

Global and Local Change: Penaeid Stocks in French Guyana

CHRISTOPHE BÉNE*

PHILIPPE MOGUEDET**

* Institut Français de Recherche
pour l'Exploitation de la Mer (IFREMER)
Station Zoologique
BP 28
06230 Villefranche sur Mer
FRANCE

** Institut Français de Recherche
pour l'Exploitation de la Mer (IFREMER)
Station de La Rochelle
BP 7
17137 L'Houmeau
FRANCE

ABSTRACT

This study is an attempt to estimate the impact of the Amazon River, regarded as a global change indicator, and different local environmental factors, on the recruitment of penaeid stocks in French Guyana. In particular, the authors try to determine whether the impacts of these global and local environmental factors overlap on temporal scales, or whether they intervene at distinguishable (preferential) time scales. For this purpose, two different time-scales were considered, the biannual and monthly scales. Estimation of the adult stock abundance was also included in the analyses through the commercial catch effort time series. Multiple time series models were estimated from the monthly series and stepwise regressions from the biannual series. The two linear models obtained were then re-estimated using non-linear algorithms. The results indicate that the Amazon River and the adult stock abundance have both significant impacts on stock recruitment at the biannual time scale. However, at the monthly time scale, these two impacts vanish and influence of local rivers appears predominant. These results are consistent with the general hypotheses proposed in the Theory of Hierarchy, and more precisely with the concept of scale dependence usually associated with the multiple functional scales hypothesis.

RÉSUMÉ

Cette étude analyse l'impact du fleuve Amazone combiné à celui de facteurs climatiques locaux de Guyane française sur le recrutement du stock de *Penaeides* présent au large des côtes guyanaises. Il s'agit plus précisément de déterminer si l'impact de l'Amazone, reconnu comme un indice de changement global, agit aux mêmes échelles de temps que les facteurs locaux, ou si, au contraire, chacun de ces deux types de facteurs agissent à des échelles temporelles distinctes. Pour cela, l'échelle mensuelle et l'échelle bi-annuelle sont considérées. L'influence de l'abondance du stock des adultes matures est, elle aussi, testée par l'introduction de la série des Captures Par Unité d'Effort (CPUE). Les séries mensuelles sont étudiées par les techniques d'analyse de séries temporelles multivariées alors que les séries bi-annuelles sont analysées par régressions multiples pas à pas. Les deux modèles linéaires obtenus sont ensuite réestimés par un algorithme d'analyse non linéaire. Les résultats indiquent que les impacts de l'Amazone et de l'abondance des adultes sont significatifs à l'échelle bi-annuelle. À l'inverse, ces impacts disparaissent à l'échelle mensuelle, et l'influence du débit des fleuves locaux apparaît cette fois prépondérante. L'ensemble de ces résultats est à rapprocher des concepts développés par la Théorie de la Hiérarchie et en particulier de celui de dépendance d'échelle généralement associé à l'hypothèse d'échelles fonctionnelles multiples.

L'interaction entre phénomènes d'échelles distinctes reste une des questions scientifiques les plus épineuses posées aux spécialistes de toutes les disciplines : on peut dire qu'elle est l'un des problèmes scientifiques les plus fondamentaux (...). Elle féconde aujourd'hui la réflexion dans tous les domaines scientifiques. Frontier, 1990.

INTRODUCTION: GENERAL CONCEPTS AND METHODOLOGICAL APPROACH ADOPTING AND APPLYING THE ESSENCE OF 'GLOBAL VERSUS LOCAL CHANGES'

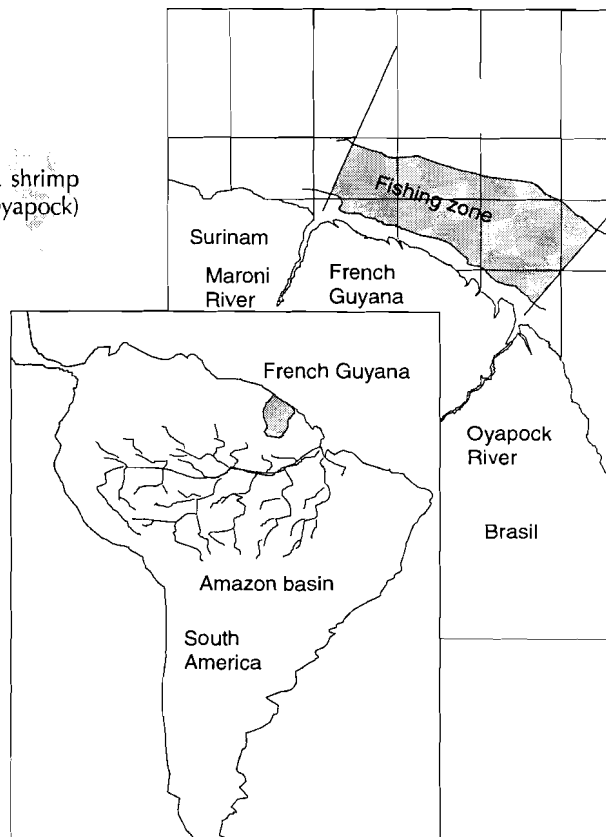
In ecology, every ecosystem analysis points out the complexity and multiplicity of nature's spatial evolution (spatial heterogeneity), and dynamics (temporal variability) and shows that the biotic and abiotic processes generally take place over overlapping spatial and temporal scales. The acknowledgment of multiple spatial and temporal scales is the essence of the approach of the present volume, devoted to 'Global versus Local Changes in Marine Ecosystems': it recalls that marine resources evolve within and because of global and local changes.

Shrimp species do not appear to be an exception: shrimp life-cycles are known to be highly environmentally-dependent (Garcia and Le Reste, 1981; Dall, 1981; Staples and Vance, 1986; Gracia, 1989; Hettler, 1992). No consensus, however, seems to emerge from the abundant literature to identify any key factor (Dall *et al.*, 1990). For illustration, the climatic factors generally assumed to have impact on shrimp recruitment includes rainfall, river flow, water temperature, sea level, salinity, turbidity, even upwelling index or solar and moon cycles (Staples *et al.*, 1984; Lam *et al.*, 1989).

This non-exhaustive list not only emphasizes the complexity of recruitment processes in marine ecosystems in general and in shrimps in particular; it also shows that only impact of locally-recorded factors have been analyzed (local rivers, local rainfall, temperature of the shrimp living area, etc.). Thus, it should be interesting to make an attempt to revisit this issue from simultaneous local and global points of view.

The French Guyana shrimp stock may represent a pertinent choice to lead this kind of investigation. Indeed, the southern limit of the area is located 450 km northwest from the Amazon River's mouth (Fig. 1), which is usually regarded as providing a global climatic index. The question which immediately arises is to know whether it would be possible to estimate the impact of the Amazon River on the dynamics of a locally-delimited process such as the recruitment of the shrimp stock off French Guyana and how this global factor interacts with other, locally-generated, environmental factors. In other words, do the global and local impacts overlap on temporal and spatial scales, i.e., do they intervene at the same spatial scale and with the same temporal frequency on the dynamics of the recruitment, or conversely, do they have specific impact scales?

Fig. 1: Geographical location of the French Guyana shrimp fishery with respect to the local rivers (Maroni and Oyapock) and mouth of the Amazon River.



1. DEPTH-DEPENDENT DISTRIBUTION OF THE RESOURCE, AND ITS IMPLICATION FOR RECRUITMENT INDEXES

When no direct estimations of recruitment are available, commercial fishery data are used. Generally, the CPUE (Catch per Unit of Effort) series of the smallest commercial category is used as proxy for recruitment. However, the analysis may be invalid if the resource distribution is depth-dependent. If it is so, and the fleet shifts its spatial distribution of effort, this inshore (or offshore) effort re-location induces a change in the pattern of the catch composition. This change introduces a subsequent modification in cpue and especially in the series that is used as a surrogate for recruitment. This shift does not correspond to any variation in the actual recruitment level, but only reflects change in the fleet fishing strategy.

Shrimp spatial distributions are depth-dependent. It is widely observed that for a given species, largest individuals are generally found in deep-water zones while the smallest individuals live in shallow-water zones (Dall *et al.*, 1990). This is a consequence of a life-cycle where juveniles develop inshore, generally in estuarine nursery grounds, and the adult migrate offshore as they grow. The occurrence of such a depth-dependent distribution has been empirically confirmed in the case of the French Guyana shrimp *Penaeus subtilis* (Venaille, 1979).

The bias in recruitment indicator induced by the depth-dependency of the resource, combined with the spatial modification of the commercial fleet effort may be partially circumvented by taking the fleet's distribution into account. In our case, this was done by introducing an indicator related to the spatial distribution of the fishing effort.

2. CHOICES OF TEMPORAL SCALES AND STATISTICAL TECHNIQUES

For the French Guyana, all climatic and/or environmental factors generally assumed to have an impact on shrimp life cycle (cf. the listed variable above) display clear-cut seasonal patterns (Fig. 2,a,c). From this, it ensues that a six-month scale might be appropriate to identify climatic inducing changes and/or biologically-induced responses involved at an intermediate temporal in the recruitment process.

However, equatorial penaeids spawn throughout the year, although spawning intensity may not be uniform in all months (Crococ, 1985; Dall *et al.*, 1990). This constancy of the spawning cycle suggests a dynamics characterized by a relatively high frequency, which might be mismatched by considering a bi-annual time scale. A shorter temporal scale (of the order of the month) is therefore also required. We thus adopted two scales, one biannual, other monthly. Based on these two different analyses were conducted, a short-term recruitment variability analysis (applied to the raw 1979-1990 monthly recorded series), and a medium-term analysis applied to the bi-annually re-scaled series. These bi-annual series were obtained by a 6-month moving average procedure applied to the monthly series. Then, we used multiple time series models for the monthly analysis and stepwise regressions for the bi-annual analysis.

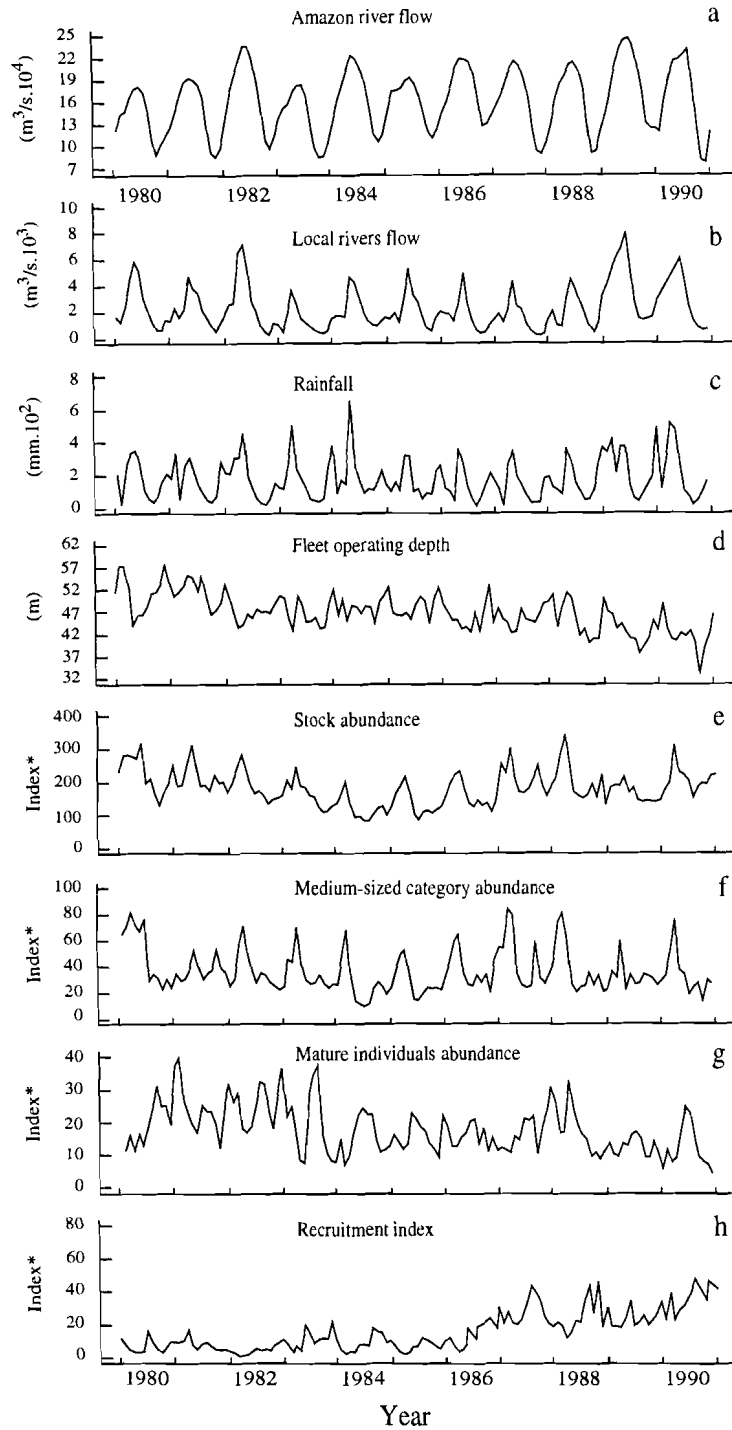


Fig. 2: Monthly time series of the variable used in the analyses, 1980-1990. Abundance and recruitment indices (*): CPUE (kg/day at sea) see Table 1 for details on series; sources : a-b: ORSTOM, c: Météo France, d-h: IFREMER.

3. CHOICES OF DEPENDENT AND EXPLANATORY DATA SERIES

The shrimp stock data was provided by (i) data sets recorded by the IFREMER station in Cayenne and (ii) captains' log-book records. The Amazon river discharge and series of environmental local factors (discharge of the French Guyana Rivers and rainfall) were provided by the stations of ORSTOM and Météo-France in Cayenne, respectively. Table 1 gives details on the explanatory variables included in the bi-annual model and Table 4 on those included of the monthly analysis. The series are shown in Figures 2 e-h. As mentioned above, in the absence of any direct estimation, the recruitment indicator is the CPUE of the smallest commercial categories of shrimps caught by the commercial fleet (i.e., the categories 61/70 + 71/80).

The presence amongst the explanatory variables of the CPUE of a medium-sized category (indicated as LogMed in Tables 1 and 4) calls for explanation. Since the fleet dynamics is likely to have an impact on catch composition (see above), one may assume the catch of mature individuals to be particularly sensible to changes in the fleet's spatial distribution. Conversely, the CPUE of the medium-sized category, distributed in middle depth-water zones, is expected to be less biased by the fleet's movements.

Indicators of	Notation	Lags	Remarks
Stock size	LogStock	t-2, t-1	total CPUE (kg/day at sea)
Mature individuals	LogLarge	t-2, t-1	CPUE of categories U10 + 11/15
Mature individuals	LogMed	t-3, t-2	CPUE of categories 31/35 + 36/40
Rainfall	LogRain	t-2, t-1	French Guyana coastal rainfall (mm)
Local rivers flow	LogRiver	t-2, t-1	Cumulated Maroni and Oyapock flows
Amazon River Flow	LogAmaz	t-2, t-1	Amazon flow
Fleet Sounding	Sound	t	Averaged fleet operating depth (m)

Table 1: Data used for stepwise regression analysis (set of biological and environmental (climatic) variables tested at the bi-annual scale). The third column indicates the different timelags at which the variables were tested in the model.

The other factors included in the model (Fig. 2 a,c) are the rainfall on the coastal zone of French Guyana, the flow of two local rivers (the Maroni and the Oyapock Rivers) (see Fig. 1) and the discharge of the Amazon River. Also, the fleet's operating depth was also included as indicator of the spatial distribution of fishing effort. All variables except fleet soundings were log-transformed to stabilize the variance.

4. MODEL IMPROVEMENT: INTEGRATING NON-LINEARITY

The estimation procedures for both time series analyses and stepwise regression are based on linear procedures. We complemented these analyses by re-estimating the models through non-linear regressions. Several algorithms [Alternative

Conditional Expectations (ACE) (Breiman and Friedman, 1985), Additivity and Variance Stabilization (AVAS) (Tibshirani, 1988), or Generalized Additive Interactive Modeling (GAIM) (Hastie and Tibshirani, 1990) offer the possibility of this non-linear re-estimation. We used Breiman and Friedman's ACE algorithm.

5. RECRUITMENT VARIABILITY ANALYSIS

5.1. Medium term (bi-annual) variability analysis

5.1.1- Linear approach

The explanatory variables were included in the model at the different lags indicated in Table 1. Since results obtained by backward and forward stepwise multiple regressions are usually unstable when the variables are correlated (Belsey *et al.*, 1980. Koslow *et al.*, 1987), the only variables maintained in the model were those which appeared stable.

The final models obtained by backward and forward regression ($F_{\text{remove}} = F_{\text{enter}} = 4.41$, $v_1 = 1$, $v_2 = n-p$, $n = 24$) are similar (Table 2). They both indicate that, relying on linear estimations, only fleet operating depth (Sound) lagged at 0 has a significant impact on the recruitment indicator (Rec). The final linear model is thus:

$$\text{LogRec}_t = f(\text{Sound}_t) \quad (1)$$

where $f()$ is a linear function with $R^2 = 41\%$

These results emphasize the impact of the fleet effort distribution on the recruitment indicator. Note that in other respects, the environmental factors which were tested have non-significant linear impact on the recruitment indicator.

Selection:	Backward	Dependent Variable: (Log Rec _t)		
R ² = 0.409	R ² adj. = 0.378	M.S.E. = 0.3762	d.f. = 19	F remove = 4.41
Variables in Model (1) (Sound _t)	Estim. Coef. -0.1572	F variables (1) 13.1682		
Selection:	Forward	Dependent Variable: (Log Rec _t)		
R ² = 0.409	R ² adj. = 0.378	M.S.E. = 0.3762	d.f. = 19	F enter = 4.41
Variables in Model (1) (Sound _t)	Estim. Coef. -0.1572	F variables (1) 13.1682		

Table 2: Final linear models after stepwise (forward and backward) regression analysis.

5.1.2- Non-linear approach

Releasing the linear constraint implies re-testing all the potential explanatory variables and identifying the form of their optimal transformations using the ACE algorithm. The bias introduced in the recruitment series by the fleet spatial distribution can be partially removed by detrending the recruitment series. The recruitment series was thus detrended with the procedure described in Makridakis *et al.*, (1983). Two non-linear analyses were then conducted simultaneously, one with the log-transformed recruitment indicator, and one with the detrended series. They are noted as log-analysis and detrended analysis, respectively (see Table 3 for details).

Analysis	Log analysis	Detrend analysis
Log-transformation of the dep. variable	Yes	No
Detrending of the dep. variable: remove the bias induced by the fleet dynamics	No	Yes
Dependent variable:	Recruitment (LogRec)	Recruitment (RecDtrd)
(Sound) variable included	Yes	No
Explanatory variables:	Sound, LogAmaz, LogMed	LogAmaz, LogMed

Table 3: Structure of the two analyses conducted for the non-linear approach.

Results of the analysis are displayed in Figure 3. For the log-analysis, the impact of the (Sound) series on the (LogRec) variable is still significant. Amongst the other variables which appear to have non-linear, simultaneous impacts on both (LogRec) and (RecDtrd) variables, only two offer transformations which were qualitatively similar. They are the flow of the Amazon (LogAmaz) lagged at 1 (i.e., 6 months) and the CPUE of the medium-sized category (LogMed), lagged at 2 (one year). The other variables were thus removed and the final non-linear models for the log-analysis and the detrended-analysis were estimated. They have the form:

$$\varphi(\text{LogRec}_t) = \phi_1(\text{Sound}_t) + \phi_2(\text{LogAmaz}_{t-1}) + \phi_3(\text{LogMed}_{t-2}) \quad (\text{log-analysis}) \quad (2)$$

$$\varphi'(\text{RecDtrd}_t) = \phi_2'(\text{LogAmaz}_{t-1}) + \phi_3'(\text{LogMed}_{t-2}) \quad (\text{detrended-analysis}) \quad (3)$$

where φ and φ' are the optimal linear transformations of the dependent variable, and ϕ and ϕ' are the optimal non-linear transformations of the explanatory variables. The R^2 are 73% and 48% for (2) and (3), respectively. The difference in these R^2 values is due to the presence of the (Sound) series in model (2), which explains a large fraction of the $t\text{LogRec}$.

Thus, the release from linearity allows the identification of two climatic factors (Amazon flow and the medium-sized category) which are significant. The non-linearity of their optimal transformation (i.e., the fact that straight lines would fit the optimal transformations poorly (see Fig. 3)), offers an explanation for the fact that the linear-based estimations proposed in the previous section failed to identify these variables as significant.

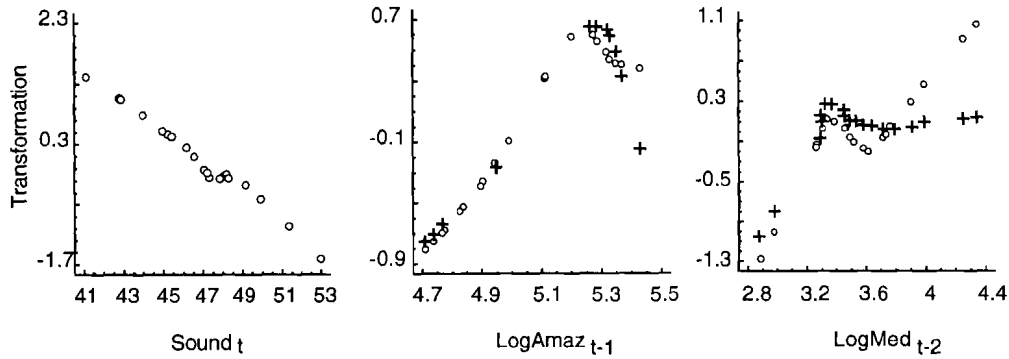


Fig. 3: Non-linear, bi-annual analyses: optimal transformations of the explanatory variables for both log-analysis and detrended analyses. (see Table 3 for details). Open dots: log-analysis ($R^2= 0.738$). Crosses: detrended analysis ($R^2= 0.485$).

5.2. Analysis of short term (monthly) variability

5.2.1- Linear approach

The multiple time series procedure used here is similar to the one described in Tiao and Box (1981), i.e., we used the Wisconsin Multiple Time Series program (WMTS-1) developed by Tiao *et al.* (1980). Table 4 indicates the series tested and the transformation adopted. All climatic variables (i.e., rainfall and river flow) were deseasonalized by a $(1-B^{12})$ backward shift operator for stationary purpose. The partial auto and cross-correlation analyses over 16 lags indicate that positive auto-correlation of the dependent variable (Rec) occurs at lag 1, 5, 9, 11, and 12, while negative cross-correlations with the sounding (Sound) and the local rivers flow (RiverDiff) are significant at lags 1 and 11, and 6, respectively (Table 5). The model parameters were then estimated using WMTS-1. The series parameter included in the range ± 2 S.E. (S.E. standard error) were removed from the model (see Tiao and Box (1981) for procedural details). Table 6 shows the variables and their estimated parameters for the final linear model such as identified following the Tiao and Box's method. The R^2 coefficient reaches 75 %. The analysis of the residuals cross-correlation matrix indicates no lack of fit. The final linear model is:

$$\text{LogRec}_m = 0.78 \text{LogRec}_{m-1} + 0.23 \text{LogRec}_{m-12} - 0.62E-04 \text{RiverDiff}_{m-6} \quad (4)$$

Variable	LogStock	LogLarge	LogMed	RainDiff	RiverDiff	AmazDiff	Sound
Indicator of:	Stock	Mature	Mature	Rainfall	Local rivers	Amazon	Fleet Sound
Transf.	Log_e	Log_e	Log_e	$(1-B^{12})$	$(1-B^{12})$	$(1-B^{12})$	—

Table 4: Multiple time series analysis. Set of explanatory variables tested at monthly scale. The third row (Transf.) indicates the transformation applied to the variable. $(1-B^{12})$: backward shift operator.

(l)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
yy (l)	+				+				+		+	+				
yx1(l)	-										-					
yx2(l)						-										

Table 5: Sample Partial Auto and Crosscorrelation matrices $yy(l)$ and $yx_i(l)$. The matrix is given in term of indicator symbols such as defined in Tiao and Box (1981) (a sign (+) denotes a partial coefficient value greater than $2n^{1/2}$, a sign (-) denotes a value less than $-2n^{1/2}$, a sign (.) denotes non-significant value with respect to the above criterion). y: Rec, x_1 : Sound, x_2 : RiverDiff, (l): lag being tested.

Predictor series	Model specification	Parameter estimates	Estimated S.E
Rec	(1,1,1)	0.787	0.495E-01
Sound	(1,2,2)	0.573	0.731E-01
RiverDiff	(1,3,3)	0.723	0.673E-01
RiverDiff	(6,1,3)	-0.628E-04	0.285E-04
Rec	(12,1,1)	0.237	0.534E-01
Sound	(12,2,2)	0.414	0.714E-01

Table 6: Final multiple time series model identified by the WMTS-1 program. $R^2 = 75.5\%$. The variables Rec, Sound, and RiverDiff are coded 1, 2, and 3, respectively in model specification (l, i, j) (l) indicates the lag, (i) the series being regressed, and (j) the predictor series. All parameter estimates are greater than 2S.E.

5.2.2- Non-linear approach

The linear model (4) was then re-estimated using the ACE algorithm (Fig. 4). The non-linear transformation procedure resulted in an increase of the R^2 from 75 to 81%. The forced addition of the sounding series into the model (open dots in Fig. 4) improves the R^2 value by only 2%. This indicates that, at the monthly scale, the impact of this variable on the recruitment indicator vanishes. Therefore it was not maintained in the final form of the monthly model (5). All the other climatic variables were also systematically tested in the non-linear model. None of them, however, displayed a satisfactory optimal transformation. The final non-linear form of the model (crosses in Fig. 4) is therefore:

$$\varphi(\text{LogRec}_m) = \phi_1(\text{LogRec}_{m-1}) + \phi_2(\text{LogRec}_{m-12}) + \phi_3(\text{RiverDiff}_{m-6}) \quad (5)$$

Note that in (5), the release from linearity improves the coefficient of correlation with respect to (4), but does not change the structure of the predictor function which remains $\{\text{LogRec}_{m-1} : \text{LogRec}_{m-12} : \text{RiverDiff}_{m-6}\}$. Conversely, it may be recalled that Amazon flow and the medium-sized category were included in the non-linear model for the bi-annual analysis.

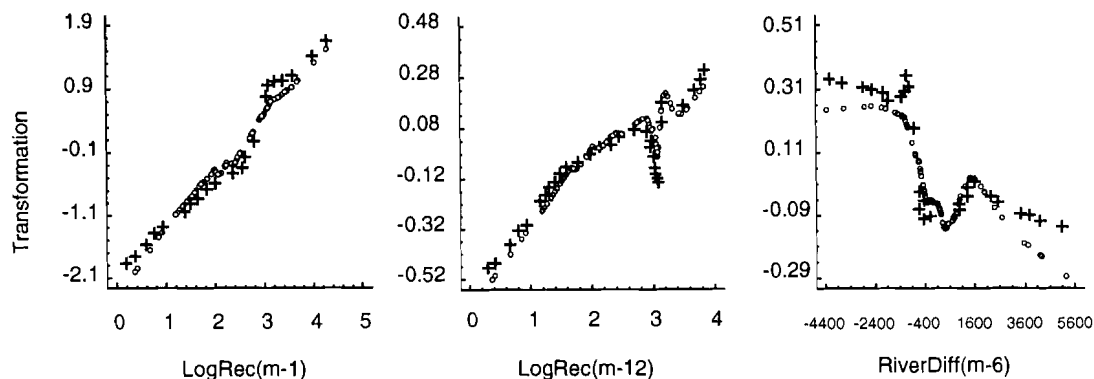


Fig. 4: Non-linear monthly analyses: optimal transformations of the explanatory variables common to the two models. Open dots: model with forced adding of (Sound), indep.var.= (Log Rec_m), predictor function= {(Log Rec_{m-1}), (Log Rec_{m-12}), (Sound_m), (River Diff_{m-6})}, R²=83.1% (the (Sound) transformed curve is not shown). Crosses: model without (Sound): final model of the form (5): indep.var.= (Log Rec_m), predictor function {(Log Rec_{m-1}), (Log Rec_{m-12}), (Sound_m), (River Diff_{m-6})}, R²=81.7%.

5.2.3- Impact of fleet dynamics on the recruitment index

In the case of the French Guyana fishery, it appears that the spatial distribution of fishing effort has an impact on the composition of the landings, and therefore on the recruitment index. This suggests that studies which do not take into account the fleet dynamics dimension when the resource is known to have spatially-structured distributions will the actual causes of long-term changes in the recruitment series. In this case, the bias might even have caused misleading conclusions concerning long term environmental and/or climatic impacts on recruitment fluctuations. Removal of this bias may be done by removing the trend in the series. In the present case, the transformation of the two climatic explanatory variables (LogAmaz_{t-1}) and (LogMed_{t-2}), with or without the detrending procedure, are similar (Fig. 3). One may therefore assume that these environmental factors actually intervene in the long term dynamics of recruitment, whereas the distribution of fishing effort impacts on the long term indicator of recruitment. The difference is slight but important.

5.3. Limits of interpretation

Biologically speaking, the above results appear easy to interpret in the context of the life cycle of *Penaeus subtilis*. The (LogMed) variable lagged at 2 in models (2) and (3) represents the abundance of the individuals about to mature, 9 to 15 months before recruitment. This one year delay corresponds to the time required to pass through the different life cycle steps separating the two stages concerned. On the other hand, the presence of (LogAmaz_{t-1}) in models (2) and (3) and (RiverDiff_{m-6}) series in model (5) are also biologically explainable. These series represent the discharge flows of the Amazon

and the local rivers 6 months ahead of the recruitment, respectively. This corresponds to the periods of egg spawning and inshore migration of the larvae. Both Amazon and local rivers seem therefore to impact on the first stages of the cycle, which are usually assumed to be critical stages in penaeid life cycle. Particularly, for the Amazon River case, this impact appears to be dome-shaped. This recalls the theoretical pattern already shown by other studies, especially on pelagics (Cury and Roy, 1989).

We will however remain careful and be more deeper in biological interpretations. Several previous studies have stressed the apparent non-linear relationship between river discharge and recruitment abundance (Garcia and Le Reste, 1981; Garcia *et al.*, 1985; Staples *et al.*, 1984; Browder, 1985; Gracia, 1989; Dall *et al.*, 1990). These studies thus agree with the shape of the relationship between recruitment and the Amazon River identified here. Some other papers propose linear negative relationship between river flow and recruitment (Barrett and Gillespie, 1975; Lhomme and Garcia, 1984; etc.), while a large number of studies suggest opposite results i.e., linear, positive relationship (Racek, 1959; Le Reste, 1978; Vances *et al.*, 1985). What is therefore needed is now to perform other analyses based on similar methodologies (non-linearity combined with time series techniques, introduction of fleet effort distribution and simultaneous use of two distinct time scales) in order to generalize the present results.

6. GLOBAL VERSUS LOCAL CHANGES: A STIMULATING CONCEPT

6.1. On non-linear techniques

In the shrimp literature, linear regressions have been useful to draw attention to potential impacts of environmentally-induced factors. However, a large number of articles have stressed the non-linear (or even more non-monotonous) nature of the relationships between environmental variables and resource biological states. It is time now to move beyond the linear domain. Critics of linear techniques are not new and certainly not restricted to biology (Prigogine and Stengers, 1979; Stewart, 1992). In the present case, the changes in predictor function and the subsequent improvement of the model following the use of the non-linear transformations highlight the methodological importance of these techniques. It is admitted that present non-linear algorithms (ACE, AVAS, GAIM) have still to be improved and must be considered and used with caution (Cury *et al.*, 1995). These algorithms, however, have the advantage to exist and to be available to biologists. They have been used by pelagic specialists for several years (Mendelsohn and Cury, 1987, 1989). A similar step has still to be taken with regard to research on shrimp. It is time now to adopt non-linear techniques, even if this implies a re-questioning of the conclusions based on classical techniques.

6.2. Beyond the classical problem of pertinent observation scales

For phenomena characterized by several scales of perception, there is generally a correspondence to the main functional scales (Wiens *et al.*, 1986; Rahel, 1990; Frontier, 1990). Consequently there are usually as many models and explanatory theories as perception scales. In the case where global and local factors are involved, this issue becomes

central for the methodological approach (Turner *et al.*, 1989). Furthermore, when the environmental and climatic factors impacting on the system are multiple, complex, and diversified, as is the case for penaeid stocks, thinking in terms of global versus local functional dynamics necessarily raises the question of pertinent observation scales. There are, however, no good, a priori, answers to this question. The pertinent scales can only be identified a posteriori by the natural frequencies of the phenomena studied (Urban *et al.*, 1987; Burel *et al.*, 1992). In those circumstances, ecological processes with unknown sources of variability or which are only partially understood, raise additional methodological difficulties. Some ad hoc solutions may be available. Thus, when a seasonal pattern is known to characterize a large number of the factors assumed to influence the dynamics — as it is usually the case for penaeid stock (Dall *et al.*, 1990) — this seasonality may indicate the optimal scale to adopt. In our case, this natural temporal time scale (frequency) allowed us to propose two different time scales susceptible to capture, a sizeable part of shrimp variability.

6.3. The Amazon River, a global factor

The Amazon River can be viewed as an indicator of global change, for two reasons. Factors are defined as being global (or local) not in terms of their intrinsic features, but rather with respect to other factors also included in the analysis. The mouth of the Amazon River is located 450 km south of the French Guyana - Brazil border. Thus, it can be considered as a non-local factor vis-à-vis the other explanatory variables, which integrate 'locally-generated' variables.

However, the Amazon River lines up to general expectations about global factors for a second reason. A global factor should provide or contain information relevant to the Earth's global climate. With a discharge volume of $5.2 \cdot 10^{12} \text{ m}^3/\text{year}$, the Amazon represents about 20% of the World's water discharge into the oceans (Oltman, 1968). The flow ratio Amazon/local rivers indicates, moreover, that, on the average, over the period 1979-1990, the Amazon annual discharge was 65 times stronger than the combined discharge of local rivers. The magnitude in the ratio thus justifies treating the Amazon to be qualified as a global factor with respect to the other variables, which conversely may be considered as indicators of local changes.

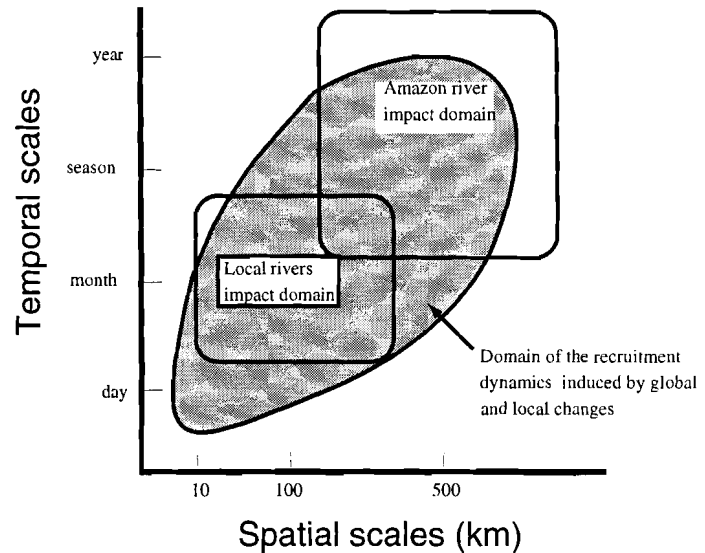
6.4. Scale dependence and the coherence of space-time scales

The fact that a river considered as a global factor appears to have a significant impact at the bi-annual but not at the monthly temporal scale, may indicate a space-time (de)limitation of its domain. Whereas the bi-annual level of shrimp recruitment dynamics is influenced by the Amazon, its impact vanishes at shorter scales. On the other hand, the discharge of the local rivers does not seem to impact the long term dynamics of shrimp abundance but is significant at the monthly scale. Shrimp recruitment dynamics thus seem to be characterized by several functional scales.

This notion of multiple functional scale is quite usual in ecology, particularly in the Theory of Hierarchy and its concept of scale dependence (Wiens, 1989; Burel *et al.*, 1992; Müller, 1992). This concept states that impacts of phenomena that spread over large spatial scales are more slower than those acting on smallest spatial scales. One may be tempted therefore to refer here to the 'concept of coherence of scales'. The term dependence when used in 'dependence of scales' implies a notion of causality and a formal relationship between space and time. On the other hand, the term 'coherence' merely refers to a logical, but not empirically established relationship between the temporal and spatial dimensions of the factors.

The observations presented here on *Penaeus subtilis* off French Guyana are in agreement with expectations of coherence of scales (Fig. 5): the Amazon River turns out to have an impact at a relatively long-term scale, while the impact of the local rivers is effective at higher frequencies, observable at monthly scales.

Fig. 5: Coherence of scale (scale dependence) in the case of the French Guyana shrimp recruitment dynamic: the Amazon River affects system dynamics at a longer temporal scale (the bi-annual scale), while local factors generate impacts at a smaller scale (monthly). This creates a virtual relationship between spatial and temporal scales in accordance with the classical concept of scale dependence.



6.5. Global versus local: avoiding misleading simplifications

Thinking in terms of global versus local changes is not merely tantamount to comparing or even to opposing two different spatially- or temporally-scaled impacts. First of all, the two notions (local and global) have no absolute, but only relative dimensions. They are only defined with respect to each other.

Nevertheless, it is on a more fundamental field that the view is erroneous which tends to reduce this concept to an oversimplistic opposition between two scales. Not only are the two notions relative and not absolute, but also their contrast between them is disputable. They are not two opposite poles excluding one another, as sometime asserted, but rather different parts of a continuum along scales. Furthermore, the different levels are not independent from one another. The same environmental factor may not restrict its impact to one given level but 'spread out' on several levels. One may expect, for instance, that the local rivers have a temporal domain which covers a larger scale than the monthly scale used here, probably of several months.

For these reasons, the dynamics of shrimp recruitment we observed, is the emergent result of a combination of interacting dynamics characterizing different hierarchical (space-time scaled) levels, and not merely the result of addition (superposition) of dynamics at two or more scales. The dynamics of biological systems are not simply 'piled up' at diverse scales (Fig. 6; Burel *et al.*, 1992).

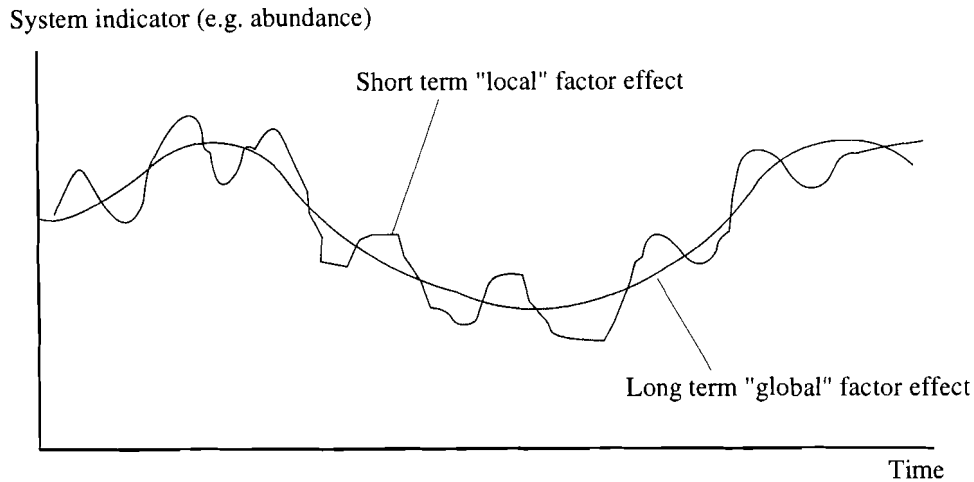


Fig. 6: Representation of the misleading notion of 'addition of effects' (instead of 'combination of effects'). This oversimplistic approach does not allow for emergent properties. We should consider systems as emergent responses to combined effects acting within and between functional levels rather than as simple addition of 'compartmentalized' responses specific to distinct functional levels.

The conclusion is therefore that one should not strive any longer to 'integrate' the dynamics of a given level by analyzing variability of this unique level. We have to widen the space-time dimension of our investigations to neighbouring levels, to identify the specific but also the interlevel mechanisms acting within and between the system levels. Within this conceptual framework, we shall not think in terms of 'Global versus Local Changes', as the two notions are in fact inseparable. Rather, we should think in terms of 'Global and Local Changes'.

ACKNOWLEDGMENTS

The authors would like to thank P. Cury, C. Roy (ORSTOM), and R. Mendelsohn (PFEG) for the welcome, and for the technical advice generously offered during the authors' two-week visit to the Pacific Fisheries Environmental Group, Monterey, California. The authors are also indebted to A. Ducouret (Météo-France, Cayenne) and P. Vauchel (ORSTOM, Cayenne) for providing rainfall and river flow data, respectively.

REFERENCES CITED

- Barrett B. and M.C. Gillespie. 1975. Environmental conditions relative to shrimp production in coastal Louisiana. *Louisiana Wildlife and Fisheries Commission Techn. Bull.*, 15: 1-22.
- Belsey D.A., E. Kun and R.E. Welsch. 1980. *Regressing diagnostics: identifying influential data and source of colinearity*. John Wiley, New-York.
- Breiman L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. *J. Am. Stat. Assoc.*, 74: 829-836.
- Browder J.A. 1985. Relationship between pink shrimp production on the Tortugas grounds and water flow patterns in the Florida Everglades. *Bull. Mar. Sci.*, 37(3): 839-856.
- Burel F., J. Baudry, P. Clergeau, P. Constant and M.-C. Eybert. 1992. Approche spatiale des phénomènes écologiques: échelles et hiérarchie. *Bull. Ecol.*, 23(1-2): 93-101.
- Crococ P.J. 1985. Appraisal of some factors relevant to the development of penaeid prawn population reproductive models. In: P.C. Rothlisberg, B.J. Hill and D.J. Staples (eds.). *Second Australian National Prawn Seminar*. Cleveland, Australia. 159-164.
- Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.
- Cury P., C. Roy, R. Mendelssohn, A. Bakun, D. Husby and R. Parish. 1995. Moderate is better: exploring nonlinear climatic effects on the California northern anchovy (*Engraulis mordax*). In: R.J. Beamish (ed.). *Climate and northern fish populations*. *Can. Spec. Publ. Fish. Aquat. Sci.*, 121: 417-424.
- Dall W. 1981. Osmoregulation ability and juvenile habitat preference in some penaeid prawns. *J. Exper. Mar. Biol. Ecol.*, 54: 55-64.
- Dall W., B.J. Hill, P.C. Rothlisberg and D.J. Staples. 1990. The biology of the *Penaeidae*. In: J.H. Blaxter and A.J. Southward (eds.). *Advances in Marine Biology*. Acad. Press, 27, 489 p.
- Frontier S. 1990. Les outils mathématiques nouveaux du transfert d'échelle. In: C. Mullon (ed.). *Le transfert d'échelle. Séminar 4*, ORSTOM: 379-403.
- Garcia S. and L. Le Reste. 1981. Cycles vitaux, dynamique, exploitation et aménagement des stocks de crevettes pénaeides côtières. *FAO Fish. Doc. Tech.*, 203, 210p. FAO, Rome.
- Garcia S., M. Lemoine and E. LeBrun. 1985. Seasonal and long-term variability of recruitment in French Guyana shrimp fishery on *Penaeus subtilis*. *FAO Fish. Rep.*, 327, Suppl., FAO, Rome.
- Gracia A.G. 1989. Relationship between environmental factors and white shrimp abundance in the southwestern Gulf of Mexico. *An. Inst. Ciec. Mary Limnol. Univ. Autom. Mexico*, 16(1): 171-182.
- Hastie T. and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, London.
- Hettler W.F. 1992. Correlation of winter temperature and landings of pink shrimp, *Penaeus duorarum*, in North Carolina. *Fish. Bull.*, U.S., 90: 405-406.
- Koslow J.A., K. R. Thompson and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. *Can. J. Fish. Aquat. Sci.*, 44: 26-39.
- Lam C.F., I.D. Whitaker and F.S. Lee. 1989. Model for white shrimp landings for the central coast of South Carolina. *North Am. J. Fish. Manag.*, 9: 12-22.
- Le Reste L. 1978. *Biologie d'une population de crevettes, Penaeus indicus, sur la côte nord-ouest de Madagascar*. Trav. Doc. ORSTOM. 99: 1-291.
- Lhomme F. and S. Garcia. 1984. Biologie et exploitation de la crevette pénaeide au Sénégal. In: J.A. Gulland and B.J. Rothschild (eds.). *Penaeid shrimp, their biology and management*. Fishing News Books, Farnham: 111-114.
- Makridakis W., S.C. Wheelwright and U.E. McGee. 1983. *Forecasting: methods and applications*. 2nd edition, John Wiley, New-York.
- Mendelssohn R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44: 408-421.
- Mendelssohn R. and P. Cury. 1989. Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis* off the Ivory Coast. *Can. J. Fish. Aquat. Sci.*, 46: 1686-1697.
- Müller F. 1992. Hierarchical approaches to ecosystem theory. *Ecol. Model.*, 63: 215-242.
- Oltman R.E. 1968. Reconnaissance investigations of the discharge and water quality of the Amazon River. U.S. Geol. Survey. Circ., 552, Washington D.C.

- Prigogine I. and I. Stengers. 1979. *La nouvelle alliance*. Gallimard, Paris, 439 p.
- Racek A.A. 1959. Prawn investigations in eastern Australia. *Res. Bull. State Fish.*, New South Wales, 6: 1-57.
- Rahel F. 1990. The hierarchical nature of community persistence: a problem of scale. *Am. Nat.*, 136: 328-344.
- Staples D.J., W. Dall and D.J. Vance. 1984. Catch prediction of the banana prawn, *Penaeus merguensis*, in the south-eastern Gulf of Carpentaria. In: J.A. Gulland and B.J. Rothschild (eds.). *Penaeid shrimps: their biology and management*. Fishing News Books Ltd: 259-267.
- Staples D.J. and D.J. Vance. 1986. Emigration of juvenile banana prawns *Penaeus merguensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. *Mar. Ecol. Prog. series*, 27: 239-252.
- Stewart I. 1992. *Dieu joue-t-il aux dés? Les nouvelles mathématiques du chaos*. Flammarion, Paris, 441 p.
- Tiao G.C., G.E.P. Box, M.R. Grupe, G.B. Hudak, W.R. Bell and I. Chang. 1980. *The Wisconsin Multiple Time Series (WMTS-1) program. A preliminary guide*. Dep. Stat. Univ. Wisconsin, 75 p.
- Tiao G.C. and G.E.P. Box. 1981. Modeling multiple time series with applications. *J. Amer. Stat. Assoc.* 76: 802-816.
- Tibshirani R. 1988. Estimating transformations for regression via additivity and variance stabilization. *J. Am. Stat. Assoc.*, 83: 394-405.
- Turner M.G., V.H. Dale and R.H. Gardner. 1989. Predicting across scale: theory development and testing. *Landscape Ecol.*, 3: 245-252.
- Urban D.L., R.V. O'Neill, and H.H. jr Shugart. 1987. Landscape ecology. *Biosci.*, 37: 119-127.
- Vances D.J., D.J. Staples and J. Kerr. 1985. Factors affecting year-to-year variation in the catch of banana prawn (*Penaeus merguensis*) in the Gulf of Carpentaria, Australia. *J. Cons.*, Cons. int. Expl. Mer, 42: 83-97.
- Venaille L. 1979. La pêcherie de crevettes péneïdes du plateau guyano-brésilien. *Bull. Inst. Pêches marit.*, 297: 1-18.
- Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology*, 3: 385-397.
- Wiens J.A., J.F. Addicott, T.J. Case and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. In: J. Diamond and T.J. Case (eds.). *Community Ecology*. Harper & Row, New York: 145-153.