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The effects of flood regime and fishing effort on the overall abundance of an exploited fish community in the Amazon floodplain

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Abstract

Freshwater fishing is highly developed in the Amazonian basin, and the problems of managing the fish resource are becoming increasingly acute. The global model of exploited stock dynamics has proved inadequate for explaining the variations observed in catches from one year to the next. Following the results of recent studies in maritime fishing, this work aims to identify the contribution of environmental variables (hydrological parameters have been selected) to the explanation of variations in the abundance of the exploited fish community. An abundance index is calculated based on the catch per unit of effort statistics and the surface of the considered basin. Using a 12-year time series, the results show that the effect of the fishing effort on the index of abundance is negligible when viewed alongside the flood regime parameters for the years prior to the catch. The effects revealed are, in chronological order of appearance: 1) a positive effect of the water level during the flood regime peak three years previous to the catch, probably associated with recruitment for a number of species; 2) the effect of the water level during its rise two years before the catch, which may well be related to competition phenomena; and 3) the effect of severe low-water levels two years before the catch, possibly due to mass natural mortality during the severest periods of low-water. Because there are complex migratory movements of fish populations either side of low-water periods, only the estimated biomass during the flood appears to be an accurate reflection of the mean biomass in the environment. Linear models are presented, where the abundance index is a function of the hydrological parameters previously identified. The model with 3 variables corresponding to the 3 evidenced effects, explains more than 83% of the variations in the annual abundance indices.

Keywords: Amazon, floodplain, fish community, fishing, fish biomass, hydrological parameters, models.

Effets du régime hydrologique et de l'effort de pêche sur l'abondance globale d'une communauté exploïtée de poissons dans la plaine inondée amazonienne.

Résumé

La pêche en eaux douces est particulièrement développée dans le bassin amazonien et les problèmes d'aménagement de la ressource piscicole deviennent de plus en plus aigus. Le modèle global de dynamique des stocks exploités s'est avéré inadapté pour expliquer les variations interannuelles de la capture. Suivant les résultats d'études récentes en pêche maritime, ce travail se propose de mettre en évidence une contribution de variables environnementales (en l'occurrence des paramètres hydrologiques) pour expliquer les variations d'abondance d'une communauté exploitée de poissons. Un indice d'abondance est calculé à partir des statistiques de prises par unité d'effort de pêche et de la superficie du bassin considéré. Les résultats montrent que l'effet de l'effort de pêche sur l'indice d'abondance est négligeable comparé à celui des paramètres de crue au cours des années antérieures. Les effets observés sont par ordre chronologique: 1) un effet positif de la hauteur d'eau pendant le maximum de la crue 3 ans avant la capture, probablement associé au recrutement de la plupart des espèces, 2) un effet de la hauteur d'eau pendant la montée d'eau 2 ans avant la capture qui pourrait être attribué à des phénomènes de compétition et 3) un effet de la hauteur d'eau en étiage 2 ans avant la capture, dû vraisemblablement aux mortalités en masse de poissons pendant les étiages sévères. Les mouvements migratoires complexes de certaines populations de poissons dans les périodes entourant l'étiage font que seuls les indices de biomasse estimés à partir des données de crue semblent refléter la biomasse moyenne dans le milieu. Des modèles linéaires, exprimant l'indice d'abondance en fonction des paramètres hydrologiques précédemment identifiés, sont proposés. Le modèle comportant 3 variables qui correspondent aux 3 effets observés, permet d'expliquer plus de 83 % de la variabilité des indices d'abondance annuels.

Mots-clés : Amazone, plaine inondée, communautés de poissons, pêche, biomasse, paramètres hydrologiques, modèles.

INTRODUCTION

Over the past twenty years fishing in the fresh waters of the Amazon basin has been highly developed: the catch for the whole basin is estimated at nearly 200,000 t per year (Bayley and Petrere, 1989). Problems concerning the management of the fish resource are therefore becoming more and more acute. The first studies on fishing in the region concentrated on the market in Manaus, the main landing point in the Western Amazon of Brazil, with a volume of landings of approximately 30,000 t per year (Petrere, 1978 *b*; 1982). These studies highlighted the complexity of the fishing sector, within which various fisheries could be identified. Amongst these was one which was preponderant in terms of commercial catches: a multispecies, multigear fishery, developed in the Amazon floodplain (Mérona and Bittencourt, 1993 *a*). For this fishery, large variations were observed between yearly catches but authors' attempts to fit these to the global model of exploited stock dynamics (Schaefer, 1954) were unsuccessful. This type of model, based on a hypothesis of equilibrium, supposes that mortality rates from fishing (measured by the fishing effort) is the only, or at least the main, factor in variations in abundance. In a certain number of cases this hypothesis has been shown to be lacking, and a number of authors have suggested taking into account environmental variables which may contribute to the abundance of stocks (Boudreault *et al.*, 1977; Sutcliffe *et al.*, 1977; Summers and Rose, 1987; Fréon, 1983 and 1986; Cury and Roy, 1987). These studies concerned marine fisheries, with the most pertinent environmental variable being the water temperature. In the fluvial context, the flood regime, the periodic variation in water level or flow, is considered to be an essential environmental parameter (Junk *et al.*, 1989). Fluctuations in commercial fishery catches have been linked to successive variations in the range of floodwater levels over previous years (Anonymous, 1971 *a*, *b*; Welcomme, 1979 and 1986; Novoa, 1989; Quiroz and Cuch, 1989). As Welcomme (1979) underlined, a large part of the fluctuations observed in fishing catches could be due to variations in fishing efforts, even if the abundance remained constant. The use of an abundance index, which is more representative of the real biomass of fish in the environment, would offer a clearer interpretation of variations in fishing catches.

In this case study, we analyze a series of 12 years of landing data including information on fishing effort. Its purpose, based on an abundance index that we define and discuss below, is to highlight yearly variations in abundance, and then to test two non-exclusive hypotheses; 1) abundance is dependent on the fishing effort and 2) abundance is dependent on the hydrological conditions of previous years. In the latter hypothesis we attempt to establish which phase of the hydrological cycle is decisive for abundance.

The environment

After descending from the Andes mountains, the Amazon river covers some 5,000 km which separate it from the Atlantic Ocean over a vast low-lying depression (with a slope of 15 mm/km for the last 1,500 km), thus forming around its bed a huge floodplain with an area of more than 180,000 km^2 (Bayley and Petrere, 1989). The "*Lago do Rei*" is a lake on this floodplain inside a sedimentary island (Careiro Island), located a few kilometres downstream from the town of Manaus, at the level of the confluence of the Amazon with the Rio Negro (*fig.* 1). The lake is a shallow, flare-shaped basin with a surface area of approximately 100 km^2 at "normal" flood, and a depth no greater than 10 m. It is connected with the river by a channel (the "*Parana do Rei*") which is open all year round, thus implying a close correlation between the water level of the Amazon river itself and that of the lake.

One of the most marked characteristics of the Amazon basin floodplain system is the seasonal alternance of flood, or high-water stage, and low-water stage, that we measure here by the height of water in the river. The data were supplied courtesy of the National Department for Natural Resources and Energy

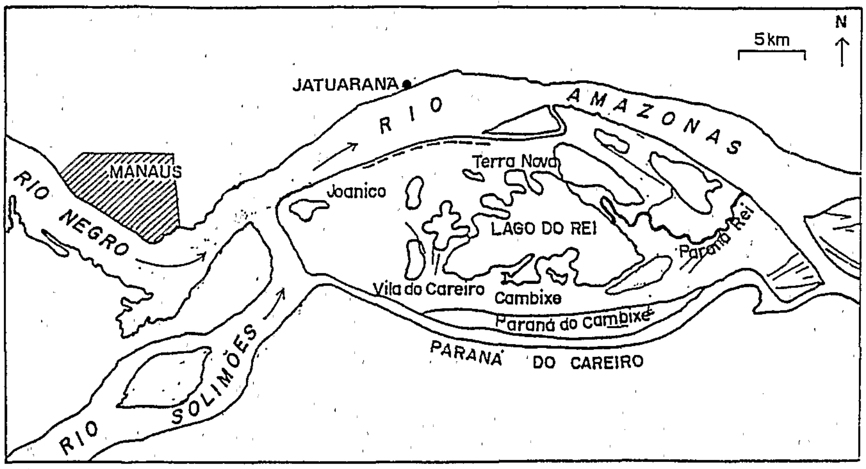

Figure 1. – Definition of area under study.

(DNAEE). We have chosen the data of the limnimetric station nearest to the area of study: that of Jatuarana, exactly opposite Careiro Island, on the north bank of the Amazon (*fig.* 1). The scale is not calibrated for altitude, and water heights are therefore relative. Observations at this station started in 1977. For the preceding years, data have been recreated based on a series of water levels recorded in the port of Manaus, a data series which has been in existence since the start of the century. Although Manaus is located on the bank of a different river, its proximity with the confluence and the dam effect exerted by the Amazon on its tributary, result in a highly significant correlation existing between the two series of monthly averages as well for the raw data ($r=0.999$ for $n=124$) as for the moving averages after removing the seasonal effect ($r=0.999$ for $n=112$).

The water level of the Amazon river varies considerably between the high-water maximum which occurs at the end of June and the low-water minimum which varies from year to year between the months of September and December. The maximum range in water levels is nearly 12 m.

The flood regime varies from one year to the next (*fig.* 2). In the period of 1970-1988 considered in this study, the difference between the highest and lowest high-water levels was 3.7 m, while the difference between the most severe and least severe low-water levels was 4.7 m. The time-scales for the durations of the flood and low-water stages also varied considerably.

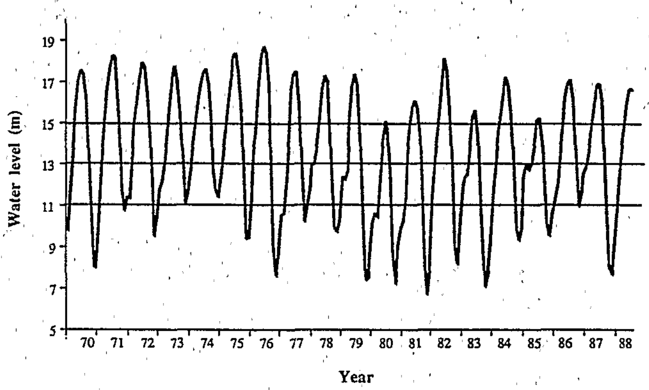

Figure 2. – Variations in monthly average height of water at Jatuarana limnimetric station on the Amazon river between January 1970 and June 1988.

Fishery

The "*Lago do Rei*" fishery has been described in detail by Mérona and Bittencourt (1993 *a*). The data are provided by a landing data collect system on the Manaus market, set up and described by Petrere (1978 *b*). Two commercial fisheries were identified: one operating out of the channel at the outlet of the lake and concentrating on migratory fish at the time of their migration; the other fishery operating on the lake itself. The annual catches for these two fisheries have developed along parallel lines. In this study we concentrate on the lake-based fishery, for which the relationship between fishing effort and catch is more clearly linked to the density of fish.

The catches are multispecies (*fig.* 3). The landing data identify 25 commercialized products corresponding to approximately 40 species of fish. Seven main species represent 94% of the catches for the period 1976-1988. Two of them are migratory species: the Curimata (*Prochilodus nigricans*), an iliophageous fish of medium size (standard length: 40 cm) which is found at every stage of its life cycle, and the Tambaqui (*Colossoma macropomum*), a large fruit-eater which can reach 30 or 40 kg in weight, and which is only captured in the "*Lago do Rei*" during its juvenile stage (1 to 3 kg). The other products correspond to species which are known to be sedentary. The Tucanaré (mainly *Cichla monoculus*) is a fish-eating cichlid;

the Acaras (above all *Astronotus ocellatus*) are other micro-predatory Cichlidae; the Aruana (*Osteoglossum biccirhosum*) is an omnivore; the Pescadas (*Plagioscion squamosissimus* and *P. montei*) are shrimp predators and the Cuiu (*Pseudodoras niger*) is a large omnivorous Doradidae.

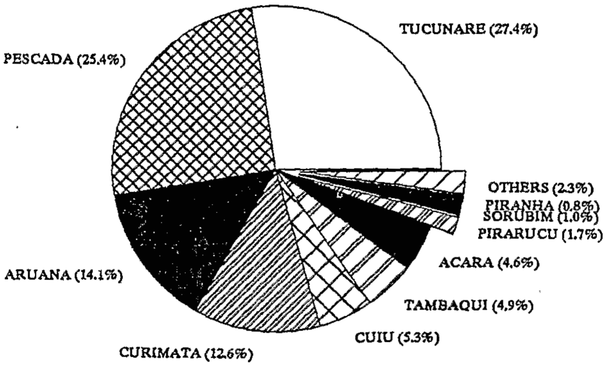

Figure 3. – Specific composition of landings from "*Lago do Rei*" on the Manaus market in the 1976-1987 period.

Fishing techniques vary greatly and are tailored to fit seasonal fishing conditions. Gill nets are mainly used during low-water periods, either singly or combined with fishing rods or hand lines. During periods of high-water, long lines and tridents are used.

Total landings, fishing efforts and catch per unit effort (CPUE) per year varied considerably from one year to the next (*fig.* 4). There was a tendency for the volume of landings to decrease, with a noteworthy peak in 1979. Fishing efforts went through two distinct phases, the first up to 1981 when values were high (average = 15,317 fisherman.day), and the other from 1982 to 1988 when values were low (average = 4,709 fisherman.day). The CPUEs showed no distinct tendency and there was no relationship between effort and CPUE.

The same group of 5 products constituted most of the landings throughout the period under study. There was, however, a distinct modification in the proportion of two species from 1984 onwards, when the Curimata species replaced the Pescada in the landings.

METHODS

Definition and estimate of the abundance index

The unit of fishing effort used was the fisherman.day, *i.e.* the number of days spent fishing multiplied by the number of fishermen participating (Petrere, 1978 *a*). The unit has the advantage of being usable for all types of fishing techniques. On the other hand, as there were no drastic changes in fishing techniques and practices during the period considered, this unity leads to a measure of fishing effort close to the real impact on the stocks (effective effort: Laurec and Le Guen, 1981).

The year was defined based on hydrological criteria. Over the series of average monthly water levels from 1970 to 1987, the average was 13.42 m (minimum 6.7 m and maximum 18.7 m). We arbitrarily fixed the limits defining periods of high-water and low-water stages at $13+2=15$ m and $13-2=11$ m respectively, where the level of 11 m during the rise in water level corresponded to the start of the hydrological year (*fig.* 5). We thus obtained four periods, whose duration varies from year to year, defined as follows:

– the rise from 11 to 15 m,
– the peak in high-water above 15 m,
– the drop from 15 to 11 m
– the low-water stage under 11 m.

An abundance index was defined based on the relationship:

$$C=f.q'.D=f.q'.B/A \quad \text{(Gulland, 1969)}$$

where C: catch in tons; f: effort in fishermen.days; q': constant; D: weight density per surface unit; B: absolute biomass; A: area of the system.

From these basic relationships we define an abundance index, proportional to the biomass of the stock as:

$$I=q'.B=A.C/f$$

The coefficient q' is linked to the catchability q by the relation $q'=q$. A (Laurec and Le Guen 1981). Therefore, in calculating the biomass index, we make the hypothesis of an inverse relationship between catchability and area.

The calculation of the abundance index demands an estimation of the surface area of the lake. The lake could be considered as a sector of a sphere whose height is very small compared with the radius of the sphere (Anonymous, 1988). In that way, the average area A of the lake during the period under consideration is approximately proportional to the corresponding average depth of the lake. As the lake is in constant communication with the river, its depth can be considered directly proportional to the water level in the river. Therefore the corrected water levels in Jatuarana ([1]) were used to calculate the index. The indices are calculated each year, from 1976 to 1987 for each of the hydrological periods.

The correlation matrix between the abundance indices for each period showed significant correlations

([1]) A measure made in April 1987 (Nunes de Mello, pers. comm.) gave a maximum depth equal to the water level in Jatuarana minus 5.72 m.

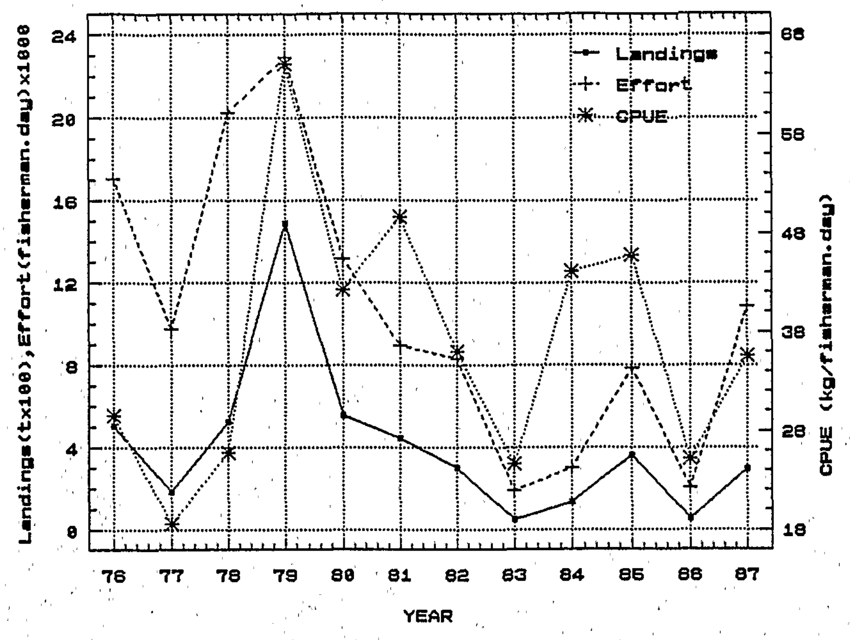

Figure 4. – Inter-annual variations in total landings (t × 100), fishing effort (fisherman.day) × 1 000 and catches per unit of effort for lacustrine fishing on the "*Lago do Rei*" between 1976 and 1987.

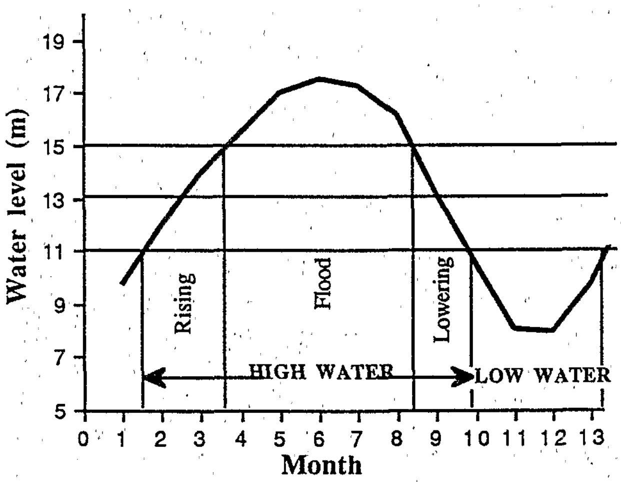

Figure 5. – Breakdown of hydrological cycle and definition of periods.

Table 1. – Correlation matrix between the abundance indices for the different phases of the hydrological cycle. The first number is the correlation coefficient, between parentheses the number of pairs; the number in italics is the corresponding probability.

		Lowering	Low-water
Rising	0.739 3 (12)	0.639 (10)	0.390 6 (12)
	0.006 0	*0.046 6*	*0.209 4*
Peak		0.860 2 (10)	0.318 6 (12)
		0.001 4	*0.312 9*
Lowering			0.430 2 (10)
			0.214 6

between the indices for the periods of rising water, floodwater and lowering water (*table* 1, $p<0.05$). On the other hand, the low-water indices clearly stood out from the rest ($p>0.1$). We therefore divided the hydrological year into two phases: one including the rise in water, the high-water peak, and the drop in water level until it returns to the 11 m mark, which we term High water, and the other when the water level is lower than 11 m which we term Low water. We thus had two apparent abundance indices per year (appendix 1). There was no significant autocorrelation in the two series of abundance indices.

Statistical analysis

The water level data used were the monthly averages of daily values between 1970 and 1987. Only two series (September and October) showed significant autocorrelations with a lag of one year. The analysis of the relations between the abundance indices and the hydrological parameters or fishing effort was pursued in two steps. The first one was a bivariate analysis of the correlation coefficients between the abundance indices (dependent variable) and the annual fishing effort or hydrological parameters (independent variable). The values for the two abundance indices were firstly correlated with the monthly average water levels for the year corresponding to the catch, thus providing 12 correlation coefficients. The operation was then repeated with the monthly average water levels for the years preceding the catch with lags from 1 to 5 years. We calculated two correlation matrices: one for linear correlations and the other for exponential correlations. This process enabled us to define a limited number of environmental variables corresponding to the average water level for that month and the lag at which the correlation was maximum. These variables are noted using three letters to define the month and a number to define the lag (e. g.: Jan1 = average water height in January of the year preceding the catch).

The next step consisted in fitting linear models to the original data using a multiple regression procedure. Two series of models were tested:

$$I = a + a_0 . f + \Sigma a_i . env_i + e \qquad a_0 < 0 \qquad (1)$$

$$I = e^{a + a_0 . f + \Sigma a_i . env_i} + e \qquad a_0 < 0 \qquad (2)$$

where I: abundance index, a, a_0, a_i: model coefficients. The a_0 coefficient is limited to negative values which are the only meaningful values to test a dependence of abundance on fishing effort. Positive values lead to exclusion of the term $a_0 f$ from the model.

f: fishing effort in fisherman . day,

env_i: environmental variable.

These models corresponded to the introduction of an environmental component into the conventional models of stock dynamics (Cury and Roy, 1987).

They were adjusted by means of multiple regression. The variables were introduced in order of decreasing significance. The procedure and all the statistical treatments are pursued by the "Statgraphics" software.

RESULTS

Bivariate analysis: abundance index, monthly water level or fishing effort relationships

The highest correlations were obtained from the linear correlation for the high-water index and from the exponential correlation for the low-water index. The variations in the correlation coefficient between the indices and monthly water levels suggested several possible influences on abundance (*fig.* 6, *table* 2).

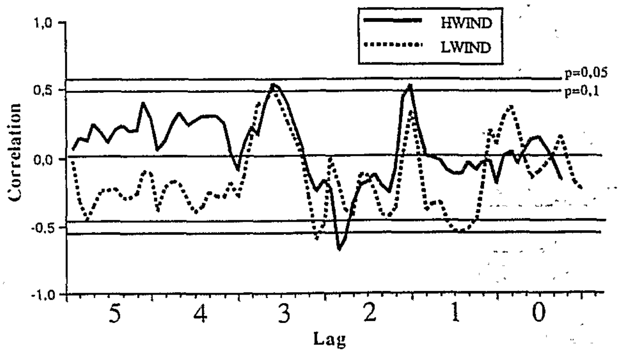

Figure 6. – Variation in the value of the coefficient of correlation between high- and low-water abundance indices (respectively HWind and LWind) and monthly average heights of water.

Table 2. – Correlations between high-water (HWind) and lower-water (LWind) abundance indices and selected variables. The correlations are linear for Hwind and exponential for LWind. Effort = fishing effort of the current year; Effort01 = sum of fishing efforts of the current and the previous year; other variable names are the first three letters of the month and the lag in years. Between parentheses the probabilities of the correlations.

	HWind	LWind
Effort	+0.5199 (*0.0832*)	+0.1959 (*0.5417*)
Effort01	+0.5516 (*0.0785*)	−0.0067 (*0.9843*)
May3	+0.5641 (*0.0561*)	+0.5238 (*0.0805*)
Nov3		−0.6096 (*0.0353*)
Feb2	−0.6903 (*0.0129*)	
Dec2	+0.5237 (*0.0806*)	
Jul1		−0.5148 (*0.0868*)

For the high-*water index*.

– The level of water in May and in June at a lag of 3 years has a positive effect on the index. The period corresponds to the end of the rise in water and the maximum high-water period, *i. e.* this parameters is related to the extent of the flood.

– The level of water in February and March at a lag of 2 years has a negative effect on abundance. The period is a time when during certain years there is a temporary halt that occurs in the rise in water, an event which is locally named the "repiquete".

– Finally, the level of water in November and in December at a lag of 2 years (a time of the year generally corresponding to the end of the low-water period), has a positive effect on abundance.

The relation between abundance index and fishing effort was positive. Taking into account the effort of the previous year (Effort01), justified if the exploitation covered at least two age classes of fish, did not change this result.

For the low-water index, there were three periods which also showed an effect on biomass.

– May at a lag of 3 years, in the same way as the high-water index,

– November at a lag of 3 years, corresponding to low-water period, *i.e.* a few months before its effect becomes evident on the high-water index,

– June and July at a lag of 1 year, corresponding to the drop in water with a negative effect.

No relation whatsoever could be found between abundance index and fishing effort.

Multivariate analysis

Whatever the index taken into account, the introduction of an effect of the fishing effort does not seem appropriate. The variables Effort and Effort01 do not have any significant effect ($p>0.1$) and are positively correlated to the abundance index.

For the high-water index, the linear models are those which produced the highest correlations and are presented here. The first variable to enter the model was Feb2 which alone produced a significant model ($p=0.01$), explaining 48% of the variability of the index (*table* 3, *fig.* 7 *a*). Adding successively Dec2 and May3 produced models at 2 and 3 variables both highly significant ($p<0.01$) (*table* 3 and *fig.* 7 *b*, *c*). More than 83% of the variability of the index were explained by the 3 variables model.

For the low-water index, we present the result of the exponential model which described better the index variations. Models with 1, 2 and 3 variables were significant ($p<0.005$) and explained respectively 37, 68 and 75% of the variability of the index series (*table* 3 and *fig.* 7 *d*, *e*, *f*). However, two variable coefficients in the 3 variables model were far from significant ($p>0.1$).

DISCUSSION

In calculating the abundance index, we made the assumption of an inverse relationship between catchability (*i.e.* a combination of vulnerability and accessibility) and area on a yearly basis. Average vulnerability in a given period most probably does not change with the mean water level during the period. The efficiency of fishing gear is of course dependent upon hydrological conditions but, in this artisanal-type multi-gear fishery the fishermen have a good knowledge of the aquatic environment and constantly select the appropriate gear to optimize their catch. On the other hand, accessibility can indeed vary with the water level in the considered period. A higher flood leads to inundation of more marginal vegetated areas, thus enabling the fish to take refuge in areas which are inaccessible to fishing gear and boats. Conversely, in the low-water period, a lower mean water level leads to a higher proportion of the water column accessible to the fishing gear. The hypothesis of a coefficient q' approximately constant for a given period is therefore acceptable:

$$q'=q.A.$$

The relationship between the effort in a given year and the corresponding abundance indices all show a positive trend. If effort represents a measure of the mortality rate due to fishing, then an increase in effort should lead to a reduction in biomass. This is true even if we take into consideration that there may be variations in catchability due to variations in effort. The observed relations therefore have to be interpreted as a dependence of effort on abundance. In other words, the fishermen adjust their effort in relation to the abundance of fish; when the latter is low they diminish their effort, either by going to other fishing grounds and stocks of fish, or simply by stopping altogether. These artisan fishermen are extremely adaptable. The absence of any causal relation between the fishing effort and the abundance index indicates that the effort developed locally has a negligible influence on the abundance of fish in comparison with that of the hydrological factors. The conclusion is of primary importance for future management. The inhabitants of the island, most of them subsistence fishermen, all express the anxiety that the activities of "foreign" fishermen will decrease the abundance of what they consider to be "their" fish. The fear is therefore unjustified, at least when one considers the whole of the fish community, although some prized species could be threatened.

The analysis showed no significant effect of hydrological parameters on the concomitant abundance index. During the high-water period it is probable that the exploited fish biomass may not be dependent on water level during the current year, as will be discussed in the following section. However, severe low-water periods result in mass natural mortality (pers. observations) and thus biomass should be affected. Higher values of correlation (although not significant) between low-water abundance index and water level during the low-water period of the current year are in fact observed (*fig.* 6).

Finally, it is thus the water levels of previous years which account for more variance in abundance indices. Firstly, it should be noted that there is no correlation between the high-water and low-water abundance indices. The low-water indices are generally lower than the high-water indices. The observation is to be related to the behavioural patterns of fish in floodplains, in particular to the phenomena of lateral migration (Welcomme, 1979; Cox Fernandes, 1988; Mérona and Bittencourt, 1993 *b* in press). When the floodwater starts to drop, numerous species of fish perform lateral migrations, leaving the plain for the river along which they start travelling great distances. Thus the abundance of migratory species in the plain during the low-water period is related to the extent of this movement, which in turn is most probably

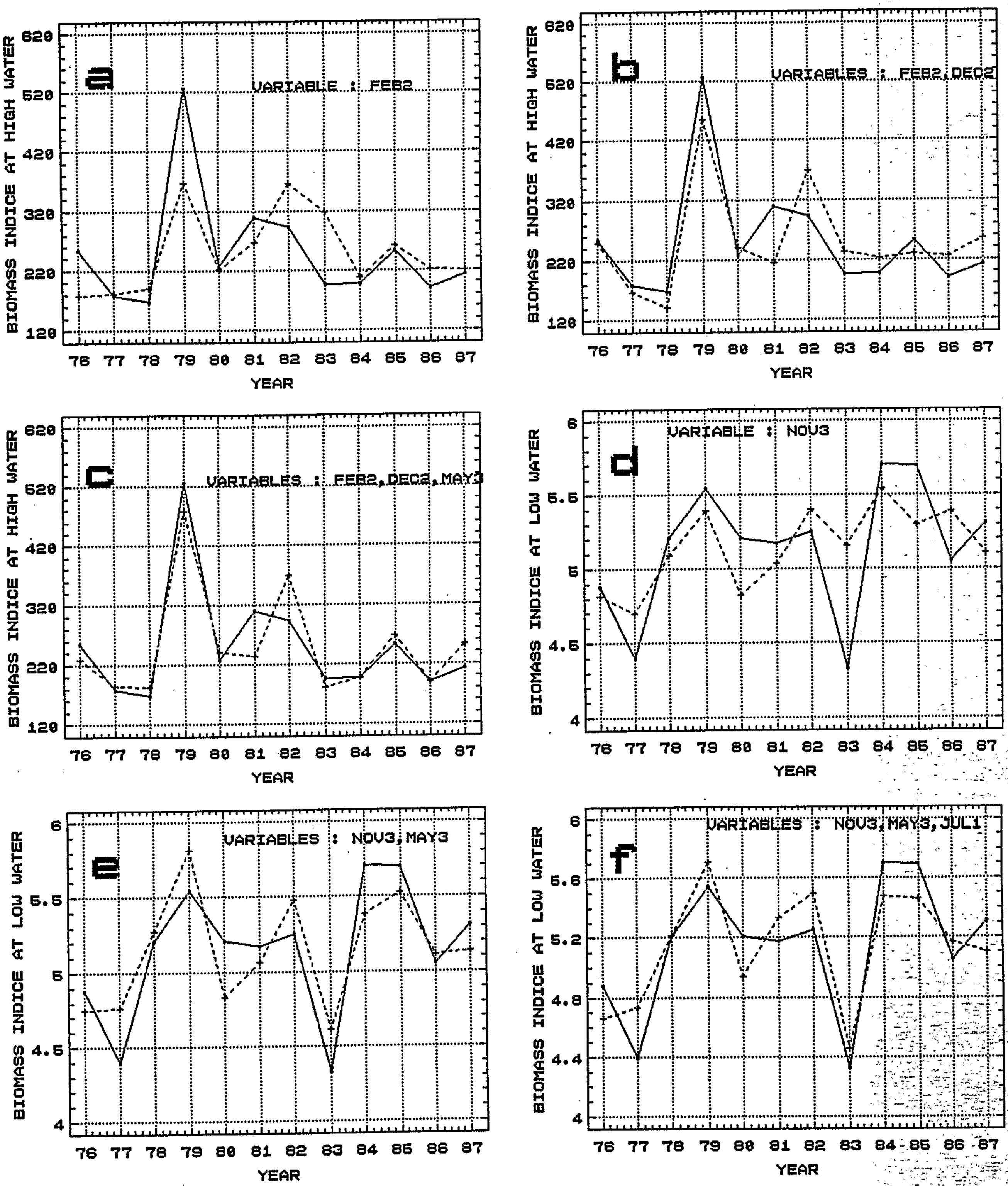

Figure 7. — Adjustment of various models to the series of abundance indices between 1976 and 1987. Full lines: observed values; dotted lines: adjusted values (*a*, *b*, *c*: High-water indices with, respectively 1, 2 and 3 environmental variables, Model: $\text{Ind}=a+a_i\text{env}_i$; *d*, *e*, *f*: Low-water indices with respectively 1, 2 and 3 environmental variables, Model: $\text{Ind}=e^{a+a_i\text{env}_i}$).

Table 3. — Parameter values for the various explanatory models for variations in abundance indices (between parentheses: standard error of estimate).

	Constant (a)	Coefficients (a_i)	Relative contribution	Probability of estimate	R^2	Probability of the model
		High-water				
Feb2	1 014.83 (*254.08*)	−61.062 4 (*20.220 8*)	100	0.012 9	0.477 0	0.012 9
Feb2	574.99 (*234.98*)	−60.802 6 (*14.819 8*)	63.84	0.002 6	0.747 2	0.002 1
Dec2		44.493 6 (*14.347 2*)	36.16	0.012 7		
Feb2		−57.487 8 (*12.707 3*)	56.96	0.001 9		
Dec2	135.51 (*288.52*)	32.880 5 (*13.395 7*)	32.27	0.039 7	0.837 3	0.001 6
May3		31.051 0 (*14.749 3*)	10.77	0.068 4		
		Low-water				
Nov3	6.660 8 (*0.632 1*)	−0.167 0 (*0.068 7*)	100.	0.035 3	0.371 6	0.035 3
Nov3	2.851 4 (*1.368 4*)	−0.175 2 (*0.051 5*)	54.46	0.007 9	0.682 4	0.005 7
May3		0.235 6 (*0.079 4*)	45.54	0.015 8		
Nov3		−0.111 9 (*0.064 4*)	49.48	0.120 5		
May3	3.864 2 (*1.455 4*)	0.257 2 (*0.075 9*)	41.37	0.009 6	0.751 1	0.008 4
Jul1		−0.116 8 (*0.078 6*)	9.15	0.175 5		

related to the hydrological parameters and the density of fish. Reproduction occurs for most species, and especially for migratory species, at the start of the floodwater period: the spawners are then distributed around the available habitats. We are making the assumption here that the distribution of spawners is homogeneous, and that the abundance indices in periods of high-water are indeed reliable indices of average abundance in the floodplain.

In this way, the annual abundance of stocks of fish, as an annual average, seems linked to hydrological parameters in three ways. The first is a positive effect of the flood during a given year on fish abundance three years later. The only data available concerning the age at which fish are captured concerns Pescadas (25.4% of landings). Worthman (1982) provides age-length curves for the two species of Pescada in similar habitats of the same region: at three years of age one of the species has an average size of 34 cm and the other an average size of 26 cm. These lengths are similar in size to those of the catches supplied by Annibal (1982). It is therefore likely that the flood affects the recruitment of the populations. Petry (1989) showed that the quantity of Characidae larvae arriving in the plain — and therefore having a chance of survival — was directly linked to the speed of the current. This result is applicable to the migratory species which reproduce in the river, which include the Curimata (12.6% of landings). Most of the other species caught are considered to be sedentary. The Pescadas have a partial spawning strategy with a maximum reproduction activity at the moment of high-water (Worthman, 1982). This fact enables us to suppose that an even greater flood favours the survival of their larvae possibly by a greater availability of food. The effect of flood on the recruitment of fish in the floodplain has been reported on several occasions. Dudley (1972) observed high abundance for age classes corresponding to years of high flood in the Kafue floodplain. Similarly, Benech (1974 and 1975) and Benech and Quensière (1983) noted a major recruitment of certain species of migratory fish in the lake Tchad system in 1970, a year of high flood for the *El Beid*. Conversely, Reizer (1974) noted the low abundance of the 1968 age class in the Senegal river, linked to a greatly reduced flood. A number of case studies have also established connections between the catch of fisheries and the flood water levels of previous years which the authors interpreted as an effect on recruitment (Anonymous, 1971 *a*, *b*; Muncy, 1973 and 1977; Welcomme, 1976, 1979, and 1986; Novoa, 1989; Quiroz and Cuch, 1989). In each case the lag in years between the floodwater and the catch depended upon the average age of the fish in the fishery. In Africa the lag-time is very short, from one to two years, as the fisheries concentrate on small species with fast rates of growth (Welcomme, 1979). Similar lag-times are observed on certain sections of the Orinoco river which are intensively exploited (Novoa, 1989). On the other hand, much longer lag-times (5 to 6 years) are reported for the Parana, a river in which the fisheries are poorly developed and concentrate on large sizes of fish (Quiroz and Cuch, 1989).

The second effect of hydrological parameters is a negative influence of the water level at the very beginning of the rise in water on the abundance index two years later. This effect could concern 1) the fish of the year, entering in the fishery two years later and 2) the one-year-old fishes whose recruitment was shown to be linked to the previous year's flood. In order to examine these two hypotheses the variables were entered in the model in a chronological way (May3 before Feb2). The residuals of the one-variable model in relation to the variable May3 were greater for high values of the variable (*fig.* 8). The introduction of Feb2 normalized these residuals. In other words, high recruitment rates resulting from high floodwater levels could be regulated the following year and therefore the second hypothesis seems to be the most probable. Although no obvious ecological data could be found to support that hypothesis, one may think of less intense lateral movements when the low water period is short, leading to an increase of competition processes.

any effect of effort on the abundance index indicates, at the very most, that it is the effort developed locally which has a negligible effect, compared to that of the hydrological factors, on the general abundance of fish in the floodplain. This somewhat restrictive conclusion can be extended, however. This result has been observed in fishing grounds near the market of Manaus, which are amongst the most intensively exploited fishing grounds of the whole region (Petrere, 1982). It is therefore reasonable to suppose that this fact can be extrapolated to the other fishing grounds of the region, and that the abundance of fish throughout the floodplain of central Amazonia is not affected by the total fishing effort in the region. This widened conclusion is also compatible with the previous results showing that, in general, fishing in central Amazonia is still far from reaching a level of exploitation corresponding to its estimated potential (Bayley, 1981 and 1982; Mérona and Bittencourt, 1988; Mérona and Bittencourt, 1991; Mérona, 1990 a and *b*).

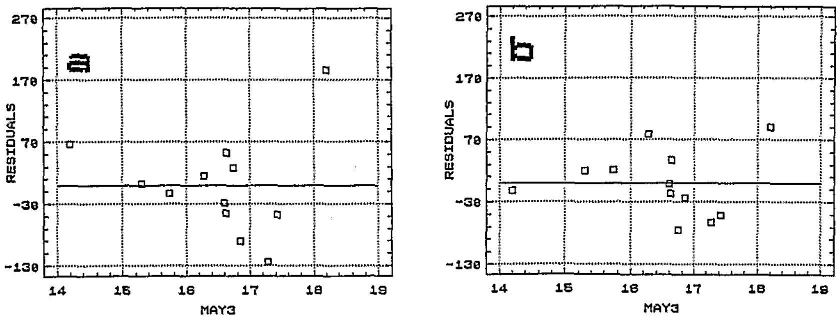

Figure 8. — Distribution of the residuals for the models with one (May3: a) and two (May3, Feb2: b) variables for the high-water abundance index as a function of the variable May3.

The third effect resulting from hydrological parameters, a positive one of the height of water in November and December on the abundance index of the floodwater two years later, is easier to interpret. These months correspond to the end of the low-water period and so low values of water level reflect a very long period of low-water. It is well known that particularly severe low-water levels result in the massive death of fish from all age groups in the plain (Welcomme, 1979) leading to a drastic diminution of biomass.

Some of the effects detected on the high-water index are also observed on the low-water index. These are the flood at a lag of 3 years and the low-water period at a lag of 2 years although the variable involved for this latter effect (Nov3) precedes that of the high-water model (Feb2). This shows that the abundance of fish during low-water periods is somehow related to the general abundance of fish in the plain. Other parameters, however, seem to play a complex role. No convincing interpretation could be found for the effect of the flood at a lag of 1 year. The phenomena of lateral migration occurring before the low-water period have been described by Cox Fernandes (1988). These movements of fish primarily concern migratory species such as the Curimata, but can also occur with species which are reputed to be sedentary (pers. observations). The movements do not appear to be directly linked to reproduction but seem to result in reduction of fish population density in the plain. In addition, as we have already discussed, it is possible that the catchability which we supposed to be constant is quite the opposite: that during the low-water period it is linked to the average water level.

In this study we have isolated a specific site of fishing within a much larger fishery. To what extent can our conclusions be generalized? The absence of

In addition to this, the effects of hydrological parameters have been observed throughout the exploited community of fish. One of the most abundant species in the catch is migratory. If we accept the hypothesis of a homogeneous distribution throughout the plain after reproduction has taken place, then the abundance observed for a given site can be generalized to the whole of the flooded habitats. For other, reputedly sedentary species, while the local abundance for each of them can vary from site to site, overall multispecies abundance could be more simply linked to the general productivity of the plain and therefore to the flood regime parameters.

CONCLUSION

Based on these data concerning a multispecies commercial fishery in central Amazonia, we have been able to show that the corrected catches per unit effort were not dependent on the fishing effort developed. This conclusion is not, of course, incompatible with the existence of phenomena of over-fishing of certain species since some species replacement was observed in the composition of annual catches. Analyzing the effort/CPUE relationships for certain fish which are particularly prized by the fishermen is nonetheless difficult, due to the highly multispecies nature of the catch.

We show that the abundance of the exploited community of fish is largely determined by the hydrological events of the previous years. The model containing three variables enables us to explain a major part of the variability in abundance indices. The relationship between flood regime parameters and fish abundance seems nonetheless to be complex, and an enhanced understanding of the ecology of the populations making up the community will be necessary before making any mid-term forecasts.

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APPENDIX 1

Landings, effort, abundance indices (high-and low-water abundance indices) and mean monthly water level in Jatuarana.

Year	Landings (tons)	Effort (fishermen/ day)	HWind	LWind	Mean monthly water level (metres)											
					Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec
1970					9.76	11.99	13.92	15.53	17.02	17.56	17.32	16.16	13.23	10.53	8.04	8.00
1971					9.74	12.73	14.64	16.50	17.54	18.26	18.22	17.15	15.02	11.72	10.75	11.39
1972					11.32	13.78	14.93	16.01	17.14	17.96	17.65	16.35	14.28	11.46	9.55	10.41
1973					11.75	12.18	13.30	14.69	16.27	17.51	17.75	17.02	15.55	13.41	11.05	11.75
1974					12.73	13.69	14.74	15.92	16.85	17.44	17.61	16.89	15.03	12.78	11.75	11.41
1975					12.31	13.66	14.88	16.18	17.28	18.27	18.40	17.54	15.93	12.64	9.40	9.47
1976	502.43	17005	253.577	131.585	11.30	13.50	14.50	16.70	18.20	18.70	18.40	16.80	13.40	9.10	7.60	8.70
1977	180.81	9737	178.896	80.883	10.50	10.60	12.30	14.70	16.60	17.40	17.50	15.90	12.67	10.22	11.01	11.80
1978	521.38	20223	168.125	183.231	12.96	12.99	13.89	15.15	16.63	17.28	17.02	15.46	12.41	9.92	9.74	10.22
1979	1488.25	22887	526.617	254.706	12.38	12.23	12.69	15.05	16.74	17.37	16.81	14.16	10.40	7.42	7.54	8.63
1980	553.85	13113	227.654	182.359	10.19	10.63	10.44	12.52	14.20	15.07	14.73	12.55	8.75	7.23	9.03	9.88
1981	443.44	8935	309.608	175.921	10.25	11.40	13.36	14,81	15.73	16.03	15.67	14.32	10.62	7.27	6.70	7.90
1982	298.48	8295	292.438	191.091	11.40	13.22	14,45	14.84	17.43	18.11	17.53	15.79	12.74	8.97	8.17	10.15
1983	46.01	1866	195.839	75.647	11.92	12.33	12.53	13.81	15.29	15.63	14.44	10.85	8.36	7.08	7.64	9.09
1984	131.85	2989	197.004	300.329	11.44	12.99	14.64	15.54	16.62	17.21	16.89	15.52	12.92	9.83	9.30	9.91
1985	359.27	7848	252.420	297.141	12.40	13.01	12.69	13.03	13.87	15.14	15.19	14.10	12.52	10.15	9.51	10.59
1986	51.28	2042	189.439	156.710	11.30	12.03	13.72	15.18	16.22	16.90	17.11	16.12	13.24	10.95	11.69	12.49
1987	293.61	10821	211.773	202.711	12.85	13.55	14.73	15.72	16.82	16.92	16.05	13.79	10.69	8.00	7.67	9.13