is the natural mortality and K is the growth coefficient calculated with the Von Bertalanffy equation.

Parameters a and b of the length-weight relationship were obtained from information in the database described above, with the addition of the fish sampled in the present study (total $n=642$). A power function was fitted to the data:

$$W = a(Tl^b) ;$$

where W is the weight in grams; a is the condition factor; Tl is the Total length of the fish in centimetres, and b is the power exponent. These observations were plotted and calculated for pooled sexes.

No information is available regarding fishery-mortality patterns at age for these fisheries, and a number of assumptions and simplifications were required. For determining the age-dependent mortality curves, length-frequency distributions were analysed separately for the two fishing fleets. It was assumed that these length-frequencies approximately expressed the fishing mortality-at-age by the two fishing fleets.

Normally, the fishing mortality-at-age induced by a trawl fishery is represented by an ogive. In the present case, information obtained with a trawl skipper and several fishery inspectors indicated that only fish of small sizes are available to the trawl gear. This was supported by the age composition of the trawler catch. Thus, it was opted to describe the pattern of fishery mortality at age by an unimodal curve (similar to that for the artisanal fleet) rather than by a commonly used sigmoid. For the artisanal fleet, the length distribution from the database ($n=500$) of Pérez-Cifuentes *et al* (1999) was used. The samples collected in that study came from gillnets, hooks and lines of different sizes, and a unimodal fishing mortality curve was utilised to described their pooled effects.

A yield per recruit model was constructed using the biological information on growth, mortality and reproduction, as well as the following relationships:

Fishing Mortality F_i :

$$F_i = F \cdot \frac{e^{-p \cdot i}}{1 + e^{Rg \cdot (Tc - i)}}$$

where i is age and p , Rg and Tc are the chosen selectivity parameters for each of the fleets and F the total instantaneous fishing mortality by each fleet.

Catch equation:

$$C_{i_t} = \frac{F_i}{F_i + M} \cdot N_{i_t} \cdot (1 - e^{-(F_i + M)})$$

where i is age, t is time, M is natural mortality, and F is a measure of the age specific fishing mortality.

Survival equation:

$$N_{i_t} = N_{i_{t-1}} \cdot e^{-(F_i + M)}$$

where N_{i_t} is the number of survivors at time i , F_i is the age-specific instantaneous rate of fishing mortality and M is the natural mortality.

Profit equation:

$$P_{PV} = \sum^i Y_{i_t} \cdot (pr - c) \cdot (1 + d)^{-(t-t_0)}$$

where P_{PV} is the present value of the profit, Y is the yield of age group i in year t , pr and c the unit price and cost, and d the discount rate. Price varied with fish size, which in turn varied with fleet. Also costs were allowed to vary with fleet, reflecting different expectations and profit margins. Thus, the determination of exact prices and costs was not very important in the simulations, as long as they represented plausible (relative) values.

The yield per recruit model used in the present work incorporates smooth functions instead of parameters. Thus ogives rather than knife-edge processes were used. The time step was weekly. The MBAL for spawning stock values were used as reference points for a precautionary management. MBAL is a minimum biological acceptable level, which has been set at 20% of the virgin spawning stock biomass.

In the first two scenarios an attempt was made to describe the relative yield brought about by many combinations of total fishing mortality F and age of first capture T_c . A single-fleet with a very steep age-selectivity ogive, in the fashion of common knife-edge approximations, was simulated first. The purpose of this theoretical analysis was to find the optimal combination of F and T_c with regard to Y/R . This pattern corresponds to the trivial optimal strategy: fish are allowed to grow unharmed to a critical (optimal) age past which they suffer full fishing mortality. This theoretical optimum was then compared with that resulting from the assumed fishing pattern of the artisanal fleet. The only differences in the two scenarios are thus the form of the selectivity curve (steep sigmoidal vrs unimodal curve) and the age at first capture.

The 3rd, 4th and 5th scenarios simulate the real fleet interactions observed in the fishery. Thus, hypothetical (unimodal) selectivity patterns were attributed to both the artisanal and trawl fleets, with basis in the length-distributions in the catches. The total instantaneous fishing mortality induced by each fleet is unknown and the F was allowed to vary freely for each fleet. This yielded many possible curves of Y/R and

profit/R for combinations of F_a and F_t . The curves were represented as isopleths in contour plots. The analysis was repeated for different expectations of cost and price structures of the two fleets.

Different prices/costs were assumed for each fleet with base on talks with the fishermen and registered first-hand sales. For the artisanal fleet the unit price was set to 8 Quetzales (approx. 1 euro) per pound, because this was the price paid for fish purchased in this study. For the trawlers the price was set equal to Q 4.01 (approx. 0.50 euro), the average price at harbour during the 4th trimesters of 1999- 2001, based on data communicated by UNIPESCA (unpublished). The prices for the trawl fleet do not account for the price (nil) of those fish that were high-graded at sea. The costs were set in the following way: for the artisanal fleet, they are assumed to be 75% of the unit price, leaving a 25% profit margin. For the trawlers, they were assumed to be either 33% or 0% of the unit costs of the artisanal fleet. The discount rate was assumed to be constant at 5%.

RESULTS

The total size distribution of the fish sampled ranged from 10.4 cm to 49 cm (Fig. 4), with an overlap in the sizes captured by the two fleets (overlap range: 20 cm and 25 cm TL). Past this size fish were only captured in artisanal operations.

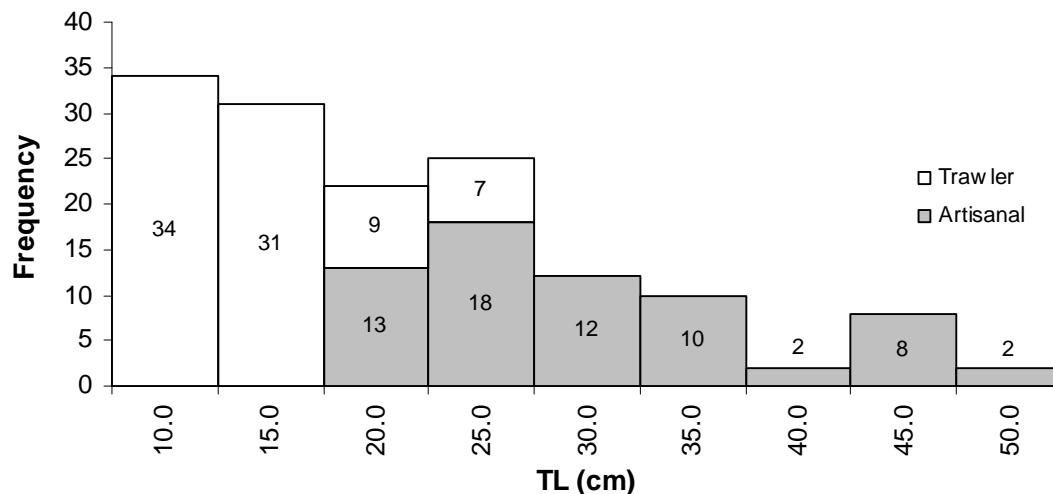


Figure 4. Total Length (TL) frequency distribution of *L. guttatus* collected in the samples.

Marking of otoliths

The sagittae otoliths of *L. guttatus* are oblique with a concave under side and a convex upper side. The thickness changes with time, making it more difficult to observe inner rings in older fish. Whole and sectioned otoliths revealed the presence of rings (Fig. 6), and the number of rings increased with size. A linear regression fits the relation between otolith length and the total length (Fig. 5) Therefore, this structure was considered to fulfil the minimum requirements for ageing for *L. guttatus*.

Otoliths did not follow an expected pattern of ring formation, irrespective of counting method (Figure 6). The expected pattern of ring formation is one of larger distances between rings in early ages and a decrease in these distances at older ages. The opposite was observed in whole otoliths: the distances between rings increased, as the fish grew older and then remained constant until the last mark.

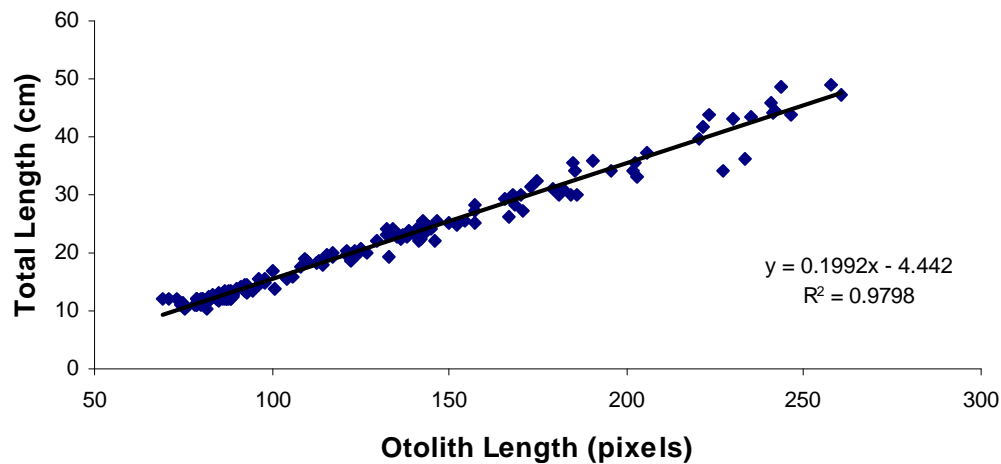


Figure 5. Relationship between whole Otolith Length (pixels) vrs Total Length (cm) for *L. guttatus*.

Defining the first year zone was also a difficult task for whole otoliths owing to the frequent occurrence of diffuse and irregular rings around the centrum (as seen in Fig. 6). For sectioned otoliths, the first rings were difficult to observe in the big fish, and none could be determined in random pictures of small fish. A test made with random pictures of big otoliths showed that more rings were counted in sectioned otoliths than in whole otoliths of the same individuals.

In some of the otoliths, a “jump” or void between rings could be observed, giving rise to the suspicion of the existence of a “missing ring”. This void pattern was observed even in fish that had an otherwise normal pattern of ring deposition, i.e. decreasing distance between rings. This pattern was also found in sectioned otoliths. This jump can be seen from the 2nd to the 3rd ring in the whole otolith view, and from the 4th to the 5th ring in the sectioned otolith view (Figure 6). Despite unclear patterns in otoliths, attempts were made to fit growth curves, but these were restricted to readings performed on whole otoliths.

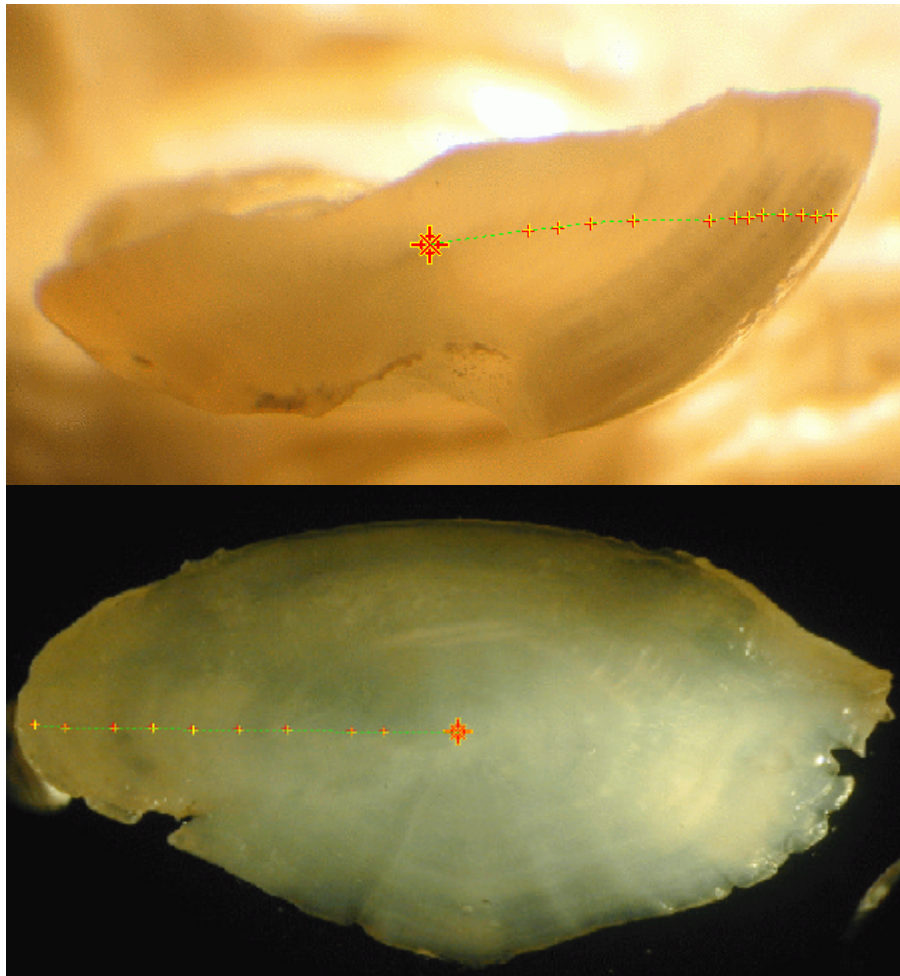


Figure 6. Sectioned (above) and whole otolith (below) of a single individual (male, 43.8 cm TL). Unclear pattern in the ring formations (above) and diffusive rings (below) gave rise to discrepancy in age estimations.

Marking of vertebrae:

Pictures of 132 whole fish vertebrae revealed the presence of clear rings, and a linear relationship between the number of rings and the size of the fish was observed (Figures 7 and 8).

Vertebrae showed clearer ring definition, and deposition seemed to follow the expected pattern. Therefore the criteria to interpret the zones as age was considered more consistent than for otoliths. For the same individuals, the number of rings was

higher in vertebrae than in otoliths, and no problems were experienced with the definition of the first ring.

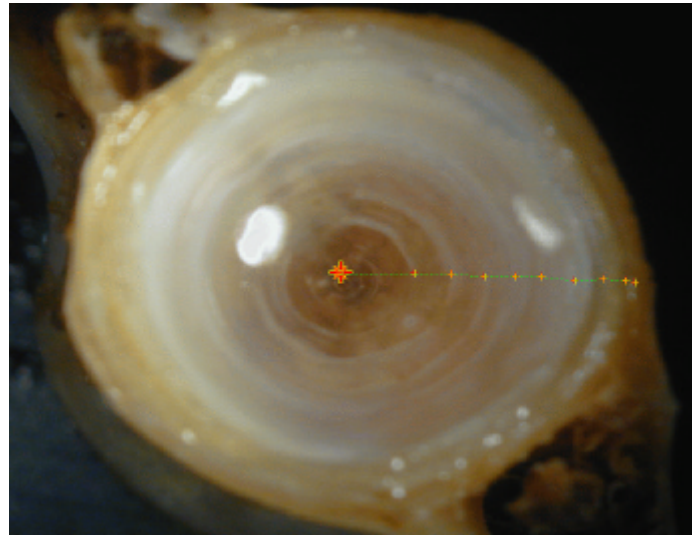


Figure 7. Picture of a marked vertebrae (male, 43.7 cm TL, same individual as in Figure 6).

There was a strong linear relation between the total length and the radius of the vertebrae, and this is the main requirement for acceptance of an ageing structure (Brennan & Cailliet 1989).

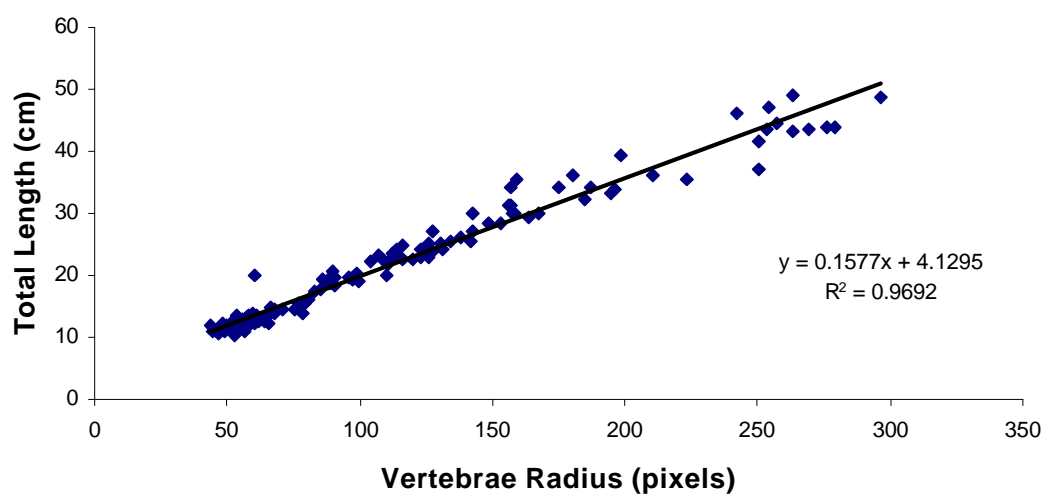


Figure 8. Relationship between Vertebrae Radius (pixels) and Total Length (cm) for *L. guttatus*.

Back-calculated lengths-at-age from vertebrae readings were calculated assuming that ring formation occurs as an annual event (Table 1). Although some slight increases in back-calculated size were observed for older age classes this trend was not strong and it showed some variability for the different age groups. This seems to imply that the technique employed to define the first year was consistent in vertebrae. The back-calculations showed that rate of increase in size decreases with age, as expected. For the age class 7.8 and further, the sample was too small ($n=7$) to make meaningful analyses. Comparison of back-calculated length-at-age for the older cohorts exploited by the artisanal fishery with the observed length-at-age of fish caught with trawls (< 3.8 years) failed to reveal statistical differences (paired t-test; $n=4$; $p>0.05$). Thus, the samples can with some confidence be considered to originate from the same stock.

Table 1. Fraser-Lee back-calculated lengths-at-age for *Lutjanus guttatus* aged with vertebrae.

<i>n</i>	Years	0.8	1.8	2.8	3.8	4.8	5.8	6.8	7.8	8.8	9.8
2	0.8	11.25									
58	1.8	11.94	13.29								
28	2.8	14.19	18.76	20.61							
14	3.8	15.19	20.40	24.93	27.41						
9	4.8	13.34	18.52	23.17	27.11	29.20					
5	5.8	13.81	19.28	24.06	28.17	31.27	33.68				
9	6.8	14.12	19.30	24.78	29.16	33.70	37.92	40.52			
4	7.8	13.13	19.03	24.31	27.81	31.13	35.42	38.70	41.00		
2	8.8	14.34	19.54	24.69	28.74	31.94	36.66	40.32	43.55	45.45	
1	9.8	13.48	19.34	23.65	27.75	32.40	35.95	40.53	44.38	47.41	48.70
Average Length-at-age (cm)		13.15	16.56	22.89	27.90	31.44	36.22	40.04	42.21	46.10	48.70

Marking of Scales

The scales presented a lack of clearness in the ring formations, and therefore, the technique was abandoned as a possibility to age the fish.

Age interpretation and growth

With whole otolith counts, the youngest fish aged were 0.8 years old, and this corresponded to the length-interval 10.4 -16.8 cm. The oldest fish aged were 5.8 years corresponding to the length range from 36.2 cm to 48.7 cm. For vertebrae, the

youngest fish aged were 0.8 years old and the oldest 9.8 years (male of 48.7 cm TL). The growth curves fitted to the individual observations after the two readings are plotted in Figure 9. The length-at-age intervals were relatively wider for vertebrae than for otoliths, and more extreme outliers were identified, especially in the age class 2.8 years (see Fig. 21 in appendix).

For the younger age classes it was possible to count more rings in otoliths than in vertebrae. An overlap between the two growth distributions for young fish, from 0.8 years until 3.8 years of age, was observed. Past this age more rings were marked in vertebrae than in otoliths from the same fish and the curves broke apart.

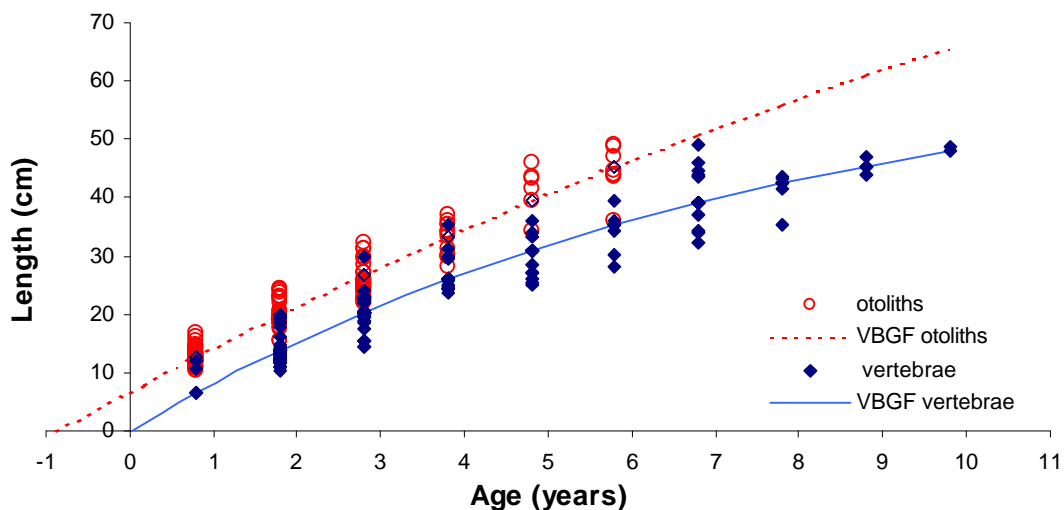


Figure 9. Von Bertalanffy Growth Function (VBGF) as determined from whole otoliths and vertebrae readings.

The parameters of the VBGF obtained with whole otoliths were: $L_{max} = 153.9$ cm; $K = 0.05$ yr⁻¹; $t_0 = -0.85$ yr. The results for vertebrae were: $L_{max} = 66.4$ cm, $K = 0.13$ yr⁻¹, and $t_0 = 0.03$ yr. The bias corrected 95% confidence percentiles obtained after bootstrapping the vertebrae data were: $L_{max} = 44.99$ to 137.79 cm; $K = 0.05$ to 0.29 yr⁻¹ and $t_0 = -0.7$ to 0.66 yr. The bootstrapped confidence intervals of the Von Bertalanffy parameters approximately followed bell-shaped curves (appendix, Figure 22).

The growth curves obtained after reading otoliths and vertebrae were statistically different (ARRS: $F= 114.31$, d.f.=3, 266, $p<<0.1$). A paired t-test showed clear differences in length-at-age for individual fish marked with the two methods ($n= 132$, $p<<0.001$). This is confirmed in a bias plot (Figure 10) that shows that as fish grew older, differences between readings become wider. Owing to the differences between ageing methods and the consistent results obtained with the vertebrae, otoliths were detracted from further analysis.

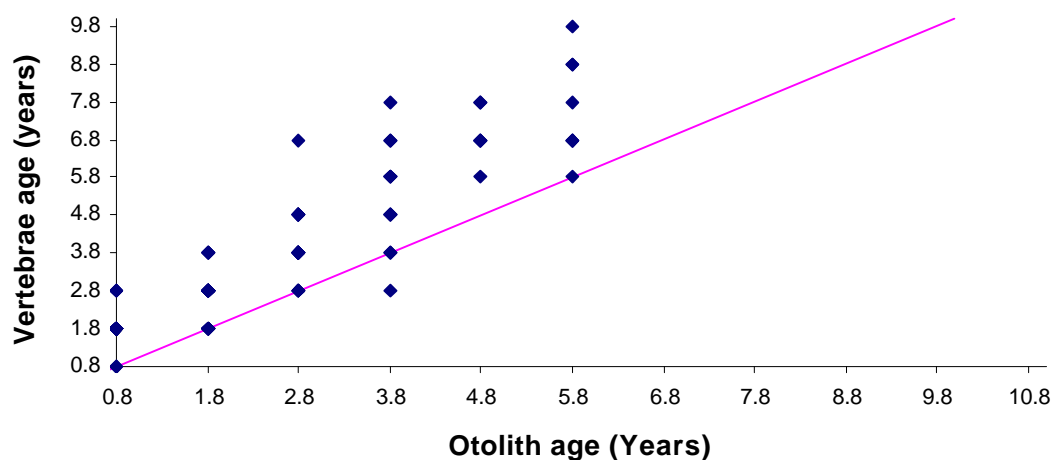


Figure 10. Bias plot: Difference in age reading using whole otoliths and vertebrae. The 45° line shows the line of agreement.

Gonad inspection allowed sex identification for 57 females and 74 males. The VBGF for separated sexes using the vertebra method is shown in Figure 11. The respective equations for males and females are: $L_{t_m} = 75*(1-e^{(-0.10*(t-018))})$ and $L_{t_f} = 61.6*(1-e^{(-0.16*(t-0.025)})$. No statistically significant difference could be demonstrated in the test of coincidence of growth curves for the two sexes (ARRS: $F=2.26$ d.f.=3, 141, $p>0.05$). Therefore the data were pooled together for further analysis. Males seemed to reach older ages than females but sampling of big fish was limited and that trend is uncertain.

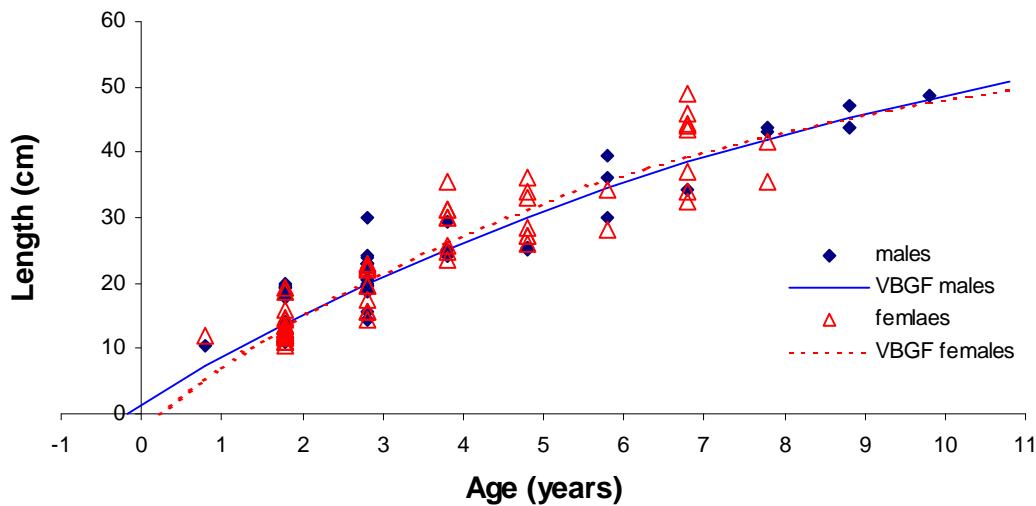


Figure 11. VBGF for separate sexes, based on vertebral counts ($n=77$ males and $n=70$ females).

Maturation

The age-at-maturity T_m calculated for females was 4.5 years (L_{50}). Females initiated maturation from approximately 3 years (observed data) and the full-adjusted probability was reached at about 7 years (Figure 12).

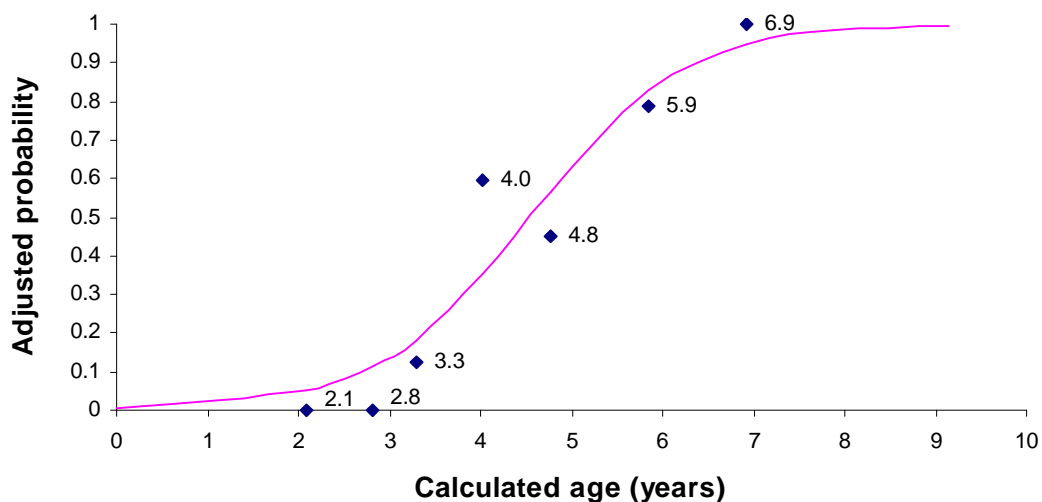


Figure 12. Maturity ogive calculated for females of *L. guttatus* ($n=278$)

Other population parameters

Assuming the best value for $k=0.13$, as determined with vertebrae, the natural mortality M was calculated to be 0.2867. The equation used to obtain this parameter has been determined specifically for snappers and groupers (Ralston 1987).

The parameters of the length-weight relationship were calculated to be $a= 0.0197$ and $b= 2.8977$. Figure 13 presents the length-weight relationship for the total data, which resulted in a high R^2 . The addition of the small fish caught by the trawler improved the fit of the curve for pooled sexes. In a previous study (Pérez-Cifuentes *et al* 1999), only bigger fish obtained from the artisanal catches were utilised in the length-weight relationship.

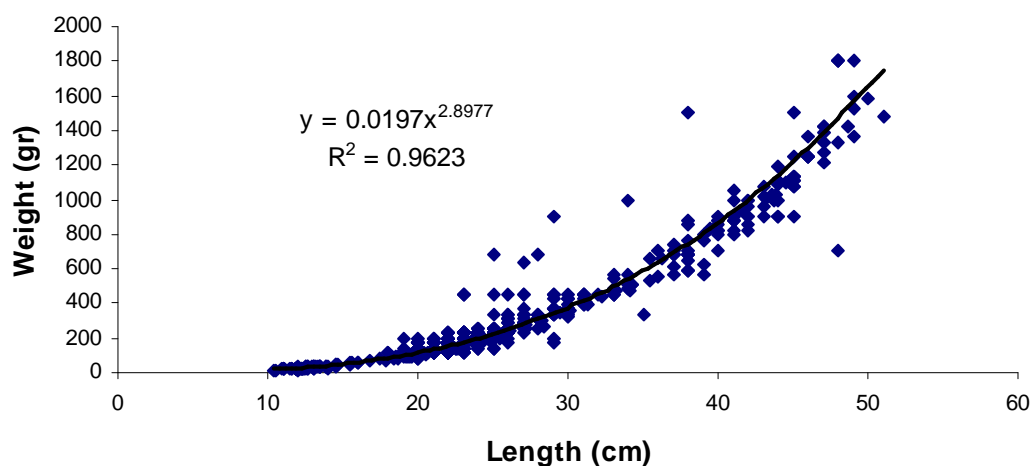


Figure 13. Weight-length relationship for *L. guttatus*, pooled sexes ($n= 504$).

Selectivity of the fleets

No information exists about the selectivity characteristics of the different fishing gear in Guatemala for *L. guttatus*. In this section, the age distribution of the catches is shown, and age-dependent fishing mortality patterns that might fit these data are suggested. Most of the fish sampled in the trawler catches were 1 year old, but fish up to 3 years old also occurred, although in minor quantities. In contrast, the

artisanal fishery showed a clear peak for fish aged 3 years old. Further, fish up to 13 years of age (estimated according to the VBGF) were present in the artisanal catches.

The length-distributions in the catches suggested two unimodal curves to express selectivity-at-age, with peaks (T_c) at age 1 for the trawler and age 3 for the combined artisanal fleet (observed data). The curves suggested in figure 14 are described by the parameters shown in Table 2. The curves were forced to reach the same height (probability of 0.5) but have slightly different shapes. The curve for the artisanal fleet was made such that it provided relatively high fishing mortality for fish older than the age-at-first-capture (long tail to the right). This should mimic the effects of the combined artisanal fleet, which is a heterogeneous composition with regard to gear type (gillnets of different mesh-sizes and different sizes of hooks and lines).

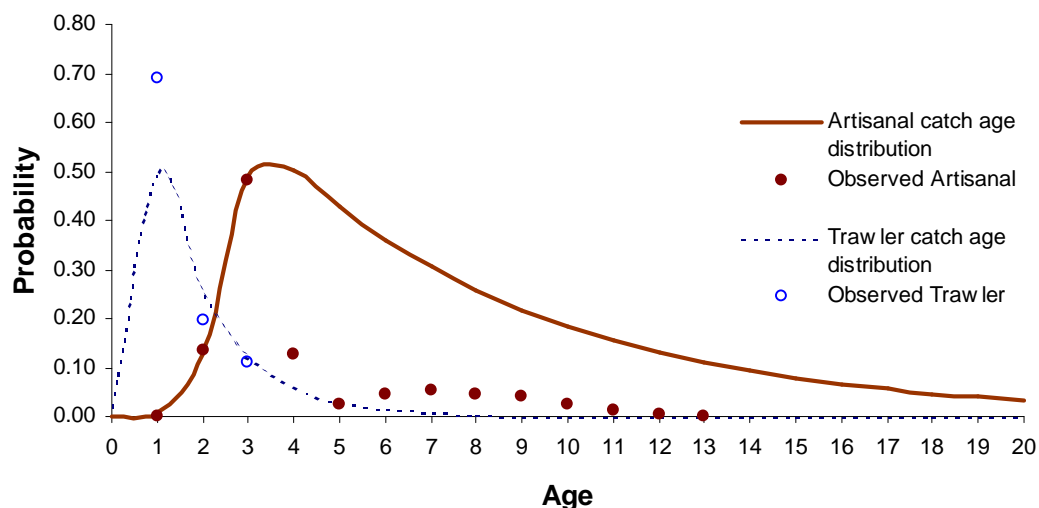


Figure 14. Age distribution of *L. guttatus* in the samples of the catches by the artisanal and trawler fleets. The age-dependent mortality patterns are shown as curves.

Scenario Modelling

The parameters obtained above (Table 2) were used for scenario modelling. In scenario 1 (Fig. 15), a theoretical case is presented showing the outcomes of leaving one fleet to fish alone at an optimum $T_c=6$ (nearly knife-edge). Under this setting yield is described by a flat-top curve, and spawning biomass does not decline to values lower than the critical MBAL 20% irrespective of fishing mortality. The

results of scenario modelling for this hypothetical fleet are shown in Figure 16. Highest yields are obtained for combinations of T_c between 4.5 and 7.5 years, and $F > 1.5$ owing to the flattop nature of the curves. Past an age $T_m > 8$ the Y/R decreases because there will very few larger fish left to catch. The functions were modified to simulate a more realistic situation where this single fleet imposed an unimodal fishing mortality pattern, as expected from e.g. gillnets (scenario 2, Figure 17). This fishing pattern had close resemblance to that of the artisanal fleet, as suggested in Figure 14. Since the artisanal fleet is targeting fish mainly under the optimal T_c , strong changes were observed in the curves: the yield showed a more defined peak, but general lower yields. Further, the spawning biomass curve clearly declined to critical levels, even for moderate values of fishing mortality.

Table 2. Values of parameters suggested for the trawler and artisanal fleet.

Parameter	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
L_{max} (VBGF)	66.4	66.4	66.4	66.4	66.4
K (VBGF)	0.13	0.13	0.13	0.13	0.13
t_0 (VBGF)	0	0	0	0	0
M (natural mortality)	0.2867	0.2867	0.2867	0.2867	0.2867
a (length-weight)	0.0197	0.0197	0.0197	0.0197	0.0197
b (length-weight)	2.8977	2.8977	2.879	2.879	2.879
MaxAge (set to...year)	30	30	30	30	30
T_m (maturation)	4.51	4.51	4.51	4.51	4.51
R_{tm} (maturation)	1.201	1.201	1.201	1.201	1.201
F artisanal F_a	variable	variable	variable	variable	variable
T_c artisanal T_{ca}	6	2,5	2,5	2.5	2.5
R_{tca}	10	3	3	3	3
P_{ra}	0	0,17	0,17	0.17	0.17
F trawler F_t	0	0	variable	variable	variable
T_c trawler T_{ct}			0.2	0.2	0.2
R_{tct}			19	19	19
P_{rt}			0.7	0.7	0.7
Recruits	1	1	1	1	1
Step (weekly)	52	52	52	52	52
U_p artisanal (price)				8	8
U_c artisanal (cost)				6	6
U_p trawler (price)				4.01	4.01
U_c trawler (cost)				1.98	0
Discount rate	0.05	0.05	0.05	0.05	0.05

An interaction scenario between the trawlers (Ft) and the artisanal fleet (Fa), was simulated using the “real” age-dependent selectivity suggested above (scenario 3; Table 2). There were clear indications that the best yield is attained for moderate fishing mortality by the artisanal fleet (Fa) and very low mortality by the trawlers (Ft) (Figure 18). This reflects the different T_c 's associated with the two fleets. Although the fishing pattern for the artisanal is lower than optimal, trawlers seem to be catching fish far smaller than the critical size.

The simulation of the discounted profits obtained in the fishery (both fleets combined) is shown in Figures 19 and 20, for two different cost structures (scenarios 4 and 5). The simulated scenario is otherwise similar to the previous simulation (scenario 3) in terms of all other parameters. In the first case the trawler fleet is assumed to have unit costs of production that are 33% of those of the artisanal fleet. In scenario 5 a more extreme situation is explored, and the trawler fleet is assumed to have nil costs of production for this by-catch species. The profit patterns are very similar, indicating that it is more profitable to allow an exclusive fishery by the artisanal fleet, irrespective of the costs of production of the two fleets. Thus, under the no-cost assumption (scenario 5) optimal profits are obtained for Fa values around 0.6-1.6, while the values for the trawler Ft ranges from 0.0 to a maximum of about 0.1.

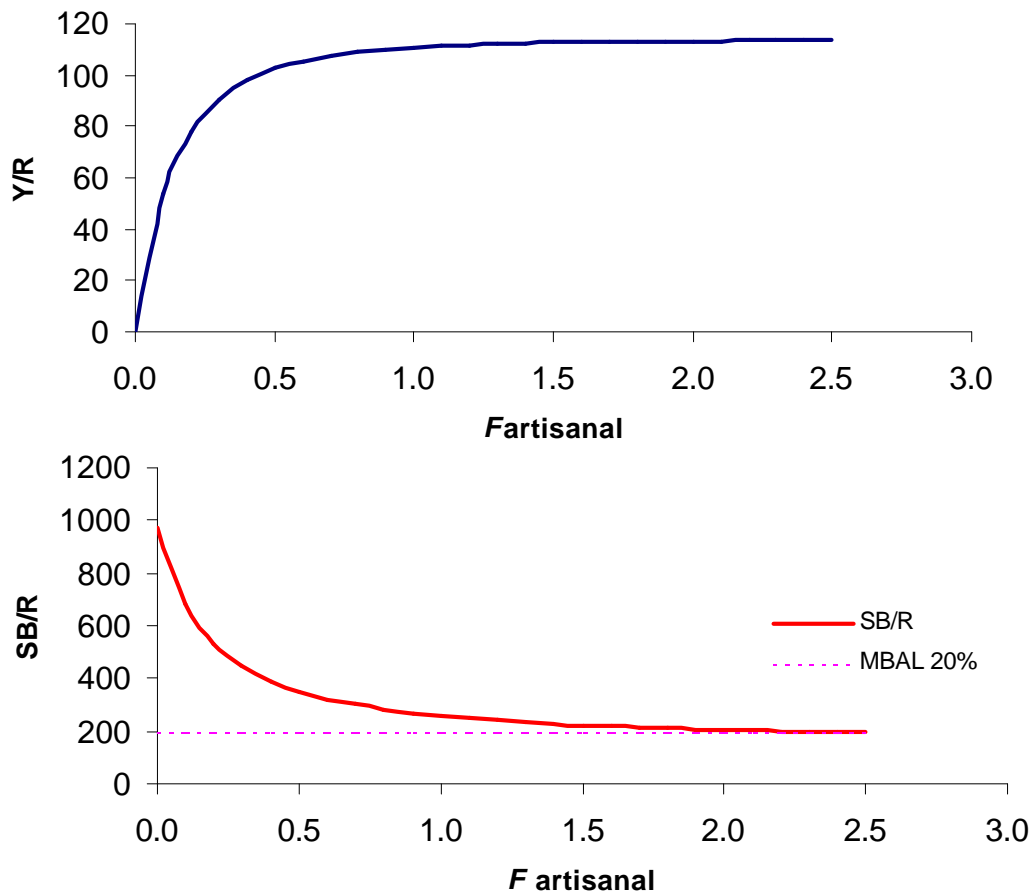


Figure 15. Yield-per-recruit (Y/R) and spawning biomass per recruit (SB/R) curves for a hypothetical fleet applying knife-edge like fishing mortality (F) to *L. guttatus*. Parameters described in Table 2 for scenario 1.

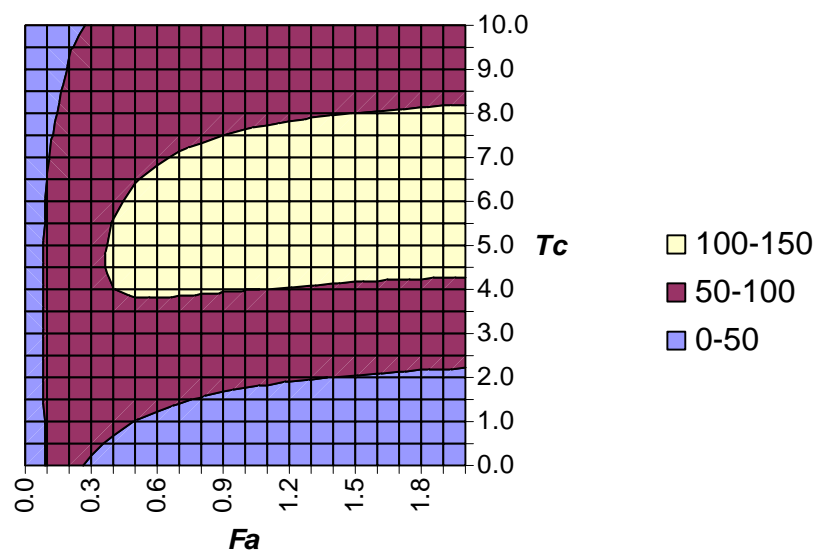


Figure 16. Yield-per-recruit for a single-fleet targeting *L. guttatus* in a approx. knife-edge manner, for different combinations of age at first capture T_c and fishing mortality F_a .

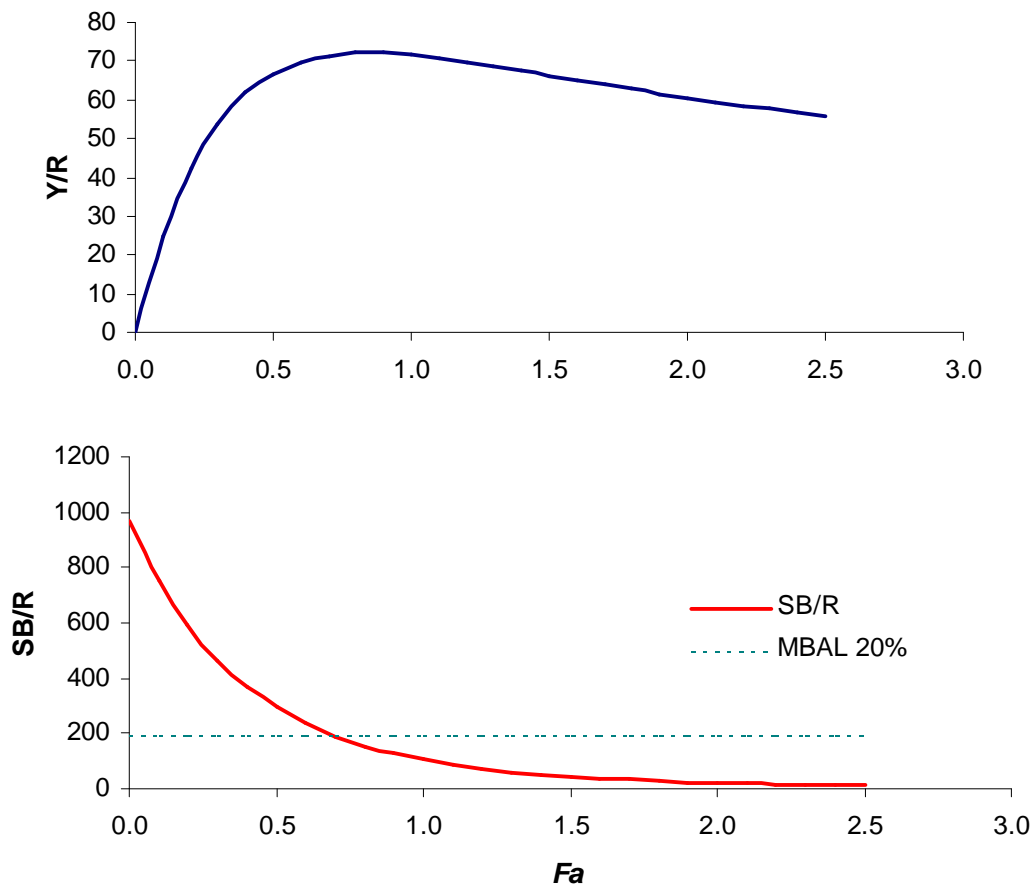


Figure 17. Yield-per-recruit (Y/R) and spawning biomass per recruit (SB/R) curves for a single-fleet with characteristics similar to the artisanal fleet with regard to age-dependent fishing mortality (F_a) for *L. guttatus*. Parameters described in Table 2, scenario 2.

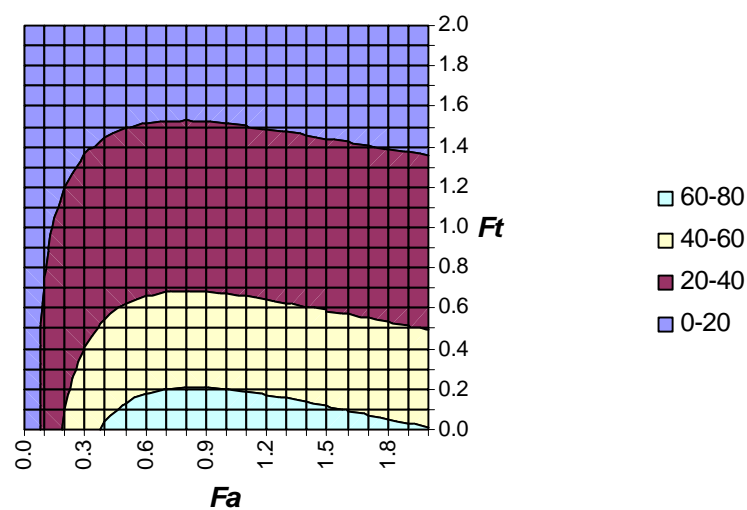


Figure 18. Yield per recruit for combinations of the artisanal fishing mortality F_a and the trawler fishing mortality F_t . Parameters in table 2, scenario 3.

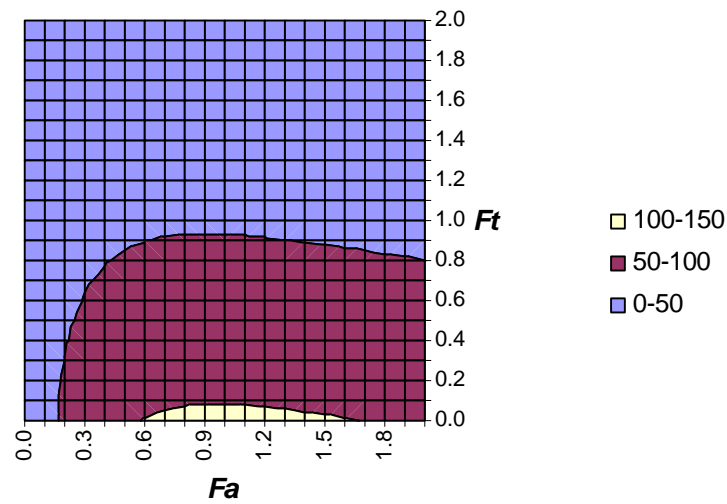


Figure 19. Profit per recruit for combinations of the artisanal fishing mortality F_a and the trawler fishing mortality F_t , assuming costs of production of the trawler fleet to be 1/3 of those of the artisanal fleet (scenario 4, parameters in table 2). The currency of profit is given in relative units.

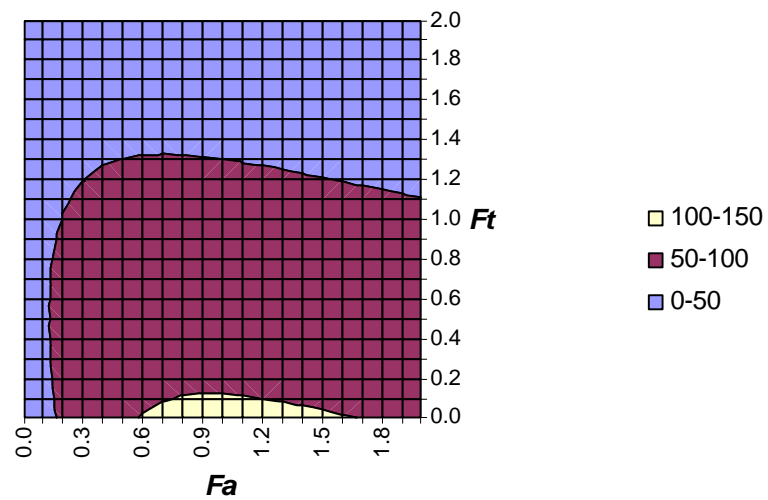


Figure 20. Profit per recruit for combinations of the artisanal fishing mortality F_a and the trawler fishing mortality F_t , assuming unit costs of production of the trawler fleet to be nil (scenario 5, parameters shown in table 2). The currency of profit is given in relative units.

DISCUSSION

The present observations and those from other works (e.g Saucedo-Lozano and Chiappa-Carrara 2000, Ixquiac 1998), indicate that small (mostly immature) *L. guttatus* are predominant in the catches of shrimp trawlers. This may be related to feeding characteristics of the species. Rojas (1996-1997a) found that *L. guttatus* below 20 cm TL feeds principally on shrimps, and Saucedo-Lozano & Chiappa-Carrara (2000) made similar findings for fish in the range 6 to 14.9 cm. Both authors agree that bigger sizes feed predominantly on fish. It would seem likely that fish above 20 cm TL leave the shrimp grounds to obtain other types of food. Thereafter they may become available to the artisanal fleet, and this is reflected in the small overlap of sizes between fishing gears (frequency distribution in Fig. 4). Back-calculated lengths of fish caught by the artisanal fleet were similar to the observed lengths-at-age of snappers sampled by trawls. This is further indicative that they might be representative of the same population.

Ageing otoliths of *L. guttatus* was a difficult task because of the occurrence of diffusive marks near the nucleus and the lack of consistency in the growth pattern. However, the relationships between the size of the hard-structures and fish length were strong, and this mirrors previous results obtained with lutjanids (e.g. Burton 2002, Newman 2002, Wilson & Nieland 2001). Under this criterion these structures were considered useful for ageing. On defining the first ring, Brennan & Cailliet (1989) mentioned that the rings are not simple fine lines that encircle the origin of growth, but should consistently describe depositional patterns associated with winter or summer growth zones. The problem of defining the first ring has been mentioned for *L. campechanus* (Wilson & Nieland 2001) for which the first annulus appeared as a defined “smudged” of opaque material. He attributed the phenomenon to the protracted spawning season and the rapid growth rate of juvenile red snapper. For whole otoliths, the parameter t_0 showed a high negative value ($t_0 = -0.85$ yr), and this can be a consequence of erroneous marking of the first ring in the present work. This can be supported by the analysis of the 1.8 age class: this age-class was clearly better represented in vertebrae than in otoliths ($n=58$ compared to $n=33$), and this can be indicative of better marking in vertebrae.

The phenomenon of counting more zones in sectioned than in whole otoliths has been described for e.g. *L. erythropterus*, *L. malabaricus*, *L. sebae* (Newman *et al* 2000a; Newman 2002) and *L. peru* (Rocha-Olivares 1998). These authors concluded that whole otoliths showed lower and more imprecise age estimates than sectioned otoliths. In the present work a larger number of rings could also be seen along the borders of sectioned otoliths, but a lack of consistency was obtained for the expected growth pattern. Further, the inner rings easily shown in whole otoliths were very difficult to locate in sectioned otoliths. Therefore, data from sectioned otoliths were considered equally unreliable as those from whole otoliths and were not utilised in the fit of the growth curves.

The expected pattern for the growth is to be fast prior to maturity, and past this stage, energy is spent to develop gonads resulting in a consistent decreasing of growth rate. Pérez-Cifuentes *et al* (1999) determined the length-at-maturity for *L. guttatus* to be 33 cm in females. Using the VBGF obtained in the present work to predict the age of the fish, this length can be converted to an age of 5.17 years. Past this length, the rate of growth expressed in the reduction of distances between rings should decrease. The expected post-maturation pattern was not found for otolith data in the present material, and this detracted from their reliability for growth analysis. Owing to the advantages in both otolith ageing techniques (clear rings in whole otoliths, border rings in sectioned otoliths), they should be combined in any further attempt to establish age, unless a more precise method can be applied.

The sample collected for the present study was not sufficiently adequate to analyse if the rings represent year marks, or to address causes of their formation. Pannela & Manooch III (1980 *in* Manooch III 1987) addressed the difficulty of interpretation of marks in reef fish, which experience constant water temperature year round. They concluded that bony structures in many tropical fishes reveal an abundance of markings, but discerning their meaning is a challenge. Nelson & Manooch III (1982 *in* Wilson & Nieland 2001) attributed the formation of transparent annuli in red snapper to the spawning season. This species has a long spawning season and a seemingly constant recruitment (Bradely & Bryan 1975 *in* Wilson & Nieland 2001). For *L. peru* the same has been mentioned and there are reports that this species also occurs in the Pacific Coast of Guatemala (Fischer *et al* 1995). It is possible then, to

evaluate if *L. guttatus* forms the marks during the peak months of reproduction, but the following questions arise: what triggers the formation of rings in juvenile fish, if temperature and spawning season are ruled out? If *L. guttatus* has a prolonged spawning season with three peak months (Pérez-Cifuentes *et al*) and the females are intermittent spawners (Rojas 1996-1997b), are then many rings formed each year?

As mentioned before there is not enough data to understand the information coded in the otoliths. Grimes (1987) reported that for *Lutjanus* the timing of reproduction involves a number of environmental cues like temperature, photoperiod and the lunar cycle. Temperature has been correlated with gonad development and preparation for spawning in lutjanids (Grimes & Huntsman 1980, Everson 1984, Arnold *et al* 1978 in Grimes 1987). There is a chance then that temperature could be correlated with the spawning season, and therefore, with the mark formations in otoliths of immature fish. Manooch III (1987) mentioned that large variation of growth rate is not expected in the tropics at least based on seasonal temperature fluctuations (If one excludes phenomena such as “El niño” and “La niña” that cyclically occur in the Central American Pacific.) An alternative explanation is the possibility of a direct relation between spawning and food abundance. This could explain the formation of the rings in both young and adult fish.

In 1998 peak precipitation months (>2500 mm) for the Pacific Coast of Guatemala were June and August (source: Insivumeh, information sent under request) while the peak months for the gonadosomatic index were August, October and January (Pérez-Cifuentes *et al* 1999). Reshetnikov & Claro (1978 in Manooch III 1987) suggested that spawning is timed to coincide with periods of high rainfall, when increased runoff introduces nutrients into coastal waters and supports greater food production for early life stages. These periods are coincident for some lutjanids that inhabit continental and large islands (Manooch III 1987). For *L. guttatus* this could be the strategy employed, but validation tests like the marginal increment analysis relation with environmental parameters should be carried out during at least one year to corroborate this hypotheses.

Growth curves for vertebrae and whole otoliths gave rise to different estimates of the VBGF parameters. The discrepancy between counts from whole otoliths and

vertebrae is reflected in the lack of overlap for old ages. Thus, age was underestimated with otoliths when compared with vertebrae. Lai and Liu (1974 *in* Manooch III 1987) also concluded that the best structures for age determination in *L. sanguineus* were the vertebrae. In the present work, vertebrae presented clearer rings, and these followed the expected grow pattern. Good estimates of growth patterns are essential for assessment models of the yield-per-recruit type. The samples of otoliths/vertebrae used in this work gave good coverage of young and old age classes and were therefore appropriate to fit the Von Bertalanffy growth curve. Older organism were also selectively collected, and their size is consider to be near the L_{\max} reported earlier for different countries: 53 cm in Guatemala (Pérez-Cifuentes *et al* 1999); 58.2 cm for the Coast of Guerrero, México (Arellano-Martínez *et al* 2001); and 60 cm in Costa Rica (Rojas 1996-1997a). Cruz-Romero *et al* (1996) used the program ELEFAN I to analyse length-frequency distributions and obtained the following results: $L_{\max} = 64.2$ cm; $K = 0.192$ yr⁻¹. These are in considerable agreement with the parameters found in present work: $L_{\max} = 66,4$ cm and $K = 0.13$ yr⁻¹. The importance of having older fish represented in the samples should be borne in mind. A simulation with the VBGF model showed that after removing the 3 oldest fishes, the growth parameters would completely change. This uncertainty around the growth parameters was dealt with as a part of the bootstrap analysis (Appendix, Figure 22). Parameters of the VBGF had wide confidence intervals but these were within a normal range for individual-based models.

The growth curves for females and males were nearly coincident, but males were aged older than females in the present study. In the work of Pérez-Cifuentes *et al* (1999), a length-frequency histogram shows that the artisanal landings contained bigger females in total length than males, starting from around 47 cm. Females in this size were not sampled in this study. Grimes (1987) reports that the number of female snappers is preponderant at larger sizes and attributes this to differences in longevity. According to Pérez-Cifuentes *et al* (1999) and Rojas (1996-1997b), males mature earlier than females and therefore, the female age-at-maturity is consider more important for management purposes. If regulations concerning gear selectivity are taken to conserve females, males will be benefited.

In order to evaluate the consequences of different fishing strategies a yield per recruit model was preferred, owing to the unavailability of fishery related data (King 1995). However, even for this simple type of model several simplifications were called for. The strongest assumptions were those that related to the shape of the age-dependent fishing mortality patterns. However, the two unimodal curves utilised to describe the action of the trawl and artisanal fleets seemed reasonable, and it is doubtful that more precise formulations would result in contrasting conclusions. The application of yield per recruit theory is subjected to various pitfalls but if precaution is taken, it can be used to assess fishing patterns (ICES 1980). Although Y/R analysis is not a good predictor for future yields because of year to year variation in recruitment, it can be useful for designing management measures (Al-Husaini *et al* 2002).

In the present work, different management scenarios were created. According to a knife-edge approach the yields would be high, and the spawning biomass would be kept in safe levels, if the age of first capture of the snapper is delayed until the age of 6 years (Figure 15, scenario 1). Simulations were also made to mimic the effects of the existing artisanal fleet that targets large, and more valuable, fish than the trawl fleet. However, even the artisanal fleet seems to be catching fish that are younger and smaller than optimal (Figure 17, scenario 2). This strategy might also result in recruitment overfishing for large fishing intensities. This is in line with the findings of Rojo-Vázquez *et al* (1999), who recommended an increase in the mesh size of the gillnets from 7.62 cm to 8.89 cm to ensure that *L. guttatus* spawn at least once before the onset of exploitation in Navidad Bay, Jalisco México.

Whereas it was possible to make some estimates of the prices for snapper fetched by the two fleets, no information is available regarding costs of production for the coastal fisheries in Guatemala. A major difficulty is to determine the costs of fishing snapper for the trawl fleet, because this is a by-catch species. A minimum cost related to sorting and dumping of unwanted by-catch can be agreed upon. However, trawl fishers can claim that no costs are associated with the fishing operation, because they intuitively place the cost totally on the shrimp, their target species, and not on the snapper. However, it is equally true that the trawl fleet markets some of (largest) snapper, and this species should thus be regarded as an associated species rather than a rejection. While it was difficult to estimate costs, the strategy followed in the current

study was to assume two extreme costs for the trawler fleet. Both the “high” and “low” cost estimates were far below the cost of fishing snapper for the artisanal fleet, and this was thus a conservative approach. However, irrespective of the cost structures utilised for the two fleets, it is likely that profitability and yields of snapper can only be optimised if the fishing mortality caused by the trawl fleet on small fish is low or absent (Figures 19 and 20). To optimise the yield of snapper selective fishing practices by the artisanal and, particularly, the trawl fleet must be considered.

A yield per recruit model is a relatively simple tool. However, even the few parameters utilised in this work were surrounded by large amounts of uncertainty, partly caused by the limited number of observations. Thus, an analysis of the effects of parameter uncertainty on model output should be performed in the future. Further, it should be borne in mind that biological interactions are far more complex than depicted in the present models, which only account for fleet interactions. Multispecies simulations of similar systems exploited by competing fleets (Christensen 1998; Santos 2002) have shown that a large number of feedback takes place, and that conclusions are often counter-intuitive. However, it is hoped that the present work is a positive contribution to the complex discussion of fleet interaction in Guatemala.

CONCLUSIONS

L. guttatus is an important commercial species in Guatemala. The industrial shrimp trawlers catch mainly small individuals as by-catch, and the artisanal fleet target commercially important sizes. Analysis of growth patterns indicates that the two fleets apparently catch members of the same population.

Different skeletal structures were evaluated for ageing *L. guttatus*, including scales, vertebrae, and whole and sectioned otoliths. Scales allow non-invasive studies but were inappropriate for age reading because they showed extremely poor ring formation. Whole and sectioned otoliths showed rings and were apparently adequate for ageing. However, secondary analysis of these structures showed unconformity with logical growth patterns, difficulty to set first-year marks, and poor von Bertalanffy estimates. Vertebrae were easy to handle and prepare, and provided clear and logical ring deposition, and thereby reliable growth patterns. It is hypothesised that ring deposition follows an annual cycle, probably related to the rainy season.

The von Bertalanffy estimates obtained from vertebral data were: $L_{max}= 66.4$ cm, $K= 0.13$ yr⁻¹, $t_0=0.03$ yr. These were in agreement with previous estimates obtained in the Eastern Central Pacific. Males and females showed similar growth patterns. The age at maturity was calculated to be 4.5 years for females. The most frequent ages in trawl and artisanal catches were 1 and 3 years old, respectively.

Age-dependent fishing mortality patterns were suggested to follow unimodal curves for the two fleets. With basis on these observations a single-species yield per recruit model that accounted for fleet interaction was developed and utilised for scenario modelling.

The artisanal fleet seems to target fish below the critical size required to maintain the highest yields and spawning stock biomass. However, and irrespective of cost structures utilised for the two fleets, it is likely that the total profitability and yield of snapper fishery can only be optimised if the trawl fleet refrains from fishing small snapper. This calls for selective fishing patterns.

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APPENDIX

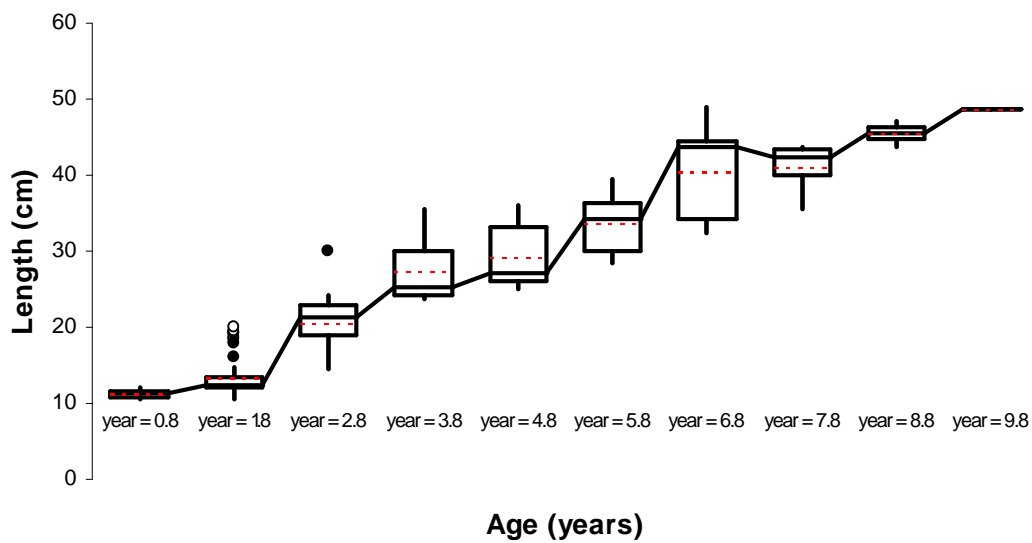
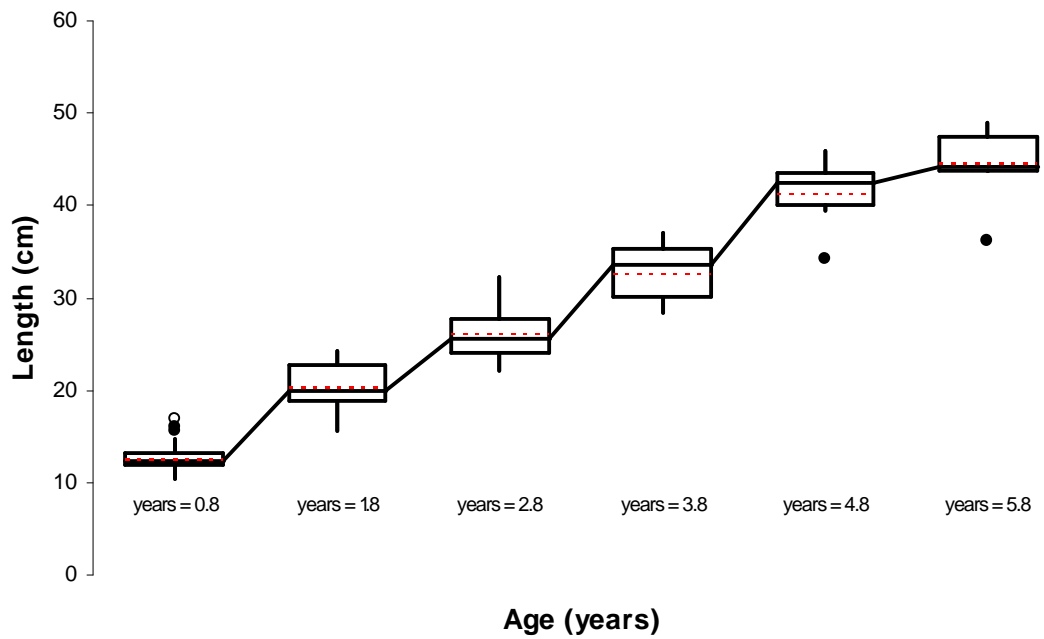


Figure 21. Boxplots for age determination using whole otoliths (upper) and vertebrae (lower). The triangles represent the age observations by year and the open circles represents extreme outliers

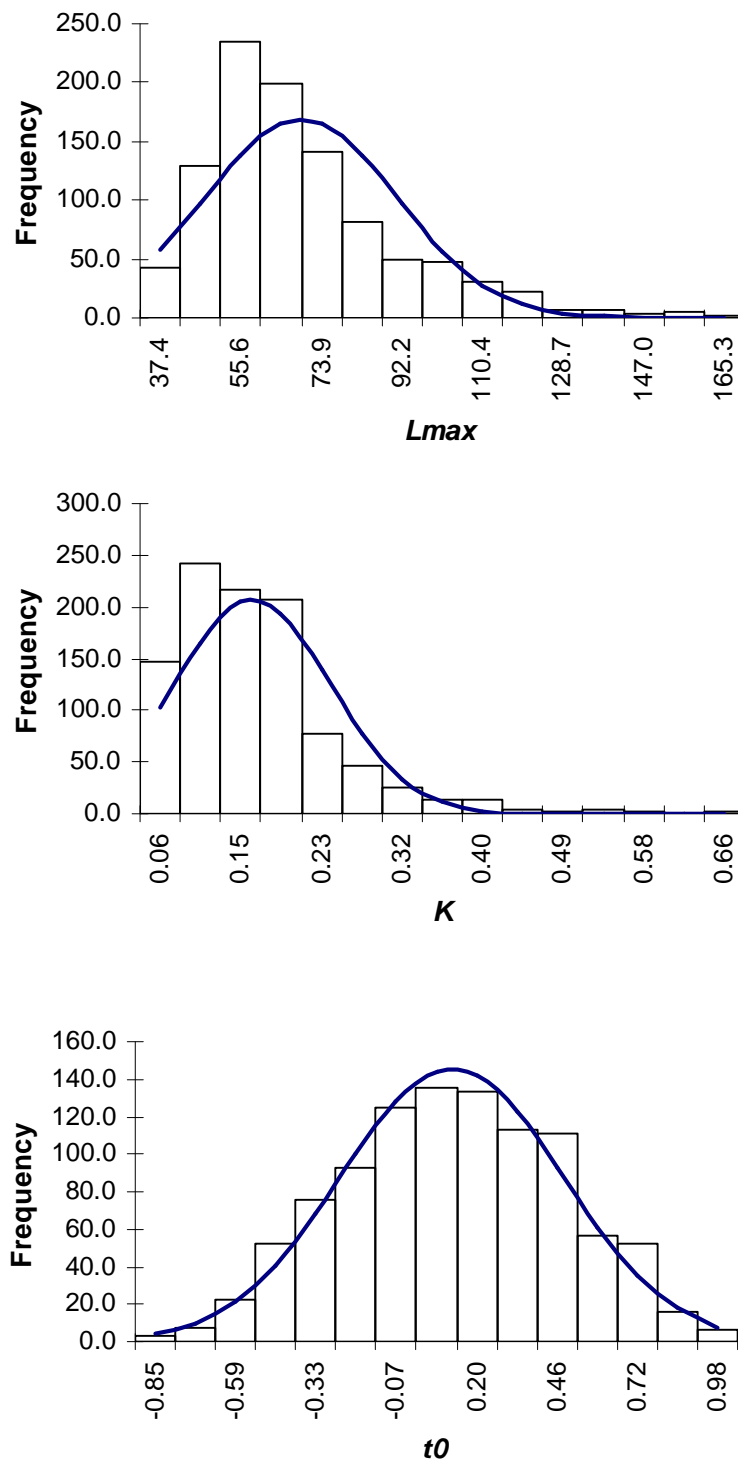


Figure 22. Bootstrap frequencies of growth parameters (L_{max} , K , t_0), determined by vertebrae for *L. guttatus* after running 1000 iterations.