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Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the Lower Amazon, Brazil

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Abstract Fishery statistics and length data series for *Colossoma macropomum* Cuvier obtained during 1992 and 1993 in the Lower Amazon, Brazil were used to describe the fishery and to estimate growth and mortality rates. Mean population parameters were L_∞ = 119.85 cm (total length), W_∞ = 33.4 kg, K = 0.228 year^{-1}, C = 0.505, Winter Point = July, M = 0.445 year^{-1}, F = 0.94 year^{-1} and L_c = 28.29 cm. Yield-per-recruit analysis showed that an excessive fishing effort and principally a very low length at first capture lead to an increase in overfishing in the region. Corrective measures are recommended.

KEYWORDS: Amazon, *Colossoma macropomum*, fishery, growth, mortality, tambaqui, yield.

Introduction

Colossoma macropomum Cuvier inhabits the river systems of the Orinoco and the Amazon. This species is characterized by its oval, laterally compressed body form, its yellow to olive green dorsum, and dark ventral markings (Saint-Paul 1985). Known as ‘tambaqui’ in Brazil, it is the second largest scaled fish in the Amazon Basin, and reaches at least one metre in total length, and 30 kg in weight (Goulding & Carvalho 1982).

Research on the autecology, and biology of *C. macropomum* from the Brazilian Amazon has been conducted by Honda (1974), Goulding (1979, 1980), Goulding & Carvalho (1982), Carvalho (1981) and Saint-Paul (1982, 1984a, 1984b). SAGRI (1990) gave a brief description of their migratory and spawning behaviour. Nevertheless, knowledge on the biology and life cycles of tambaqui is still fragmentary.

C. macropomum has been exploited commercially in the Amazon Basin since at least the end of the nineteenth century (Verissimo 1895). Today, tambaqui is an important fish in commercial fisheries and it is a preferred species for local consumption, which leads to the assumption that the fishing of this species has been very intensive. Tambaqui contributed some 36–45% (approximately 22 000–30 000 t) of the 1976–1978 fish landings in Manaus, Amazonas state (Petrere 1983), and constituted 36.1% of all fish sold in that city over 11 years (Saint-Paul 1985). However, between 1976 and 1986, tambaqui catches fell from 12 000–5000 t (Merona & Bittencourt 1991). Little has been documented about tambaqui catches in the Amazon Basin in the last 10 years. In 1992, some 209 t of tambaqui were landed in Santarém, Lower Amazon; that accounts for 2.8% of the total landings and includes this species among the ten most exploited in the region (Ruffino & Isaac, 1994).

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Information from local fishermen in Santarém suggests that size and relative abundance of tambaqui have been decreasing in recent years. Brazilian fisheries regulations state that only specimens longer than 55 cm can be caught; but fishermen routinely break this law.

Project IARA-Fisheries Resources Management of the Lower Amazon is part of a technical co-operation programme involving the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) and the German Agency for Technical Cooperation (GTZ) in the fisheries sector. It aims to provide technical support for the administration of fishery resources in the Lower Amazon. Currently, project IARA is assessing fish stock depletion in order to develop appropriate management policies and programmes for regional fisheries. This paper presents some of the first results of this project through a description of the tambaqui fishery and its population dynamics in the Lower Amazon, as a basis for the management of the fishery.

Materials and methods

Length (cm) and weight (kg) data were collected from tambaqui sub-samples selected at random from those landed at markets in Santarém (Pará State, Brazil) during 1992 and 1993. Fish were measured from the tip of the snout to the tip end of the caudal fin; total length (TL) to the nearest cm. Larger fishes were weighed on scales with a precision of 100 g; for smaller individuals, the balance used had a precision of 20 g.

Parameters a and b in the equation $W = a \times L^b$ were estimated by ordinary least-square regression after logarithmic transformation.

Individual lengths were grouped by month in frequency tables. Mean lengths were also calculated, and some differences were tested with a single t-test. The seasonal Bertalanffy growth model (Sparre & Venema 1992) was used to fit growth curves to length data series for 1992 and 1993, respectively. Growth parameters were obtained using the ELEFAN programme (Pauly 1987), and Wetherall's (1986) method. The growth performance index ($\varnothing' = \log_{10} K + 2 \log_{10} L_\infty$) of Pauly & Munro (1984) was calculated to allow comparison of the tambaqui growth parameters found here with published values.

The estimate of natural mortality (M) was obtained from Pauly's (1980) empirical relationship. Total mortality rate (Z) was ascertained by length-converted catch curves (Sparre & Venema 1992) and by the mean-length method (Beverton & Holt 1956). Relative yield-per-recruit was estimated according to Beverton & Holt (1956).

Growth, mortalities, and selection parameters were obtained using the FISAT package of Gayanilo, Sparre & Pauly (1994). Yield-per-recruit for a series of fishing mortalities and lengths-at-first-catch were estimated with the LOTUS 1–2–3 programme of Sluczanowski (1985).

For a description of the tambaqui fishery, detailed catch-per-effort data (catches, duration of fishing trip, gear type, vessel type, ice and oil consumed, number of fishermen, distance of fishing ground to Santarém and landing site) were obtained daily from the landings in Santarém during 1992 and 1993 by interviews with the fishermen or vessel owners operating in the Lower Amazon from Parintins (Amazonas state) to Prainha (Pará state) (Fig. 1).

An unbalanced analysis of variance calculated via the GLM (General Linear Model) procedure (SAS 1987) was used to study the joint effect of some non-continuous variables (gear type, vessel type, month, market, distance of fishing ground, catch period) and continuous variables (number of fishermen, duration of trip, ice and fuel consumed) on the catch-per-trip

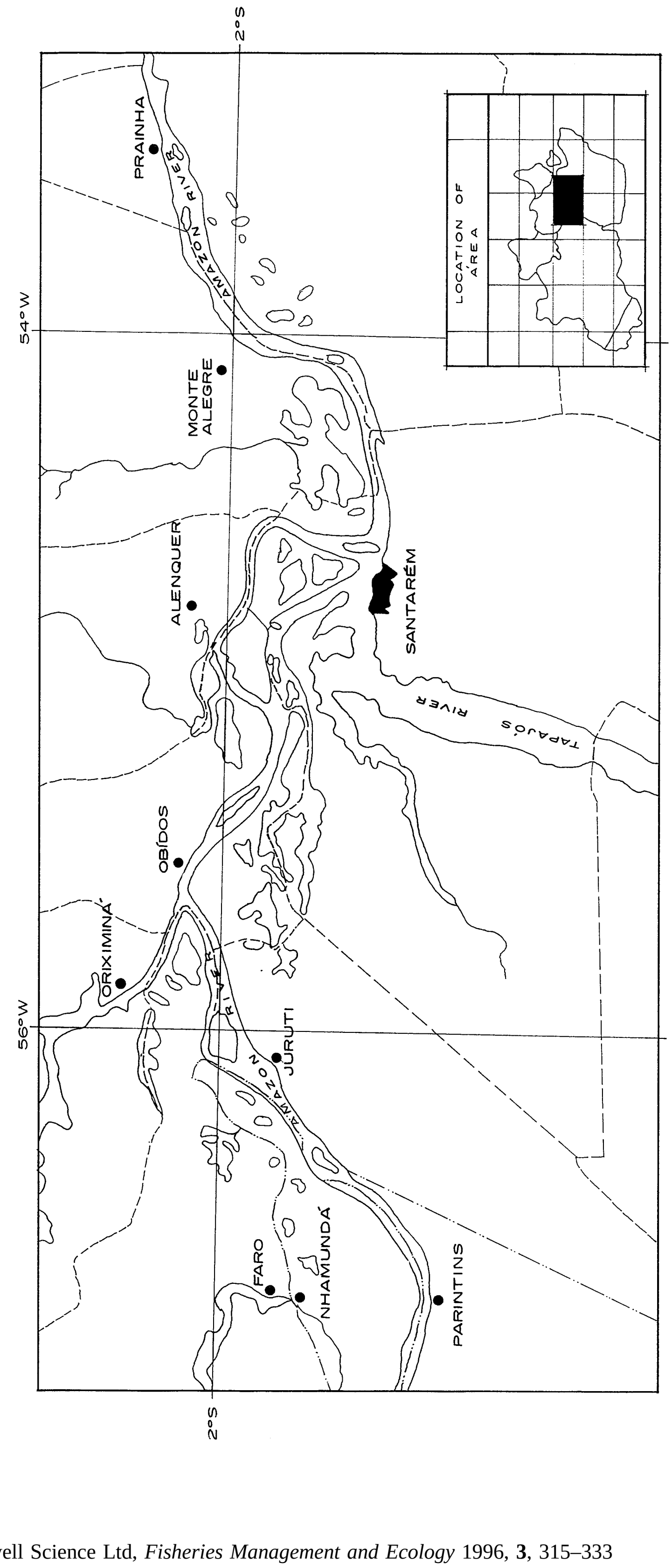

Figure 1. Map of the Lower Amazon.

Table 1. Descriptive list of all variables used in the GLM analysis for tambaqui (*Colossoma macropomum*) of the Lower Amazon.

Variable Name	Categories
Vessel type	Fishing-boat (FBo)
	Buyer-boat (Buy)
	Mixed-boat (Mix)
	Cargo or Ferryboat (CF)
	Motorized canoe (MC)
	Canoe (C)
Ice	Quantity of ice consumed on the trip (kg)
Fuel	Quantity of fuel consumed on the trip (litres)
Distance	Rank (1–4): distance from Santarém to fishing district
	1: Santarém, Alenquer, Monte Alegre
	2: Aveiros, Óbidos, Prainha, Terra Santa
	3: Parintins, Oriximiná, Nhamundá
	4: Manaus, Itacoatiara, others of Amazonas State
Period	Period that the fishery occurred (Day–D, Night–N, Day and Night–B)
Environment	Fishing ground:
	Lake (L)
	River (R)
	Flooded forest (FF)
	Channel (C)
Gear type	Type of gear used in the fishery:
	Gillnet (G)
	Gillnet with small mesh (GSM)
	Drift net (D)
	Long-line (LL)
	Castnet (C)
	Hook and line (HL)
	Mixture of various gears (VG)
Month	Landing month
Days	Duration of trip in days
Fishermen	Number of fishermen participating in the fishery
Market	Landing sites:
	Modelo market (Md)
	Uruará market (Ur)
	2000 market (M2)
	Edifrigo Ice plant (E)

of tambaqui (response variable) for 980 observations (trips) in 1993 (Table 1). The GLM procedures used the least-square method to fit the model. All continuous variables were log transformed. The sum of squares (Type III SS) was used as a measure of the relative weight that each explanatory variable has in the total variability. The significance of each variable was determined with the help of an *F*-test and the quality of the fit through r^2 (Milstein, Goldman & Hulata 1993).

Differences between the respective means of catch-per-trip, and CPUE (catch per fishermen per day), for each level of the categorical variables in 1993 were tested with a Duncan multicomparison test (SAS 1987). Following Milstein & Hulata (1993), the results shown in

Tables 2 and 3 identified means that were significantly different at a 95% level by successive letters, 'A' being larger than 'B', 'B' larger than 'C', etc.

Results

Tambaqui fishery

Annual catches of *Colossoma macropomum* landed at Santarém amounted to 209 t in 1992 and 125 t in 1993. The flood season of 1992 did not last as long as that of the following year, nor did the water level rise as much as it did in 1993. In 1992 the water level in the river rose to only 6.5 m in May (wet season) and decreased rapidly to 2.5 m in November (dry season). By contrast, in March of 1993 the water level was already at 7 m and reached 8 m in May; it fell to just 3.2 m in the dry season (Fig. 2). Total catches were higher in 1992, when the rainy season was shorter. Fishing operations are probably more productive when the fish are more concentrated.

Monthly patterns also reflected the differences between both hydrological years, the changes being more drastic in 1992 (Fig. 2). In general, catches were low at the beginning of the year and increased in the flooding months. They reached a peak in April, when the water level was high, and hit a low between June and August, increasing slightly with the dry season (around September) only to abate again in the final weeks of the year.

The total number of trips, fishermen and fishing days, as well as the CPUE (expressed as catch fisherman^{-1} day^{-1}), showed the same trend, with two yearly peaks – the largest in April and the second one when the water was low (Figs 3 and 4). Duncan's test showed CPUE was similarly high between February and April and again in September, but lower in July (Table 2). Mean CPUE oscillated between 3 and 14 kg fisherman^{-1} day^{-1} and was higher in 1992, when the rains were less intense (Fig. 4). It should be noted that the fishery in the region is multispecific, so the fishermen never restrict themselves to catching a single species. The ratio of *C. macropomum* catches over the total catch was about 1:3 for both years. Total productivity (i.e. all species considered together) of the local fishermen, for trips that yielded tambaqui, averaged between 15 and 48 kg fisherman^{-1} day^{-1}. Each trip had, on average, a duration of 4 days and deployed four fishermen, within a range of 1–30 days and 1–24 fishermen, respectively.

Tambaqui landed in the city of Santarém were caught in lakes, rivers, and creeks of the region between the districts of Parintins and Prainha (Fig. 1). Most fishing boats travel to localities near to Santarém for fishing. About half of the catch was from the district of Santarém, 19% from Alenquer, 15% from Monte Alegre, 11% from Prainha, 3% from Óbidos, and only 2% from other more distant districts. Duncan's test showed that average values of catch-per-trip and catch per fishermen per day of boats originating from Prainha and Óbidos were significantly higher than those from other districts (Tables 2 and 3).

The fishing itself was done using one- or two-men canoes or small boats (of both single-log dugout and plank-formed hull types) propelled by either paddle, sail or low-power outboard engines. These are either sent off by themselves (for fishing grounds close enough to Santarém) or towed by larger boats that also carry ice for preservation. The latter vessels are on average 10 m long and have different denominations according to the way their owners deal with local fishermen. A fishing-boat *(barco pescador)* has its own regular crew of fishermen who always

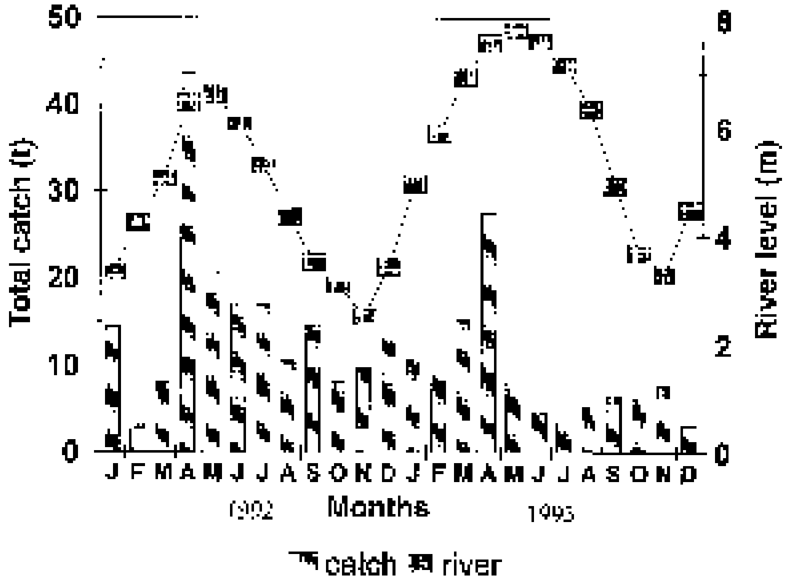

Figure 2. Catches of tambaqui (*Colossoma macropomum*) in the Lower Amazon and river water level at Santarém, during 1992–1993.

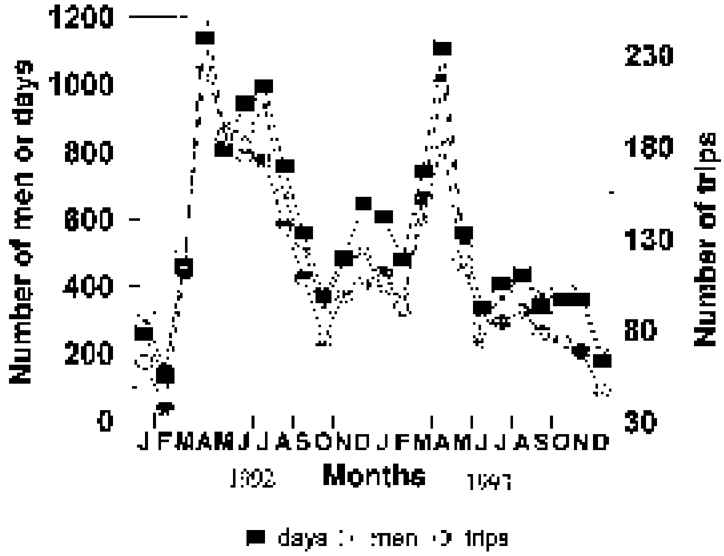

Figure 3. Fishery effort (number of fishermen, duration of trips and number of trips) of the tambaqui (*Colossoma macropomum*) fishery in the Lower Amazon, during 1992–1993.

work together: it takes them to the fishing grounds where they disperse in their respective canoes, then collects their combined catch, stores it in ice and transports the catch, fishermen and canoes back to the port. Alternatively, the crew of a buyer-boat *(barco comprador)* does not engage in fishing nor does it tow any canoes: it simply uses the vessel as transportation to riverine communities where it buys someone else's catches. A composite arrangement is

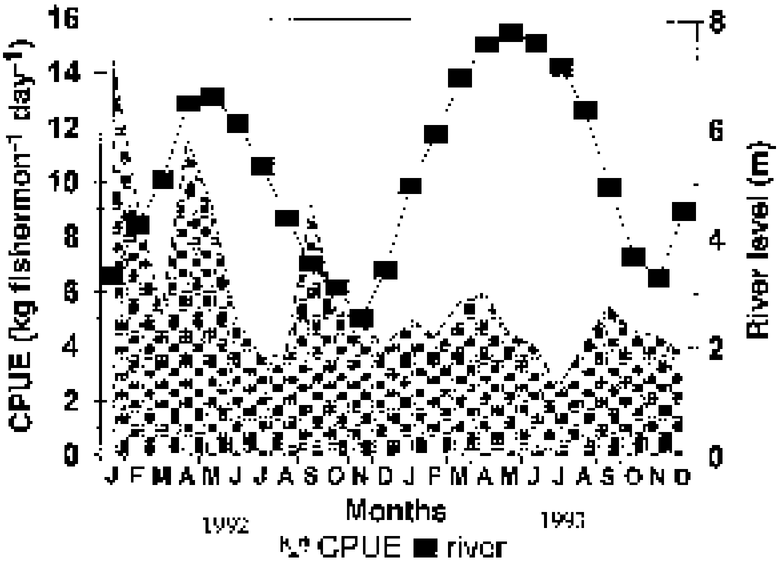

Figure 4. Catch-per-unit effort (CPUE) of tambaqui (*Colossoma macropomum*) in the Lower Amazon expressed as kg fishermen^{-1} day^{-1} and river water level at Santarém, during 1992–1993.

the mixed-boat *(barco misto)*, which tows some canoes and has its crew engaged first in fishing, then in buying from other fishermen to fill up a quota or an order. Fishermen who live in distant communities also make use of regular transportation line vessels to bring their catch to Santarém in styrofoam iceboxes aboard both passenger ferry boats *(barcos de linha)* and cargo boats *(barcos de carga)*.

Mean landing weight per trip of tambaqui for all vessel types in 1992 and 1993 was 120 and 85 kg, respectively: the higher catches were from the buyer-boats, mixed-boats and fishing boats, and the lowest ones from self-propelled outgoing canoes (Table 3). About 74% of the tambaquis landed in Santarém in that period were transported by fishing-boats, 11% by cargo or passenger ferry boats, 4% each by buyer-boats, mixed-boats and manned canoes, 2% by motorised canoes.

Tambaqui were captured by means of a large diversity of gears (Fig. 5). Gillnets accounted for 70% of the catches and a combination of gears called 'mixed-bag' (for example, gill- and castnet) accounted for 20%. Gillnets and 'mixed-bag' were used practically throughout the year. A typical gillnet for tambaqui is made of multifilament nylon, mesh sizes ranging from 150 to 240 mm stretched (Evangelista & Takitome, personal communication). In addition, $\approx$5% of the catch arose from *miqueiras* – small-meshed (80–160 mm stretched) monofilament gillnets. The remaining 5% of the catch were variously obtained by means of drift nets, long lines, castnets and, occasionally, harpoons, hook-and-line, bow-and-arrow and tridents. Castnets are used preferentially in the summer, when fish are more concentrated. Long-lines and drift nets are used in the river in September and October, the season for dourada, *Brachyplatystoma flavicans* (Castelnau), when tambaqui are also occasionally captured. Duncan's method showed significantly higher catch-per-trip performance for gillnets, followed by 'mixed-bag'; hook-and-line, *miqueira*, drift net and long-line had approximately similar results with castnet associated with the lowest mean value (Table 3).

Table 2. Results of Duncan's multiple range test for the catch fisherman^{-1} day^{-1} (kg) of tambaqui (*Colossoma macropomum*) of the Lower Amazon. Different letters identify differences at 95%. See abbreviations in Table 1.

Variable categories		Means	N	Duncan grouping	
Vessel type	Buy	7.886	12	A	
	C	5.407	276	A	B
	Mix	5.261	20	A	B
	FBo	5.042	15	A	B
	MC	3.712	29		B
	CF	3.448	276		B
Distance	2	7.184	99	A	
	3	4.919	9	A	B
	1	1.551	872		B
Period	D	5.350	492	A	
	B	4.968	401	A	
	N	4.481	87	A	
Environment	R	6.064	774	A	
	L	4.933	183	A	
	FF	3.927	11	A	
	C	3.643	12	A	
Gear type	LL	6.132	465	A	
	G	6.063	344	A	
	GSM	4.618	4	A	
	VG	4.213	118	A	
	CD	3.829	13	A	
	D	1.747	15	A	
	HL	1.469	21	A	
Month	1	5.184	84	A	B
	2	6.274	71	A	
	3	5.514	126	A	
	4	6.451	186	A	
	5	4.459	107	A	B
	6	4.107	64	A	B
	7	2.699	69		B
	8	3.887	69	A	B
	9	6.457	52	A	
	10	4.930	59	A	B
	11	4.864	55	A	B
	12	3.954	38		B
Market	Md	6.834	252	A	
	M2	4.793	67	A	
	Ur	4.543	652	A	
	E	0.963	9		B

Approximately 78% of catches in the region occurred in lakes, 20% in rivers and only 2% in other environments such as creeks or flooded forests (Fig. 6). Mean catch-per-trip and catch per fishermen per day values were not significantly different ($P > 0.05$) in lakes and rivers (Table 3).

GLM indicated seasonality was the most important factor affecting yield variability. The

Table 3. Results of Duncan's multiple range test for the logarithm of the catch trip^{-1} (kg) of tambaqui (*Colossoma macropomum*) of the Lower Amazon. Different letters identify significant differences. See abbreviations in Table 1.

Variable categories		Means	N	Duncan's grouping			
Vessel type	Buy	2.045	12	A			
	Mix	1.952	20	A			
	FBo	1.885	628	A			
	MC	1.692	15		B		
	CF	1.520	29		B		
	C	1.240	276			C	
Distance	2	2.099	99	A			
	3	1.709	9		B		
	1	1.646	872		B		
Period	B	1.758	401	A			
	D	1.722	492	A			
	N	1.222	87		B		
Environment	L	1.703	774	A			
	R	1.695	183	A			
	C	1.384	12		B		
	FF	1.251	11		B		
Gear type	G	1.934	465	A			
	VG	1.521	344		B		
	HL	1.489	4		B	C	
	GSM	1.441	118		B	C	
	D	1.412	13		B	C	
	LL	1.256	15			C	D
	C	1.105	21				D
Month	1	1.758	84		B	C	
	2	1.849	71	A	B		
	3	1.749	126		B	C	
	4	1.822	186	A	B		
	5	1.489	107				D
	6	1.516	64				D
	7	1.420	69				D
	8	1.649	69			C	
	9	1.681	52			C	
	10	1.753	59		B	C	
	11	1.906	55	A			
	12	1.491	38				D
Market	Md	2.161	252	A			
	M2	1.751	67		B		
	E	1.619	9		B	C	
	Ur	1.506	652			C	

month in which the catch took place explained 24% of the variability in the data; the market where the catch was landed accounted for 20%; quantity of ice carried on board contributed for 13%, as did the vessel type involved in the catch. The global model presented a r^2 value of 62%, and all variables were significant at 5%, with the exception of gear type and duration of the trip (Table 4).

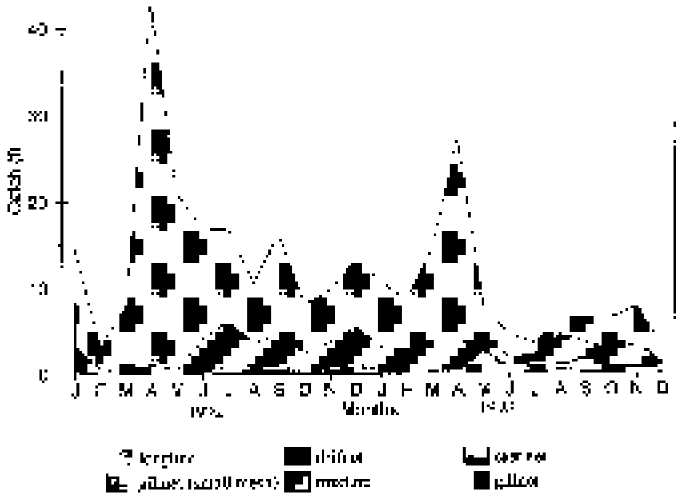

Figure 5. Catches of tambaqui (*Colossoma macropomum)* in the Lower Amazon by gear type landed in Santarém, during 1992–1993.

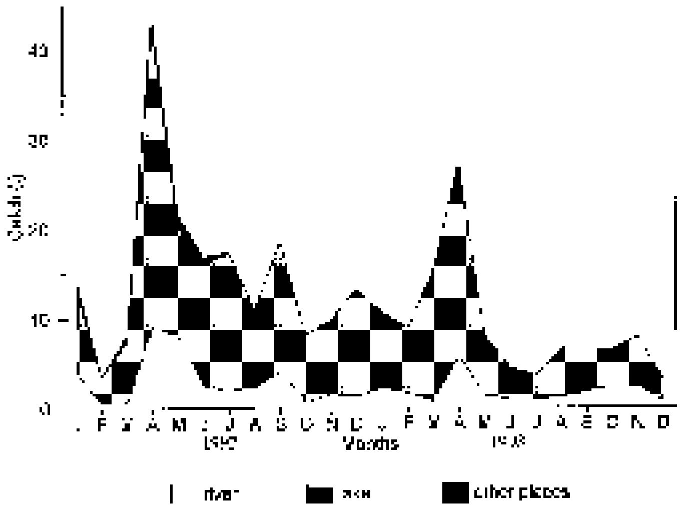

Figure 6. Catches of tambaqui (*Colossoma macropomum)* in the Lower Amazon by environment landed in Santarém, during 1992–1993.

The incoming catch was immediately sold to local markets, retailers and, in lesser quantities, to ice plants. Average monthly prices of tambaqui for first sale varied between US$ 0.50 and US$ 1.00 kg^{-1} for the 1992–1993 period. On a month-by-month comparison, prices in 1992 were slightly lower than corresponding ones in the following year. Record values were attained in April 1993, at Easter, when fish consumption always increases considerably.

Table 4. Relative contribution of each variable in the variance of the ANOVA model, *F* values and significance. df = degrees of freedom.

Variable	df	Type III SS (%)	*F* Value	Significance
Ice	1	13.50	39.85	0.0001
Fuel	1	4.03	11.91	0.0006
Days	1	0.46	1.35	0.2456
Fishermen	1	6.08	17.96	0.0001
Vessel type	5	13.24	7.82	0.0001
Period	2	3.12	4.6	0.0464
Environment	3	0.30	0.3	0.0103
Gear type	6	15.11	7.43	0.8255
Month	11	24.14	6.48	0.0001
Market	3	20.02	19.71	0.0001

Weight-length relationship

The relationship between weight and length of tambaqui for 1992 and 1993 is given by:

$$W = 0.028\ L^{2.92}$$

The correlation coefficient (r) was 0.994 for 1191 data points, with $L_{min} = 9$ and $L_{max} = 104$ cm, respectively. The value of the exponent was not significantly different from 3.0.

As for the condition factor, large changes in fat content can be detected indirectly. The highest monthly averages were in September and March (0.04) and the lowest in the November to January period (0.02).

Growth in length

Monthly length data samples were large and considered representative of the population. Tambaqui recruit to the fishery at a length of ≈20 cm. Larger fish of up to 100 cm were not frequently caught. Mean length for all data was 40.89 cm, with a standard deviation of 13.26 cm. Monthly length frequency distributions showed a polymodal pattern (Fig. 7). Monthly mean lengths were low in most cases, being higher in June and July and at a minimum in November (Fig. 8). The mean length of fish caught in lakes was significantly lower ($P < 0.05$) than that of specimens captured in rivers.

The parameters that describe the growth in length of tambaqui were more or less constant in the two years studied. Preliminary estimates of L_∞ obtained through Wetherall's method yielded 116 cm in 1992 and 118 cm in 1993. The values of L_∞ and K obtained via ELEFAN were 121.2 cm and 0.229 year^{-1} for 1992; 118.5 cm and 0.226 year^{-1} for 1993. Consequently, based on the length/weight relationship, W_∞ for each year was, respectively, 34.5 and 32.3 kg. The values of oscillation parameter, $C = 0.51$ and Winter Point, $WP = 0.58$ year for 1992; and $C = 0.50$ and $WP = 0.52$ year for 1993 indicate that the growth of tambaqui oscillated seasonally in a sinusoidal fashion, and that growth rates were about 50% lower by the end of July, when the water level was falling. Conversely, growth rates were higher at the beginning of the year, in the high water months. Estimates of growth performance index $\varnothing'$ resulted in 3.52 and 3.50, respectively (Table 5).

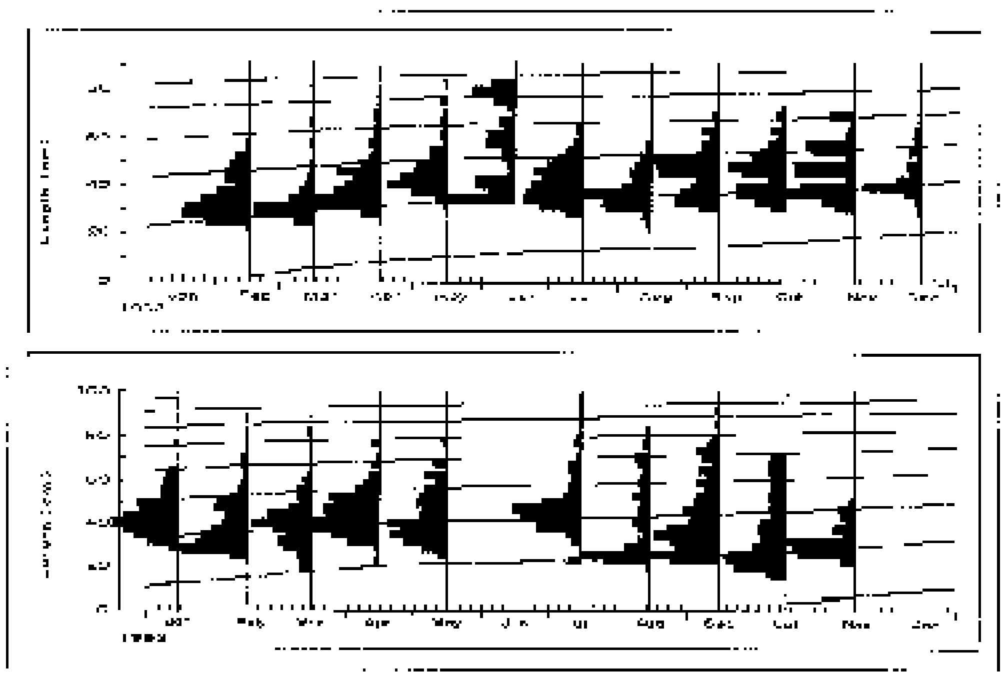

Figure 7. Length frequency data and estimated growth curves of tambaqui (*Colossoma macropomum*) of the Lower Amazon for 1992–1993.

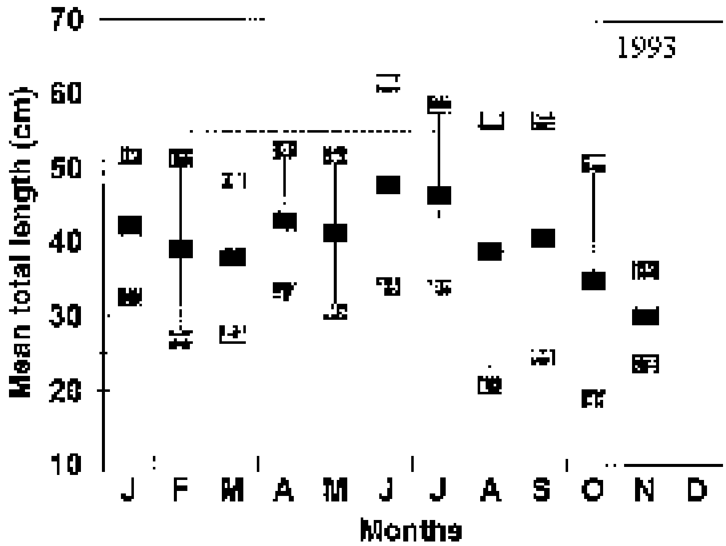

Figure 8. Monthly mean lengths of tambaqui (*Colossoma macropomum*) in the Lower Amazon landed in Santarém, during 1993. (— = length at first maturity)

Figure 7 shows growth curves, estimated from the ELEFAN, superimposed on length-frequency data. The results suggest that *C. macropomum* lives at least 13 years. Figure 7 also indicates that the fishery operated on at least 7 cohorts of the population. Table 6 shows the

Table 5. Parameters of population dynamics of tambaqui (*Colossoma macropomum*) of the Lower Amazon.

Parameters	1992	1993	1977–1978 (Petrere 1983)
K (year^{-1})	0.229	0.226	0.227
L_∞ (cm)	121.20	118.50	107.2
W_∞ (kg)	34.50	32.30	32.00
C	0.510	0.500	–
WP (year^{-1})	0.580	0.520	–
Rn	0.163	0.141	–
$\varnothing'$	3.52	3.50	3.42
M (year^{-1})	0.45	0.44	0.45
Z (year^{-1})	1.40	1.37	0.725
F (year^{-1})	0.95	0.93	0.275
E	0.68	0.68	0.38
L_c (cm)	28.50	28.07	55.00

Table 6. Length-at-age key for tambaqui (*Colossoma macropomum*) of the Lower Amazon, estimated via mean parameters and Bertalanffy's seasonal growth model. Input parameters: $L_\infty = 119.85$, $K = 0.2275$, $C = 0.5050$, $WP = 0.5500$, $t_0 = 0.0000$.

Relative age (year)	Mean length (cm)
0.5	13.49
1.0	23.84
1.5	35.13
2.0	43.38
2.5	52.37
3.0	58.94
3.5	66.10
4.0	71.33
4.5	77.04
5.0	81.21
5.5	85.75
6.0	89.07
6.5	92.68
7.0	95.33
7.5	98.21
8.0	100.32
8.5	102.62
9.0	104.29

length/age relationship estimated from Bertalanffy's model using average parameters (1992–1993) and assuming $t_0 = 0$. Mean lengths correspond to relative age, since the actual value of t_0, and therefore the actual age, could not be calculated based on length data only.

Table 7. Input parameters and estimates of total mortality (Z) to tambaqui (*Colossoma macropomum*) of the Lower Amazon.

Year Sample	Input parameters	Method	Z
1992	L = 45.22 cm and L' = 32.50 cm		
		Mean length	1.37
		Catch curve	1.44
		mean	1.40
1993	L = 53.06 cm and L' = 41.50 cm		
		Mean length	1.28
		Catch curve	1.46
		mean	1.37

Mortality rates

Using mean lengths for the estimation of total mortality of *C. macropomum*, $Z = 1.37$ year^{-1} for 1992 and $Z = 1.28$ year^{-1} for 1993 were obtained. The length-converted catch curves yielded $Z = 1.44$ year^{-1} for 1992 and $Z = 1.46$ year^{-1} for 1993 (Table 7).

Estimates of the natural mortality (M) for 1992 and 1993 were 0.45 year^{-1} and 0.44 year^{-1}, respectively, for a water temperature of 26°C. Therefore, fishing mortality (F) was 0.95 year^{-1} in 1992 and 0.93 year $^{-1}$ in 1993, and the exploitation rate $E = 0.68$ year^{-1} for both years (Table 5).

The mean length (L_c) at which 50% of the fish encountered by the gears are retained was estimated as 28.5 cm for 1992 and 28.1 cm for 1993 (Table 5).

Yield-per-recruit

The yield-per-recruit model provided an indication of the actual yield from the fishery in relation to the potential maximum sustainable yield, given a constant rate of recruitment. Figure 9 shows the relative yield curves obtained from mean population parameters for 1992 and 1993. The Y'/R value corresponding to the current rate of fishing mortality ($F = 0.94$ year^{-1} and $E = 0.68$) and the length at first capture ($L_c = 28$ cm) are indicated in the graph. The yield in such conditions is very low and increased overfishing must be occurring, as fishing pressure exceeds F_{MSY}. Thus, the fish are being caught before they can grow large enough to substantially contribute to the stock biomass. The model predicted that an increase in the length at first capture – for instance, to 55 or 65 cm – will lead, after reaching equilibrium, to an increased yield-per-recruit, even under the same fishing effort and exploitation rate. That would prevent overfishing and should result in a yield very close to the maximum sustainable yield for such L_c.

Discussion

Some hypotheses on the tambaqui life cycle indicate that immature *C. macropomum* are confined to lakes and floodplains, while adults stay in floodplains or flooded forest for only 4

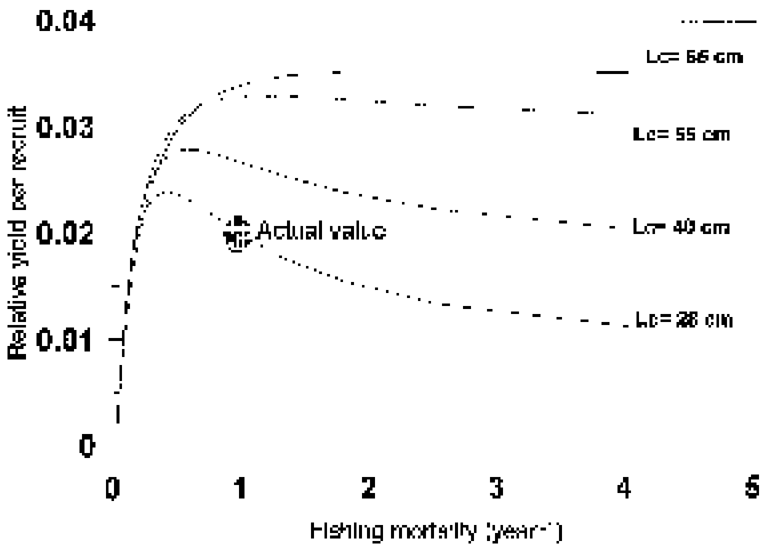

Figure 9. Yield-per-recruit curves of tambaqui (*Colossoma macropomum*) of the Lower Amazon according to fishing mortality and length at first capture.

to 7 months a year (Goulding & Carvalho 1982). During the low water season, the adults leave the lakes and enter the main river channels, moving upstream and searching for woody shore areas and other sites, until their gonads are completely mature (Goulding & Carvalho 1982). This occurs close to the first rains at the end of the year (Isaac, Rocha & Mota, in press), and according to local fishermen tambaqui cross the main channels in search of an adequate site to spawn, probably places with good water flow. Length at first maturity is supposed to be about 50–55 cm (Goulding & Carvalho 1982; Isaac *et al.* in press).

With the rise of the water level in the main channel of the river, eggs and larvae should be transported into the floodplains, i.e. into the nursery areas, while the adults swim back to the lakes or flooded forest (Carvalho 1981). In the high water season the terrestrial vegetation is flooded, increasing refuge and feeding habitats; tambaquis remain in these areas feeding on fruits and seeds and growing until the water level begins to fall again (Honda 1974; Carvalho 1981).

The fishery in the Amazon is strongly seasonal. The dry season is generally more productive because the fish are migrating, and concentrated in the main channel, providing relatively good catches. However, contrary to expectations, in the Lower Amazon tambaqui production by weight and CPUE were highest when the water level was high, in the rainy season. When flooding starts, the fishermen tend to spend more time on lakes, as the central channel of the river becomes more dangerous for fishing. The contribution of these two factors – fish movements, and the fishermen's strategy – explains the seasonal variability of the production. These results agree with the findings of Payne (1987), for the species in the Mamoré river, Bolivia.

The local fishery is artisanal, based on small-scale or subsistence fishermen, who operate in small boats of low fishing power. Many fishermen work in the remaining lakes even during the low water season, catching juvenile tambaqui that live in these habitats throughout the year. Predominance of capture in lake environments and with gillnets (probably with finer mesh) explains the small mean sizes found in the catches landed in Santarém.

Many tropical fish are fast-growing, short-lived species (Lowe-McConnell 1987). Nevertheless, *C. macropomum* appears to be a relatively slow-growing species, able to live up to 13 years. Growth parameters estimated by Payne (1987), for this species in the Mamoré river were lower than those calculated in the present study, although that author only studied a single sample. According to Payne, in the Mamoré river, scales of *C. macropomum* of 80 cm had seven annuli, which means the specimen was 8 years old assuming an annulus is formed each year. That result is at variance with the present study (Table 6). On the other hand, the estimates, either of L_∞ and K or 'a' and 'b' from the weight-length relationship, obtained by Petrere (1983) in the Manaus region were very similar to the present data (Table 6).

Abundant food supply should promote maximum growth in the flood period (Daget & Ecoutin 1976). Junk (1985), reported that several Amazon species, all of them migrant characoids, store fat during the flood as energy reserves for migration and gonadal maturation. Castelo, Amaya & Strong III (1980) reported that visceral fat content accounted for 10% of the total weight of the fish, after the rainy season. This study revealed slower growth rates when the water level began to fall, and faster growth during the flood season, which confirmed seasonality of growth.

Natural mortality is positively correlated with growth rates, so it was also low (M = 0.45 year^{-1}). Fishing mortality (F = 0.94 year^{-1}) seemed to be high, and inappropriate to the life history strategy of the species. This was reflected in the results of the Beverton & Holt (1956), yield-per-recruit model, which indicated tambaqui stocks are being overfished.

It has been suggested that the Beverton & Holt model is not suitable for managing a tropical multispecies fishery where complex interactions among species are largely unknown (Pauly 1979). However, according to Petrere (1983), *C. macropomum*, being an omnivorous fish that tends to a more herbivorous diet as it increases in size (Honda 1974), is independent of other fish species. Also, its relatively large size makes it subject only to limited natural predation. Therefore, such interaction may be infrequent, and the yield-per-recruit analysis can be considered in this respect suitable for the tambaqui fishery. On the other hand, it can be argued that the classical stock assessment models are inadequate for floodplain fish stocks, in which abundance, growth and mortality rates depend very much upon the hydrological regime. More detailed knowledge of within-year changes is necessary to apply alternative models, based on the assumption of rapid growth, low mortality during the flood, and low growth, high mortality during the dry season. Year-to-year recruitment variations may modify absolute yield but probably do not invalidate the 'average expectation' (Beverton 1983).

Yield-per-recruit analysis of tambaqui for 1976–1978 showed that the stock was then still underexploited, although the fishing fleet of Manaus was travelling further to catch the larger fish because of local depletion of stocks in lakes near that city (Petrere 1983). The author used a L_c = 55 cm because in those years the commercial fishermen did not yet catch smaller tambaqui. Nowadays, tambaqui juveniles are frequently sold in the Manaus market (Barthem, personal communication). Merona & Bittencourt (1988), fitting a 10-year dataset from landings in Manaus to the Schaeffer model, concluded that tambaqui was overfished in 1985 and 1986. Since 1980, small-sized fish species (r-strategists) like jaraqui (*Semaprochilodus* spp.) displaced the tambaqui off the first rank of the landings (Merona 1993).

The present study concluded that current values of exploitation rate and fishery mortality in the Lower Amazon are excessive and above the maximum sustainable yield. Similarly, length at first capture is very small, leading to low production. Optimum fishing mortality, to prevent overexploitation, should be 0.4 $year^{-1}$. A reduction of fishing effort in an artisanal and subsistence multispecific fishery is practically impossible. However, an increase in length at first capture could be implemented by an increase of mesh size or discarding the still-live juveniles. According to the Y'/R model, for the same level of recruitment, an increase in length at first capture will lead to an important yield magnification after attaining a new equilibrium.

The acceptance of the capture of small fish damages the reproductive potential of the species, reduces the spawning stock, and minimizes the fishermen's productivity, and profit. In addition, *C. macropomum* is a much appreciated fish for human consumption, and has an important function in the dispersion of seeds, and in the cycle of some vegetables (Goulding & Carvalho 1982). Bayley (1981) believed that, in a multigear and multispecies fishery, a depression of stocks of large and appreciated species is inevitable. Larger species are depressed but a larger diversity of smaller species of lower value can be used for consumption by lower socio-economic groups.

The enforcement of a size limit is also questionable in such a fishery. Despite *C. macropomum* being caught together with other species and with various gears, evidence is that good fishermen may combine the kind of mesh, the place and the period of their fishing, to select the desired species and sizes. Educational programmes to control size limit would contribute at least to the maximization of the fishermen's profit and protect young fishes. The tendency of modern managers should be to preserve the *status quo* in the short term. In the longer term it might be desirable to diversify the fishery to foster maintenance of a more stable species composition in the ecosystem. Probably the more practical method, which might arrest over-exploitation of large species and contribute to the protection of the fishery as a whole, would be the periodic prohibition of fishing from certain areas, e.g. those recently implemented through the 'lake reserves' by the riparian human population.

To improve the efficiency of current regulations and guarantee the sustainable exploitation of the tambaqui, it is recommended that:

- the length at first capture be increased, at least to 55 cm total length, persuading the fishermen to use nets with larger mesh, to avoid the habitats of juveniles, and to discard live juveniles in the catch;
- environmental education instruments such as posters, films, folders, TV and radio programmes be made available to explain the scientific results for both the fishermen and the lay people, as is currently being done by Project IARA;
- protection of spawning sites, and migration patterns be implemented;
- the fishery statistics database be continued and expanded so as to provide grounds for an adequate stock assessment for the whole Amazon Basin;
- the effects of 'lake reserves' be monitored as a management strategy.

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