HYPOTHESES ACCOUNTING FOR THE VARIABILITY OF SARDINELLA ABUNDANCE IN THE NORTHERN GULF OF GUINEA

Dynamics and uses of Sardinella Resources from upwelling off Ghana and Côte d'Ivoire
Accra, Ghana, 5-8 October 1993

Denis BINET

Antenne ORSTOM. IFREMER. B.P. 1049. F 44037 Nantes cedex 01
25 novembre 1993

Abstract :

Dramatic variations of the Sardinella aurita fishery were observed since the beginning of the industrial purse seine fishery, during the 1960s. A collapse occurred in 1973, after that a huge catch has been done the preceding year; but against every experts opinions, the stock recovered and unprecedented sustained landings were recorded from the mid-1980s up to the early 1990s. The fishery spred westward along the Cote d'Ivoire and the fishing season almost extended all along the year. The fishing effort cannot account for these variations. Environmental changes were scrutinised and many papers show that they could explain a large part of the observed catch variability. Due to its thermo-haline preferences, the availability of S.aurita is directly related to the upwelling intensity, and negatively to the rivers outflows. The recruitment too, is correlated to the strength of the upwelling, through the plankton production and the feeding of larvae. Several surplus production models could account for the landing variability, up to the early 1980s. But afterwards, the stock expansion is not explained by the former models and new hypotheses were done. A second population of S. aurita was supposed settling in the western Cote d'Ivoire, in connection to possible changes in the circulation pattern. A lengthening of the previously called «short upwelling season» could have increased the forage production and hence, the recruitment issued from the first spawning period. Finally a slight cooling along the Eastern side of the Ivorian gulf could have favoured the expansion of the population from Ghana towards Cote d'Ivoire. Taken separately, none of these mechanisms can account for the whole of the observed changes, but together, they seem to explain a part of the complex stock-environment relationships.

Résumé :

Des changements surprenants de la pêcherie de Sardinella aurita ont été observées depuis le début de la pêcherie industrielle de seine coulissante dans les années 60. Un effondrement a eu lieu en 1973, après une très forte capture l'année précédente. Mais, contre tout avis des experts, le stock a récupéré et des captures record ont été régulièrement observées depuis le milieu des années 80 jusqu'au début des années 90. La pêcherie s'est étendue vers l'Ouest ivoirien et la période de pêche s'étend désormais tout au long de l'année. Ces changements ne sont pas attribuables à l'effort de pêche. Les changements de l'environnement ont été soigneusement examinés et plusieurs études montrent qu'ils peuvent expliquer un bonne part de cette variabilité des captures. En raison de ses préférences thermo-halines, la disponibilité de S. aurita est directement liée à l'intensité des upwellings et inversement au débit en mer des fleuves. Le recrutement est également corrélé avec la force de l'upwelling, via la production de plancton et la nutrition des larves. Plusieurs modèles de production ont pu rendre compte de la variabilité des prises jusqu'au début des années 80. Mais depuis, l'expansion du stock, n'est pas expliquée par les modèles précédents et de nouvelles hypothèses ont été faites. Une deuxième population de S aurita pourrait s'être développé dans l'Ouest ivoirien, en relation avec des changements dans les courants côtiers. Un renforcement de la saison marine connue comme la petite période d'upwelling pourrait avoir accru la production de nourriture et donc le recrutement issu de la première période de ponte. Enfin un léger refroidissement à l'Est du golfe ivoirien pourrait avoir favorisé une expansion de la population du Ghana vers la Côte d'Ivoire. Pris séparément aucun de ces mécanismes ne peut rendre compte de l'ensemble des changement observés, mais ensemble, ils semblent expliquer pour une part les relations complexe entre le stock et l'environnement.

1. Introduction

Most coastal pelagic fisheries show variations in annual yield which are usually larger than those of demersal fisheries. However, are these variations dependent on availability or do they reflect real changes in the stock biomass? Although the real abundance of demersal fish is most accurately indicated by the catch per unit of effort (CPUE), it is difficult to assess that of pelagic species due to problems in estimating fishing effort for a non-randomly distributed prey. On the one hand, the social behavior of fish, scattered or schooling, as well as their vertical migrations, make it very difficult to assess their real abundance correctly. On the other hand, the situation of fishermen searching for fish is quite different from that of random sampling. As Mendelssohn and Cury (1987) point out, fishing effort may introduce a bias if the variance of the catch is small compared to that of the effort, in which case the catch might be viewed as constant! For all these reasons, the yearly amount of the catch may sometimes be the only index indicating real abundance variations.

2. History of the fishery in recent decades

The pelagic resources of the northern coast of the Gulf of Guinea have long been exploited by traditional means such as dug-out canoes and beach seines. The ali net (a drifting gill net) has been in use since about 1850 in Ghana (Lawson and Kwei, 1974, *in* Korenteng, 1991). However, there were very few reports of variations in fish abundance before the beginning of the industrial purse seine fishery in the Côte d'Ivoire and Ghana in the 1960s. Oral traditions among tribes of fishermen might provide additional information, but enquiries have apparently not been undertaken. The causes of abundance variations can only be determined if fish populations are regularly sampled in a sufficiently large fishery. In this respect, all indications are that fishing activity has never been as great as in recent decades. With few exceptions, such as the report of larger *Sardinella aurita* during the 1940s in Ghanaian waters and the dominance of this species off Abidjan around 1960 (Mensah and Blanchard, pers. comm., *in* Binet *et al.*, 1991), our knowledge of variations in pelagic fish abundance is limited to the period from the 1960s to now, especially in the absence of sedimentological records of scales and other skeletal pieces.

The most abundant pelagic species are *Sardinella aurita, S. maderensis, Engraulis encrasicolus, Brachydeuterus auritus* and, in certain years, *Scomber japonicus*. During the last two decades, the most striking events were the surge in triggerfish (*Balistes carolinensis*) population during the 1970s, followed recently by a sharp decline (Caverivière, 1991, 1993), and the dramatic variations in *S. aurita* landings.

The two *Sardinella* species constitute most of the pelagic fishery. Until 1980, most of the catch from Côte d'Ivoire purse seiners consisted of *Sardinella maderensis*. Since then, *S. aurita* has ranked first in Côte d'Ivoire landings.

The history of the *S. aurita* fishery during the last decades may be divided into three periods (Fig. 1) :

(i) During the 1960s, landings in the Côte d'Ivoire and Ghana were moderate but variable, ranging between 8,000 and 47,000 mt. An approximate assessment of fishing mortality (Marchal *in* FAO, 1974) determined that a sustained catch could not exceed 30,000 mt; but all landings by traditional fishermen and bait-fish caught by tuna fishing boats were not included.

(ii) In 1972, the catch suddenly increased to 95,000 mt, almost entirely fished by canoes in Ghanaian waters. After this unusually high catch, *S. aurita* virtually disappeared. After a 5-year collapse, the species progressively increased again and had completely recovered by 1978.

(iii) Beginning in 1981, a dramatic expansion took place, with high catches over several consecutive years. From 1985 to 1987, the stock yielded successively 106, 90 and 82 thousand mt per year with no collapse after such large harvests.

Population dynamics cannot clearly account for the small variations in yield during the 1960s, the high catch of 1972 or the sizeable changes occurring later. The role of the environment in *S. aurita* availability was soon noted (Marchal *in* FAO, 1974) and put forward to explain the 1972 overfishing. Annual recruitment later on was also related to environmental variations.

Wise management of living resources requires an understanding of climatic forcings on the ecosystem in order to determine the appropriate level of fishing effort. The purpose of this paper is to analyze the different hypotheses proposed in an attempt to explain how the various sources of fluctuations have affected this fishery.

2. 1. Environmental variables and availability: River floods and upwelling

Although the occurrence of *S. aurita* in coastal surface waters was first related to cold seasons, it soon became apparent that this species, in an area where the rainy season and the long cold season roughly coincide, was influenced more by high salinity than cold waters (Marchal *in* FAO, 1974). During previous decades (the 1960s and 1970s), *S. aurita* avoided waters in the western part of the Côte d'Ivoire shelf where salinity was lessened by rains and river floods, so that most of the catches came from the eastern side. During the first months of the year, the highest salinities (>35 per mil) occur in the central area where the best catches are made. These seasonal and geographical relationships between high salinity and the occurrence of *S aurita* are also apparent when yearly catches are compared with upwelling intensity index variations (Fig. 2a) (Binet, 1982). However, several years are clearly out of the correlation range, namely 1972, the overfishing year, and 1973-1977, the recovery period. In fact, why was 1972 so distant from the correlation straight line?

2. 2. The oncoming drought

Before the 1973 collapse, a negative relationship was observed between rainfall levels and the amount of *S. aurita* landed in Abidjan during July-August (Marchal *in* FAO, 1974). Bakun (1978) noted the same relationship for the Ghana fishery from 1964 to 1968, with periods of extremely good fishing being associated with strong upwelling and subnormal coastal rainfall. The negative relationship between upwelling and pluviometry was observed along all eastern boundary currents. The occurrence of upwelled waters cools the lower atmospheric layers and prevents the development of vertical clouds which cause rain. This geographical relationship has also been reported among time series indicating that interannual variability of upwelling and coastal pluviometry are correlated (Hisard, 1980; Binet, 1982).

The first year of severe drought in subsaharian Africa was 1972. The input of fresh water into the Gulf of Guinea was further reduced by the building of two dams across the Volta and Bandama rivers, and the salinity of coastal waters was not lowered by terrestrial runoff. That year, a large number of young *S. aurita* were harvested near the coast. Binet (1982) conjectured that a close approach to the shore, usually prevented by their halophilous behavior, occurred in 1972, leading to recruitment overfishing. In Senegalese waters, that year was also marked by high catches of *S. aurita*, the level of which has never been equalled (Fréon, 1991a).

A negative relationship was found between annual catches (1963-1972 and 1978-1979) of *S. aurita* from the Côte d'Ivoire and Ghana and the outflow of the Bandama and Comoé rivers (Fig. 2b). The 1973-1977 points, during which the stock was recovering, were aligned along a different straight line. These two results allowed computation of a regression between catches, upwelling and river flow, showing the climatic influence on availability (Binet, 1982).

2. 3. An inaccessible part of the biomass

These results led Laloe (1988) to suppose that a part of the stock is ordinarily unavailable to the fishery and then to develop a production model based on the assumption of an inaccessible part of the biomass. In the case of a surplus production model, it is generally supposed that biomass production is a function of exploited biomass. However, if a certain quantity of the biomass is out of reach of the fishery, this is not correct. Laloe proposed two models based on the assumption that a part of the stock biomass is not available except under a river-flow threshold at which the whole biomass becomes available.

Laloe started from the Graham-Schaeffer model:

$$dB/dt = B_t.H.(B_t-B_v) - q.f_t.B_t \qquad (1)$$

which describes the instantaneous change of the biomass as a function of exploited biomass (B_t), unexploited biomass (B_v), fishing effort (f_t) at time t, and catchability (q), H being the growth rate of the stock.

He assumed that the fishery only acts on a part of the stock, depending on the available biomass, a being the rate of inaccessibility:

$dB/dt = B_t.H.(B_t-B_v) - q.f_t.(B_t-a.B_v)$ (2)

The value of a is constant except during very low river flow (1972, 1978) when it is equal to 0. All the biomass then becomes available, giving equation (1) (Fig. 3b). Another constraint is that $q=0$ if $B_t < a.B_v$.

This model describes catch series correctly until 1980. Most interestingly, it best fits observed data during the «recovery period» of 1973-1976 (Fig 3a).

3. Upwelling, availability and recruitment

The following models include the short or mid-term hypothesized effects of upwelling on CPUE (*i.e.*, respectively availability and recruitment). Unfortunately, they take either the whole pelagic fishery into consideration (Cury and Roy, 1987; Mendelssohn and Cury, 1987) or only the *Sardinella maderensis* fishery (Mendelssohn and Cury, 1989), but not *S. aurita* alone. The theoretical basis for such straightforwardness in modeling is that an overexploited species may be replaced by another, so that the biomass of a system is more steady than that of its components. Moreover, this plurispecific approach does not account for the diversity of ecological niches or the difference in species life-spans.

3. 1. Use of a generalized stock production model

In considering the unexploited biomass B_v as a function of a climatic factor (CLIM), $B_v$avg being the average biomass and b a constant,

$B_v = B_v\text{avg}\ (1 + b.\text{CLIM})$,

Cury and Roy (1987) obtained the following model which Fréon (1984) had studied earlier:

$CPUE_i = e^{-Ao.fi}.(A + B\ CLIM_i)$

where $CPUE_i$ is the catch per unit of effort of the year i, fi fishing effort; and Ao, A, B the constants.

Cold waters reaching the surface bring nutrients into the euphotic layer, so that the planktonic food web is boosted by these inputs. It is considered that strong upwelling can enhance the stock biomass by accelerating individual growth or decreasing the natural mortality of these plankton-feeders (ORSTOM, 1976), although the exact biological mechanisms involved are unknown. However, the abundance of *Sardinella* larvae is related to upwelling intensity, and recruitment is completed at one year. Thus, the following equation gives an empirical model, including fishing effort and an upwelling index (UPW), for years i and i-1:

$CPUE_i = e^{-Ao.fi}.(A + B.UPW_i + C.UPW_{i-1})$

This model allows testing of the roles played by the different variables (Fig. 4). Fishing effort alone can account for only 18% of CPUE variability, whereas the upwelling indices for years i and i-1 account for 40%. The best fit (73%) was obtained with the 3 variables, *i.e.*, fishing effort and the two upwelling indices. An interesting result is that upwelling intensity from the catch year (i) accounts for more variability than upwelling during the spawning year (i-1).

Does this imply that planktonic abundance, providing forage for juvenile or adult fish, is more important for the availability of the resource than for spawning success and larval survival? If so, this would mean that availability is more important than recruitment for CPUE, provided that no recruitment overfishing occurred in the preceding years.

3. 2. Short-term variations and ARMA models

Mendelssohn and Cury (1987) used multivariate auto-regressive moving-average (ARMA) to model Côte d'Ivoire pelagic fish CPUE as a function of sea surface temperature (SST). Fortnightly SST and CPUE means were calculated for the main fishing areas, and the model then fills in any missing point. The results closely reproduce observed series. Thus, a cross-correlation between SST- and CPUE-computed series shows that the best fit is obtained for a one-fortnight time lag.

This is approximately the time lag needed by copepods to benefit from upwelling enrichment (Binet, 1976). The exact duration of the production transfer from nutrient enrichment to the molting of copepodites, including diatom blow-up, maturation and spawning of copepods, is usually longer. However, ontogenetic vertical migration between the Guinea Current and Undercurrent can shorten that time span (Binet, 1991). Thus, if it is determined that short-term availability of pelagic resources is indicated by upwelling intensity within a 2-week time lag, the model is coherent with planktonic production mechanisms.

Strong CPUE persistence is another noticeable result. Once fish are present, they tend to remain. The pelagic species probably come to the surface and school more often when there is abundant zooplankton on which they can feed.

3. 3. Migration patterns

Mendelssohn and Cury (1989) used space-time analysis to study a possible relationship between migration and hydrologic factors in *Sardinella maderensis* CPUE off the Côte d'Ivoire. An east-west migration was apparent in CPUE for one- and two- fortnight lags, and a reverse movement was observed in one- and four-fortnight lags. Similar patterns were noted for transformed SST. Favorable conditions were associated with frontal structure. The west-to-east movement probably reflects advection due to the Guinea Current, and the east-to-west movement changes in upwelling. Fish evidently migrate to be in the area most favorable for zooplankton enrichment.

3. 4. An exception to the «optimal environmental window»

In a study of environment-recruitment relationships among several pelagic stocks in coastal upwelling areas, Cury and Roy (1989) used optimal transformation to search for the best relationships between recruitment and upwelling intensity. They coined the expression «optimal environmental window» to mean that recruitment in a typically Ekman, wind-driven upwelling is maximal for moderate upwelling strengths. In fact, the lower the wind speed, the poorer nutrient input into the food web and recruitment are. Conversely, if the wind is too strong, sea turbulence prevents the minimal phytoplankton stratification required for growth and breaks up the patches of zooplankton, while strong offshore advection carries eggs and larvae away from their nurseries.

The *S. aurita* fishery off the Côte d'Ivoire and Ghana is an exception to this pattern since recruitment (measured by the CPUE of the year) increases continuously with upwelling intensity (measured as a temperature anomaly). These exceptional circumstances may be due to the specificity of the sea surface cooling mechanism in the northern Gulf of Guinea. True Ekman-type wind-driven upwelling cannot be considered as the only explanation for seasonal coolings (Houghton, 1976; Bakun, 1978). Other dynamic processes are probably involved (Verstraete, 1992), *e.g.*, downstream eddies created in the Guinea Current by the cape effect (Marchal and Picaut, 1977), or westward propagation of coastally trapped Kelvin waves (Moore *et al.*, 1978). Coastal shallowing of the thermocline and strengthening of the Guinea Current during boreal summer are related, in a geostrophic adjustment (Ingham, 1970), but it is impossible to say what process preceeds the other (which came first the egg or the chicken ?). Regardless of the exact mechanism of seasonal cooling, if it is not a true wind-driven upwelling, the factor enhancing plankton production cannot be correlated with turbulence or offshore transport which reduce larval survival.

3. 5. A provisional synthesis : the CLIMPROD model

An interesting attempt to account for environmental effects on recruitment and availability in the same model was performed by Fréon (1984, 1988, 1991). In a surplus production model (Schaefer), the instantaneous change of the biomass depends on the natural growth of the population and on the catch :

$$dB/dt = hB(B_v - B) - qfB$$

in which B_v is the biomass before exploitation, B exploited biomass, q catchability and f fishing effort ;

$h = k/B_v$ is a constant, k being the increasing rate of the biomass (r in terrestrial ecology models).

It is easy to introduce an environmental variable into this equation in order to simulate the effect of climate on nonexploited biomass or catchability.

Fréon (1988) began to model the biomass of *S. aurita* as a function of an upwelling index. He considered the CPUE of the year i as a function of fishing effort and upwelling during years (i) and (i-1), assuming that the enrichment caused by upwelling benefits fish during their entire life-span. The model does not fit the *S. aurita* fishery recovery period following the collapse (1974-1977) but accounts for 82% of the variance in the 11 remaining years (Fig. 5a). However, the exceptional availability of 1972 is not dealt with.

Assuming that the high 1972 catch resulted from exceptional availability due to the drought, Fréon added another climatic variable (river flow) to account for annual catchability differences. The fit of this last model is a bit better since it accounts well for overfishing (Fig. 5b). However, the maximum sustainable yield figures seem unreliable.

4. Environmental and biological changes in the 1980s

The first empirical (Binet, 1982) and then deterministic models (Fréon, 1988; Laloe, 1988; Cury and Roy, 1978; Cury and Mendelssohn, 1987) gave consistent results up to the beginning of the 1980s when the correlations broke down as a result of several changes in the fishery. This led to a new examination of climatic and biological backgrounds. The earlier correlations should not be considered as spurious since they worked correctly for about 15 years and are still partially valid. However, something seems to have changed in the main ecological factors determining the state of the ecosystem, its pelagic biomass and spatial and seasonal distribution. We are now confronted with a new system.

4. 1. Changes in the pelagic fishery

Since the beginning of the 1980s, the *S. aurita* fishery has changed considerably compared to the 1960s and 1970s. About half of the yield is caught off the western Côte d'Ivoire and not only in Ghana as in past decades. In addition to semi-industrial purse seiners, a traditional fishery using canoes and seines has spread along the Côte d'Ivoire. In 1984, the yield per fisherman in this traditional fishery was the highest in northwest Africa (Ecoutin *et al.* 1993). Moreover, the fishing season now extends over the entire year rather than being limited to the cold seasons, although landings in June (the first rainy season) remain the poorest. Finally, landings have risen rapidly (over 100,000 mt in 1985) and remained high for several consecutive years, even following the collapse in 1973 after a 90,000 mt catch.

The species composition of the catch has changed, with *S. aurita* becoming the first-ranking pelagic species. In the Côte d'Ivoire purse-seiner fishery, *S. aurita* amounted to 11% of total pelagic fish caught off the Côte d'Ivoire in 1966-1972, 6% in 1973-1980 and 51% in 1981-1988. The lengths of *S. aurita* caught by Côte d'Ivoire purse-seiners have slightly increased. During the same periods, *S. maderensis* represented respectively 43, 70 and 31% of landings. The share of *Brachydeuterus auritus* has continuously decreased, dropping from 19% in the first period to 12% in the second and 7% in the third (Marchal, 1993).

The triggerfish *Balistes carolinensis*, which was infrequent before, proliferated dramatically in every West African trawl fisheries from 1970 onwards, often accounting for more than half the fish biomass from Senegal to Nigeria (Caverivière, 1991) and ranking first in trawling surveys off the Côte d'Ivoire during the short cold seasons from 1978 to 1986 (Caverivière, 1993).

Balistes carolinensis is harvested by Ghanaian trawlers and has become an important target species. Beginning in 1981, and especially since 1986, this species has decreased slowly, notably in the Ghanaian trawl fisheries (Caverivière, 1993). Although the ecological niches of *Balistes carolinensis* and *S. aurita* do not closely coincide, both fish prefer waters with high salinity and low turbidity. Given the role this huge biomass plays in ecological processes, no relationships between variations in the abundance of the two species can be ignored.

The total pelagic biomass of the Côte d'Ivoire shelf has been assessed in more than seven acoustic survey cruises from 1974 to 1987 (Marchal, 1993). Until 1980, biomass density over the Côte d'Ivoire shelf was about a third of Ghanaian shelf density. However, in 1981 the biomass suddenly increased to the density observed off Ghana, remaining at that level in 1986 and 1987 surveys (Fig. 6). As *Balistes carolinensis* decreased, it cannot account for this biomass improvement. Undoubtedly, the biological production of Côte d'Ivoire shelf waters has increased.

All these events clearly indicate an important ecological change, which Marchal (1993) referred to as a real disruption.

4. 2. Recent environmental changes and new hypotheses.

The main climatic features of the last decade in this region were persistence of drought, a slow rise in sea surface temperature (SST), a change in the surface water cooling pattern, acceleration and veering of zonal wind and likely changes in the circulation pattern. The first three points have been clearly determined. The fourth is based on still-debatable measurements and the fifth on a set of direct and indirect observations. The links between these processes are not clearly established, but they may be more or less related to the «global change» the planet is now undergoing.

4. 2. 1. The ongoing drought

Rainfall considerably decreased, and the resulting water shortage was aggravated by the erection of dams and the filling of reservoirs (Volta Lake in Ghana, Lakes Kossou and Taabo on the Bandama River in the Côte d'Ivoire). Along the northern coast of the Gulf of Guinea (from Cape Palmas to Benin), the volume of freshwater runoff has been dramatically reduced. During the 1950s, 1960s, 1970s and 1980s, the mean annual volume of freshwater input into the sea was respectively 247, 246, 164 and 146 km^3 (Mahé, 1993). The amount of suspended sediment has probably been reduced to a greater extent because of silt retention upstream from the dams.

Mensah (1991) found two seasonal rainfall patterns along the coast of Ghana. In this respect, it is evident that any change in the rainfall pattern would concern planktonic production and fish availability. In recent years, pluviometry has improved somewhat.

Since the recovery and expansion of stock, rainfall and river runoff have never returned to previous values, whereas *S. aurita* is now present in every fishing area and during every month except June. This fits with the notion that their occurrence above the Côte d'Ivoire shelf is due to higher salinity. A lack of freshwater inflow apparently led fish to move towards the shore and surface water, so that all the biomass became available to the fishery, whereas the decrease in the *S. aurita* catch during the late 1980s seems to have been associated with a slight increase in rainfall. Caverivière (1993) explained the reduction in *Balistes carolinensis* stock in the same way. The biotope became less saline and more turbid, therefore less favorable to the species.

4. 2. 2. Wind acceleration and sea surface temperature rise

Sea surface temperature (SST) records, obtained from «ships of opportunity» or coastal stations along the Côte d'Ivoire and Ghana shelf (Fig. 8),indicate that there has been a long-term increase since the mid-1960s (Fig. 9b), (Binet and Servain, 1993). Wind-strengthening has also been recorded in ships' data sets (Fig. 9a), (Roy, 1992; Binet and Servain, 1993). SST rise and wind increase have already been reported in other tropical oceans (Bakun, 1990). However, wind-strengthening is a matter of debate since some authors have expressed doubts, citing bias due to the use of anemometer measurements instead of sea-state estimates. A gradual increase in the use of anemometer measurements of recorded data in recent decades may have produced a slow rise in velocity in the wind data base. However, several authors consider that the apparent increase was due at least in part to real changes (Bakun, 1992; see the discussion in Binet and Servain, 1993).

Roy (1992) considered that this strengthening of zonal wind stress may have enhanced planktonic production by an input of nutrients near the surface, as occurs in typical wind-induced upwelling and because of turbulence. This would have accelerated the growth of pelagic fish and improved the survival of their larvae as well as their recruitment, thus leading to higher sustainable yields. The true biological and physical processes are probably more complex since wind-strengthening in a wind-driven upwelling would have led to a drop in SST.

Bakun (1990) already noted a wind velocity acceleration in east boundary current areas and concluded that an intensification of main upwellings had occurred worldwide. However, he did not speak of colder sea surface temperatures. Are we to infer that the entire oceanic troposphere has already been warmed up by the global change?

As noted above, local wind stress alone cannot account for seasonal coolings but may play a certain role (Binet and Servain, 1993). The discrepancy apparent when global SST and wind stress values are compared might be resolved by short-term, small-scale analysis of cooling events.

4. 2. 3. New seasonal and regional cold season patterns

Surface water coolings occur from July to September (main cooling season) and January to February, March, or even April (minor cooling season). However, the minor cooling season is highly variable in time, length and intensity. Warm waters often overlie thermocline waters and interrupt cooling events for several days or weeks.

On a yearly basis, zooplankton biomass and copepod counts are negatively correlated with temperature. In fact, zooplankton abundance is only correlated with drops in SST during the beginning of the long cold season (until the end of July). After that, colder waters do not increase the zooplankton biomass (Binet, 1976). This cooling threshold is never reached during the minor cold season. Thus, intensification of the long cold season has no favorable effect on zooplankton production, whereas lengthening of the short cold season or numerous short cooling events are highly beneficial to plankton. In fact, the planktonic biomass undergoes a slow decline from October until the beginning of the next cold season. Thus, any short cooling event during the first months of the year interrupts this nutrient decline, helping to maintain forage for pelagic species.

The role of minor upwellings was clearly noted by Pezennec and Bard (1992). Timing and the location of minor cold seasons may be of major importance since they create favorable biotopes for plankton feeders such as *S. aurita* in the midst of an otherwise low food period. Conversely, the two main reproducing periods for this species occur within each of these cold seasons, thereby optimizing larval survival.

Cold surface waters are not evenly distributed over the shelf but occur on the eastern side of Cape Palmas and Cape Three Points and are then spread eastwards by the Guinea Current. Remote sensing pictures (Pezennec and Bard, 1992), in agreement with previous hydrological surveys (Morlière and Rebert, 1972), show that these plumes of cold water progressively warm up as they drift eastward. The long cold season is usually colder in Ghana waters east of Cape Three Points than along the Côte d'Ivoire (Arfi *et al.*, 1991; Pezennec and Bard, 1992). Conversely, during the short cold seasons, the cooling is more intense eastwards of Cape Palmas.

4. 2. 3. 1. Short cold season intensification

The long cold season is also referred to as the major upwelling season because the SST are the lowest. However, during the short cold seasons in 1986, 1987 and 1990, the 21°C isotherm rose to 20 m, *i.e.*, about the same depth reached during long cold seasons (Pezennec and Bard, 1992). In the Côte d'Ivoire area, the SST recorded by merchant ships indicate the long-term changes in cold seasons. The difference between January-March minus July-September average SST showed a decreasing trend from 1970 to 1990 (Pezennec and Bard, 1992) (Fig. 10), indicating that the short cold season tended to be equal in intensity to the long cold season. An obvious result was the shortening of the low plankton concentration periods. The recruitment of short cold season cohorts was apparently improved by a more evenly distributed food supply which helped to build up the new pelagic fish biomass.

4. 2. 3.2. Zonal gradient inversion

Another change occurred in the regional SST pattern during the 1980s. Although a general warming trend was evident throughout the area, the water temperature between Abidjan and Cape Three Points dropped slightly. A regular pattern of decreasing alongshore SST from Cape Palmas to Cape Three Points was clearly observed in 1979 and 1980 but then changed progressively until 1983-1984 when it was completely reversed (Herbland and Marchal, 1991). In recent years, the waters off Assinie were cooler than those off Tabou during the long cold season. The same anomaly was observed in merchant ship SST records (Binet and Servain, 1993). The temperature differences between the Abidjan-Cape Three Points and Cape Palmas-Sassandra areas is plotted in figure 11 for the two cold seasons. From the 1980s onwards, two negative multi-year anomalies occurred, *i.e.*, from 1981 to 1985 during July-September, and from 1986 to 1989 during January-March.

For *S. aurita*, the core of the biomass was east of Cape Three Points until 1980, so that these anomalous coolings might have favored a westward extension towards the Côte d'Ivoire shelf. Moreover, if these coolings were associated with plankton enrichment, the spawnings probably increased and reinforced the settlement of *S. aurita* in Côte d'Ivoire waters.

4. 2. 4. A change in the current system ?

The Guinea Current (GC) is an eastward superficial flow fed by the North Equatorial Counter-Current (NECC) off the Liberian coast (Fig. 12). The GC is not very deep, extending on average from the surface to 15 m near the coast and to 25 m offshore. It overlays the Guinea Undercurrent (GUC) flowing westward. The GUC originates from the Bight of Biafra as a return branch of the Equatorial Undercurrent (EUC). In the Bight of Biafra, the GUC can often be observed at the surface. As it runs westward, the GUC progressively drops below the GC (Fig. 13). In May 1972, Lemasson and Rebert (1973) located the dive of the GUC off the Ghana coast. The GC off Abidjan is of minimal thickness during the cold seasons, and reversals of surface circulation are common in October. It is clear that the longitude of the shear surface between GC and GUC depends on the latitudinal range and strength of their respective feeding currents (NECC and EUC).

The eastward-flowing NECC crosses a part of the Atlantic against the tradewinds. This flow migrates between a northern (summer and fall) and a southern (winter and spring) latitude, parallel to the movement of the inter-tropical convergence zone (ITCZ) between northern and southern tradewinds. Indeed, this eastward current flows in the opposite direction under the doldrums rather than the tradewinds area.

According to Philander (1986), «interannual variations in the Atlantic Ocean can be viewed as perturbation of the seasonal cycle». It may thus be supposed that an interannual change in the migration pattern of the ITCZ would induce a similar deviation in NECC latitude. The displacement of the ITCZ has been monitored at longitude 28°W since 1971 (Citeau *et al.*, 1986) (Fig. 14). The average February-April latitude of the ITCZ was farther south from 1978 to 1985 than in subsequent years. Because the NECC feeds the GC directly, a southward shift of the former may induce an offshore displacement or a broadening and a flattening of the latter along the Côte d'Ivoire and Ghana shelf. If our assumption is correct, the GC was nearest to the coast in 1978 and farthest from the coast in 1985. If the GC did not follow the coast closely, the GUC would probably flow over the shelf, nearer the surface and the shore, and dive in a more westerly longitude.

Two sets of current measurements off Abidjan (Lemasson and Rebert, 1973; Colin 1988) indicate westward surface transports in 7 and 9% of observations during «normal years» (1969 and 1970 respectively) versus 23, 29 and 35% during years of southward ITCZ shift (1968, 1983, 1984 respectively). In fact, Atlantic El Ninos occurred in 1968 and 1984 (Hisard, 1988). As Lamb (1978) observed previously, a southward shift of the ITCZ is associated with an El Nino warm event.

On the other hand, oceanographic surveys carried out during 1983-1984 showed a set of processes which can be viewed as consequences of tradewind relaxation (Fig. 12) : (i) Eastward return circulation (NECC, EUC) was intensified and equatorial upwelling weakened. (ii) High salinity waters of the EUC, which are not upwelled, spread into the Gulf of Guinea (Piton and Wacongne, 1985). (iii) This accumulation of waters reversed the sea-surface slope along the equator during the winter of 1984 (Hisard *et al.*, 1986); and there was a strong rise in sea level along the African coast (Katz, 1986). (iv) As a strengthening of poleward (southward and westward) return circulation could be expected from this accumulation of waters, some of this southward water flow was observed along the African coast (Shannon *et al.*, 1986). (v) It is supposed that the same process occurred north of the equator and that because of its increased velocity the GUC underwent higher Coriolis force, shifting northward and closer to the coast. (vi) Meanwhile, the eastward surface GC supposedly shifted to the south, so that westward flow (GUC) remained near the surface and plunged under the GC westward of the usual diving region.

4. 2. 5. One stock and two populations ?

As the main *S. aurita* fishery was centered in Ghanaian waters during the 1960s and 1970s, it was commonly assumed that the stock belonged to a single population. Nevertheless, tuna fishing boats regularly caught this species for live bait off Cape Palmas (FAO, 1974). According to several indices (spawning periods and locations, total length, spatial distribution), Marchal (1991) and Binet and Marchal (1992) considered that the *S. aurita* stock might belong to two populations. Although the distribution of this species is continuous, it would seem that the core of the Ghanaian population, composed of smaller fish, is located between Accra and Cape Three Points, whereas another population of larger fish, mainly situated near Cape Palmas, extends along the Côte d'Ivoire shelf. The *Sardinella* from Ghana spawn mainly during the long cold season, while Côte d'Ivoire fish spawn preferentially during the short cold season. Moreover, the seasonal occurrence of the two populations differs as well. The Ghanaian population appears in shelf surface waters during the long cold season, whereas fish also occur during the warm season near Cape Palmas. In fact, since the beginning of the drought, the salinity of western Côte d'Ivoire waters just decreased a little, during the previously called flooding season, so that surface waters may now be inhabited by such a halophilic species.

Until the end of the 1970s, the Ghanaian (or Cape Three Points) population provided the fishery with most of its yield. Afterwards, the Côte d'Ivoire (or Cape Palmas) population apparently developed rapidly, providing a larger part of the catch. It may be supposed that the change in the current system discussed above accounts for this new scheme of fish distribution (Binet *et al.*, 1991; Binet and Marchal, 1992, 1993).

The relationship between *S. aurita* distribution and high-salinity waters probably includes a relationship with the GUC as well. Marchal (*in* FAO, 1974) noted that «*S. aurita* maintain usually in the high salinity waters of the GUC. They would leave it to feed in surface as far as the salinity is not too low». This idea is demonstrated implicitly in a figure showing *S. aurita* stock during the warm season on the shelf bottom near the maximum salinity depth and the core of the GUC (ORSTOM, 1976).

As in the case of most pelagic species, *S. aurita* larvae undergo a downward ontogenetic migration. The youngest stages live near the surface and progressively move toward the depths as they grow older (Aboussouan, 1971). As this vertical distribution involves both currents, the eastward shift of young larvae is roughly compensated by a transport in the opposite direction when they reach the undercurrent. The vertical distribution of larvae does not exceed 20 m (Marchal, 1993), therefore reducing the advective loss of larvae out of nurseries if the shear surface is not too deep.

According to Sinclair (1988), the abundance of a population is partly determined by the advective processes that occur before recruitment. Possible changes in the current system could have benefited the Cape Palmas population.

During the 1960s and 1970s, the boundary surface between the GC and GUC was usually off Ghana. The migration of larvae between the two current layers ensured the retention of early stages above the shelf. This Ghanaian population yielded good year classes, the strength of which was dependent on the food supply, *i.e.*, on upwelling intensity. During the same time period, the larvae hatched off the western Côte d'Ivoire were advected eastward and lost, so that the recruitment of this population was very poor. From the beginning of the 1980s, a possible change in the current pattern may have favored the abundance of the latter population.

An Ocean Global Circulation Model (OGCM) simulation (Morlière, pers. comm., 1992) indicated that there was an increasing eastward flow along the Atlantic Ocean during the last decade (especially until 1987) in the upper 30 m of water between 3°N and 10°N (*i.e.*, the latitudinal range of the NECC and the GC, Fig. 12). These simulated results are not incompatible with the hypothesis (see above) of a strengthening of return circulation (the westward GUC).

Thus, the development of the Côte d'Ivoire population may have resulted from different changes in the circulation pattern :

(i) A zonal shift of the whole current system, with a westward movement of shear surface between the GC and GUC. The new boundary cutting across the Côte d'Ivoire population would have decreased its advective losses. (ii) An acceleration of both eastward and westward transports would have increased the area of eddies in surface and subsurface currents downstream from Capes Palmas and Three Points. Larger shear turbulences would have retained more larvae and brought colder waters towards the surface.

4. 2. 6. Relationships between wind veering, cooling events and current intensification

Although the aim of this paper is not to instruct physical oceanography, a biologist needs a minimal understanding of physical processes. Nonetheless, the changes which have occurred in northern Gulf of Guinea hydrology and meteorology during the last decade are not yet clearly understood.

The most prominent concern is the contradiction between rises in SST and apparent increases in wind stress. Assuming that there are locally wind-driven upwellings, the mean seasonal SST of different areas between longitude 0° and 10°W along the African coast are in rather good agreement with climatological wind stress. However, such agreement is not apparent when interannual variations are observed (Binet and Servain, 1993). The contradiction is greatest during the long cold seasons since apparent wind increase is associated with sea surface warming.

Conversely, during the rest of the year, weak negative regressions between wind and SST are indicative of probable wind-induced upwelling events (Fig. 15). During the last decade, small clockwise rotations of wind stress occurred, so that the wind component parallel to the coast rose west of Cape Three Points. These intensifications were apparent almost throughout the entire year. It may be supposed that, even in a system in which the main cooling season is not wind-dependent, these changes might have favored slight upwelling events in October-November and from January to May, accounting for the temperature decrease west of Cape Three Points.

Finally, the possible effect of a zonal circulation increase (both eastward and westward) cannot be excluded because, in the context of global warming, they could enhance cold water ascents in turbulent cyclonic eddies downstream from the two capes, *i.e.* on their eastern side. On the other hand, a shallowing of the GUC could have cooled surface waters west of Cape Three Points.

5. Discussion and Conclusion

The main hydrologic factors accounting for the non-density-dependent variability of *S. aurita* abundance were probably identified in the data base of the 1960s and 1970s. Good empirical correlations were observed between river flows, cooling indices and catches. The modeled CPUE fitted the observed data correctly, and 1972 overfishing was roughly understood.

Fish availability depends on salinity and probably on high plankton concentration, both of which are accounted for by «upwelling» indices. Recruitment and replenishment of the stock biomass are also related to plankton abundance in the preceding year. Thus, the same upwelling index may serve as a proxy for all these parameters, provided that it is used with different time lags.

Nevertheless, the exceptional catch of the mid-1980s disrupted all correlations, so that these models proved to be analytic but not predictive tools. During the 1980s, «upwelling» indices showed no particular trends, but the time of cooling events and the place where they occurred showed slight differences compared to previous decades. This new pattern may have favored a westward expansion of the Ghanaian population as well as boosting the previously small population near Cape Palmas. Possible changes in the current pattern would also have led to similar results.

Finally, in this complex ecosystem in which enrichment events did not result from a single physical factor, it is likely that each of the above-cited works provides part of the truth. However, river flow and cooling intensity, identified as the leading factors during the early decades of the fishery, no longer have the same importance in the 1980s due to large-scale changes in the environment. On a long-term basis, river runoff has considerably decreased, and surface water cooling events have increased, whereas the surrounding waters have undergone a slow warming and oceanic circulation has changed for some time. Perhaps, it would be useful to have indices of the spatial variability of the two cold seasons and of changes in the circulation pattern before introducing these factors into models. But the main problem we are facing now is to know how long will last these «new» environmental characteristics ?

REFERENCES

Aboussouan A. (1971). Oeufs et larves de téléostéens de l'ouest africain. IX. Sur la migration des larves de *Sardinella aurita* Val. à proximité de la presqu'île du Cap-Vert. *Bulletin de l'IFAN*, 33(A) : 227-236.

Arfi R., Pezennec O., Cissoko S., Mensah M.A. (1991). Variations spatiale et temporelle de la résurgence ivoiro-ghanéenne. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 162-172.

Bakun A. (1978). Guinea current upwelling. *Nature*, 271, 147-150.

Bakun A. (1990). Global climate change and intensification of coastal ocean upwelling. *Science,* 247, 198-201.

Bakun A. (1992). Global greenhouse effects, multi-decadal wind trends, and potential impacts on coastal pelagic fish populations. *ICES mar. Sci. Symp.*, 195, 316-325.

Binet D. (1976). Biovolumes et poids secs zooplanctoniques en relation avec le milieu pélagique au dessus du plateau ivoirien. *Cah. ORSTOM. sér. Océanogr.*, 14, 301-326.

Binet D. (1982). Influence des variations climatiques sur la pêcherie des *Sardinella aurita* ivoiro-ghanéennes : relation sécheresse - surpêche. *Oceanologica Acta*, 5, 443-452.

Binet D. (1991). Dynamique du plancton dans les eaux côtières ouest africaines : écosystèmes équilibrés et déséquilibrés. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 117-136.

Binet D., Marchal E., Pezennec O. (1991). *Sardinella aurita* de Côte d'Ivoire et du Ghana : fluctuations halieutiques et changements climatiques. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 320-342.

Binet D., Marchal E. (1992). Le développement d'une nouvelle population de sardinelles devant la Côte d'Ivoire a-t-il été induit par un changement de circulation ? *Ann. Inst. Oceanogr.* 68 (1-2), 179-192.

Binet D., Marchal E. (1993). The large marine ecosystem of shelf areas in the gulf of Guinea: long-term variability induced by climatic changes. in: *Large marine ecosystems : stress, mitigation and sustainability*, Ed. by K. Sherman, L.W. Alexander and B.D. Gold. AAAS Press, 104-118.

Binet D., Servain J. (1993). Have the recent hydrological changes in the Northern Gulf of Guinea induced the *Sardinella aurita* outburst ? *Oceanologica Acta* 16, 247-260.

Caverivière A. (1991). L'explosion démographique du baliste (*Balistes carolinensis*) en Afrique de l'ouest et son évolution en relation avec les tendances climatiques. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 354-367.

Caverivière A. (1993). Les ressources en poissons démersaux et leur exploitation. in :*Environnement et ressouces aquatiques de Côte d'Ivoire I. Le milieu marin*, P. Le Loeuff, E. Marchal, J.B. Amon Kothias eds. ORSTOM, Paris, 427-488.

Citeau J., Finaud L., Cammas J.-P. and Demarcq H. (1989). Questions relative to ITCZ migrations over the tropical Atlantic ocean, sea surface temperature and Senegal river runoff. *Meteorol. Atmos. Phys.*, 41, 181-190.

Colin C. (1988). Coastal upwelling events in front of the Ivory Coast during the FOCAL program. *Oceanologica Acta*, 11, 125-138.

Colin C. (1991). Sur les upwellings équatorial et côtier (5°N) dans le Golfe de Guinée. *Oceanologica Acta*, 14 (3), 223-240.

Colin C., Gallardo Y., Chuchla R., Cissoko S. (1993). Environnements climatique et océanographique sur le plateau continental de Côte d'Ivoire. in : *Environnement et ressouces aquatiques de Côte d'Ivoire I. Le milieu marin*, P. Le Loeuff, E. Marchal, J.B. Amon Kothias eds. ORSTOM, Paris, 75-110.

Cury P., Roy C. (1987). Upwelling et pêche des espèces pélagiques côtières de Côte d'Ivoire : une approche globale. *Oceanologica Acta*, 10, 347-357.

Cury P., Roy C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling area. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 670-680.

Ecoutin J.M., Delaunay K., Konan J. (1993). Les pêches artisanales maritimes. in :*Environnement et ressouces aquatiques de Côte d'Ivoire I. Le milieu marin*, P. Le Loeuff, E. Marchal, J.B. Amon Kothias eds. ORSTOM, Paris, 537-550.

FAO, (1974). Etude et mise en valeur des ressources en poissons pélagiques côtiers. Côte d'Ivoire. Conclusion et recommandation du projet. PNUD-FAO, FI : DP/IVC/66/506, Rome, 72 p. dactylogr.

Fréon P. (1984). Des modèles de production appliqués à des fractions de stocks dépendantes de vent d'upwelling (pêche sardinière au Sénégal). *Océanogr. trop.*, 19, 67-94.

Fréon P. (1988). Réponses et adaptations des stocks de clupéidés d'Afrique de l'Ouest à la variabilité du milieu et de l'exploitation. Analyse et réflexions à partir de l'exemple du Sénégal. *Etudes et Thèses.* ORSTOM, Paris, 287 p.

Fréon P. (1991). L'introduction d'une variable climatique dans les modèles globaux de production. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 395-424.

Herbland A., Marchal E. (1991). Variations locales de l'upwelling, répartition et abondance des sardinelles en Côte d'Ivoire. in: *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 343-353.

Hisard P. (1980). Observation de réponses de type «El Nino» dans l'Atlantique tropical oriental, Golfe de Guinée, *Oceanologica Acta*, 3, 69-78.

Hisard P. (1988). El Niño response of the tropical Atlantic ocean during the 1984 year. in : *Int. Symp. Long Term Changes Mar. Fish Pop. 1986*, T. Wyatt and M.G. Larraneta eds., Vigo, 273-290.

Hisard P., Hénin C., Houghton R., Piton B., Rual P. (1986). Oceanic conditions in the tropical Atlantic during 1983 and 1984. *Nature*, 322, 243-245.

Houghton R. W. (1976). Circulation and hydrographic structure over the Ghana continental shelf during the 1974 upwelling. *J. Phys. Oceanogr.*, 6, 910-924.

Ingham M. C. (1970). Coastal upwelling in the northwestern gulf of Guinea. *Bull. Mar. Sci.*, 20, 1-34.

Katz E.J., Hisard P., Verstraete J.M., Garzoli S. (1986). Annual change of sea surface slope along the Equator of the Atlantic Ocean in 1983 and 1984. *Nature*, 322, 245-247.

Koranteng K., A. (1991). Some aspects of the sardinella fishery in Ghana. in : *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 269-277.

Laloe F., (1988). Un modèle global avec quantité de biomasse inaccessible liée aux conditions environnementales : application aux données de la pêche ivoiro-ghanéenne de *Sardinella aurita. Aquatic Living Ressources* 1, 289-298.

Lamb P., (1978). Case studies of the tropical Atlantic surface circulations pattern during recent subsaharian weather anomalies in 1967 and 1968. *Mon. Weather Rev.* 106, 462-491.

Lemasson L., Rebert J.P. (1973). Les courants marins dans le golfe ivoirien. *Cah. ORSTOM, sér. Océanogr.*, 11, 67-96.

Mahé G., (1993). Les écoulements fluviaux sur la façade atlantique de l'Afrique. Etude des éléments du bilan hydrique et variabilité interannuelle, analyse de situations hydroclimatiques moyennes et extrêmes. *Etudes et Thèses.* ORSTOM, Paris, 438 p.

Marchal E. (1991). Un essai de caractérisation des populations de poissons pélagiques côtiers : cas de *Sardinella aurita* des côtes ouest-africaines. in : *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 192-200.

Marchal E., (1993). Biologie et écologie des poissons pélagiques côtiers du littoral ivoirien. in :*Environnement et ressouces aquatiques de Côte d'Ivoire I. Le milieu marin*, P. Le Loeuff, E. Marchal, J.B. Amon Kothias eds. ORSTOM, Paris, 237-270.

Marchal E., Picaut J. (1977). Répartition et abondance évaluées par écho-intégration des poissons du plateau ivoiro-ghanéen en relation avec les upwellings locaux. *J. Rech. Océanogr.*, 2, 4, 39-57.

Mendelssohn R, Cury P. (1987). Forecasting a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.*, 44, 408-421.

Mendelssohn R, Cury P. (1989). Temporal and spatial dynamics of a coastal pelagic species, *Sardinella maderensis* off the Ivory Coast. *Can. J. Fish. Aquat. Sci.*, 46, 1686-1697.

Mensah M. (1991). The influence of climatic changes on the coastal oceanography of Ghana. in : *Pêcheries ouest-africaines. Variabilité, instabilité et changement*, P. Cury et C. Roy eds. ORSTOM, Paris, 67-79.

Moore D.W., Hisard P., McCreary J.P., Merle J., O'Brien J.J., Picaut J., Verstrate J.M., Wunsch C. (1978). Equatorial adjustment in the eastern Atlantic. *Geophys. Res. Lett.*, 5, 637-640.

Morlière A. (1970). Les saisons marines devant Abidjan. *Doc. Scient.* C.R.O. Abidjan, 1 (2), 1-15.

Morlière A., Robert J.P. (1972). Etude hydrologique du plateau continental ivoirien. *Doc. Scient.* C.R.O. Abidjan, 3, 1-30.

ORSTOM, (1976). Rapport du groupe de travail sur la sardinelle des côtes ivoiro-ghanéennes. Fishery Research Unit Tema, Centre de Recherches Océanographiques Abidjan, ORSTOM. 62 p.

Pezennec O., Bard F.-X. (1992). Importance ecologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita. Aquat. Living Resour.*, 5, 249-259.

Pezennec O., Marchal E., Bard F.-X. (1993). La pêche des petites espèces pélagiques en Côte d'Ivoire in :*Environnement et ressouces aquatiques de Côte d'Ivoire I. Le milieu marin*, P. Le Loeuff, E. Marchal, J.B. Amon Kothias eds. ORSTOM, Paris, 387-426.

Philander S.G.H. (1986). Unusual conditions in the tropical Atlantic ocean in 1984. *Nature*, 322, 236-238.

Picaut J. (1983). Propagation of the seasonal upwelling in the eastern equatorial Atlantic. *J. Phys. Oceanogr.*, 13, 18-37.

Piton B., Wacongne S. (1985). Unusual amounts of very saline subsurface water in the eastern Gulf of Guinea in May 1984. *Tropical Ocean-Atmosphere Newsletter*, 32, 5-8.

Roy C. (1992). Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'Ouest : analyse et modélisation. *Etudes et Thèses*. ORSTOM, Paris. 146 p.

Shannon L.V., Boyd A.J., Brundrit G.B., Taunton-Clark J. (1986). On the existence of an El-Niño-type phenomenon in the Benguela system. *J. mar. Res.*, 44, 495-520.

Sinclair M. (1988). Marine populations : An essay on population regulation and speciation. Washington Press, Seattle and London. 252 p.

Verstraete J.-M. (1992). The seasonal upwellings in the Gulf of Guinea. *Prog. Oceanog.* 29, 1-60.

CAPTIONS OF FIGURES

Figure 1 : Annual catches of *Sardinella aurita* in Ghana and Côte d'Ivoire from 1963 to 1990, according to Pezennec and Bard, (1992).

Figure 2 : Relationships between the annual yield (Y) of *Sardinella aurita* in Ghana and Côte d'Ivoire (1964-1985) and (a) : an index of upwelling intensity (U) at Tema, (b) : the Bandama and Comoé rivers flows (F). The regression are (a) $Y(t) = 162U - 5430$ ($r=0.44$) and (b) $Y(t) = -50.3\ D(m3/s) + 56700$, ($r=0.45$). From Binet *et al.*, (1991).

Figure 3 : Global production model with unaccessible part of biomass (Laloe, 1988). a) Observed and fitted catches, with model M1. b) Equilibrium Catch-Effort relationship when biomass is totally accessible ($a=0$) or not ($a=0.453$), with model M2.

Figure 4 : A production model using fishing effort and upwelling indices (Cury and Roy, 1987). CPUE for all the pelagic species, from 1966 to 1981, observed values (solid line) and predicted values (dashed line), with the following parameters : 1) effort only; 2) upwelling indices, year i and i-1 only; 3) effort and upwelling index, year i; 4) effort and upwelling index, year i-1; 5) effort and upwelling indices, year i and i-1.

Figure 5 : Production model using fishing effort and environmental indices (Fréon, 1991). (a) : Observed and modeled CPUE of the Ivorian purse seiners using upwelling indices for abundance and catchability of *Sardinella aurita*. Adjustement without the years 1974 and 1975. (b) : Observed and modeled *S. aurita* catch of the Ivorian and Ghanaian fisheries using upwelling index and river flow to account for abundance and catchability, respectively. 1974-1978 : recovering period following the 1972 overfishing.

Figure 6 : Density of pelagic fish estimated by acoustic surveys (t/mille^2) over the Ghana and Côte d'Ivoire shelf in 1976, 77, 80, 81, 86 and 87. For 1981, the average for two cruises is given; *Balistes carolinensis* amounted 25-83 % of this biomass. During subsequent surveys *Sardinella aurita* represented 10 to 38 %, From Marchal (1993) and Binet and Marchal (1992).

Figure 7 : Annual flows (1955-1988) in m^3/s for the Bandama, Comoé and Volta rivers. Data of Bandama, Comoé and Volta at Senchi from ORSTOM and DRES Côte d'Ivoire, data for the Volta river at Akosombo from the Volta River Authority (Arma, pers. comm.).

Figure 8 : Map of the northern part of the Gulf of Guinea, indicating the positions of coastal stations along the Ivorian gulf and the 2° x 2° (S1 to S5) grids used in the processing of ships observations.

Figure 9 : Annual anomalies of : (a) wind stress modulus m2/s2; and (b) SST (°C) averaged between 0° and 10°W (S1 to S5) from ships data (1964-1990). Dashed lines represent adjusting functions. From Binet and Servain (1993).

Figure 10 : Annual differences (1970-1990) between SST in January-March (little cold season) and in July-September (great cold season), from the merchant ship data set in the Ivorian region (8°-2° West, 4°-6°N). From Pezennec and Bard (1992).

Figure 11 : Annual differences (1964-1990) between eastern and western sea surface temperature in the Ivorian gulf : SST (4°-2°W) - SST (8°-6°W), for January-March and July-September. The usual SST zonal gradient is inverted during the great cold seasons 1981-1985 and during the little cold seasons 1986-1989. From Binet and Servain (1993).

Figure 12 : Outlines of the changes in the circulation of the tropical Atlantic, due to the Inter-Tropical Convergence Zone (ITCZ) move towards the equator in 1984. NECC : North Equatorial Counter Current, GC : Guinea Current, GUC : Guinea Under Current. Italics : supposed changes. From Binet and Marchal (1992).

Figure 13 : Longitudinal section of the zonal components of the circulation off the Côte d'Ivoire to the Nigeria; 0-100 m profiles on the continental shelf at 10 to 23 nautical miles from the shore, May 1972. The zonal velocities are indicated in cm/s; each contour line corresponds to a 10 cm/s variation. E and W indicate the eastward and westward flow, respectively. The 0-contour is the shear layer separating the Guinea Current (GC) from the Guinea Under Current (GUC). From Lemasson and Rebert, (1973).

Figure 14 : Annual changes (1971-1990) of the mean ITCZ latitude in February-April, in 1/10 degrees latitude N. Data from remote sensing observations (UTIS-Dakar and Citeau pers. comm.).

Figure 15 : Regression coefficients of SST vs Alongshore Wind Stress, for every month and squares 1 to 5. 12th differencing each monthly series has been done prior to analysis to remove autocorrelations. Negative values indicate likely wind-induced upwellings. The interannual variations of the surface waters coolings in the long cold season are unrelated to the wind stress, meanwhile weak upwelling trends occur during the rest of the year, except in S1. Longitude ranges of the geographical squares S1 : 10°-8°W, S2 : 8°-6°W, S3 : 6°-4°W, S4 : 4°-2°W, S5 : 2°W-0° (See Figure 8). From Binet and Servain, (1993).

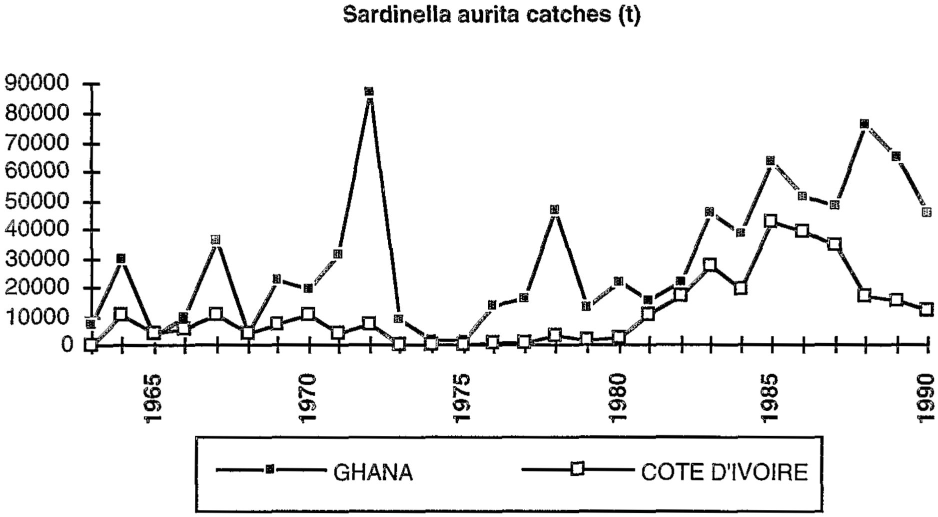


Figure 1 : Annual catches of *Sardinella aurita* in Ghana and Côte d'Ivoire from 1963 to 1990, according to Pezennec and Bard, (1992).

Fig. 2 a

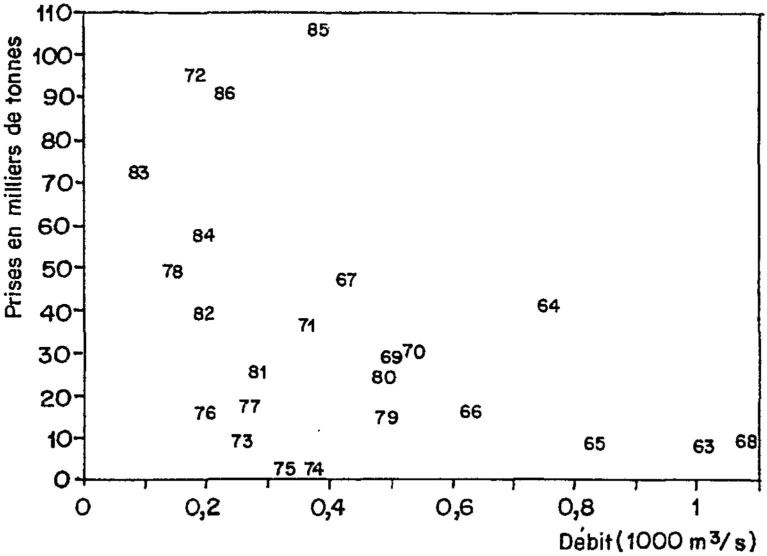


Fig. 2 b

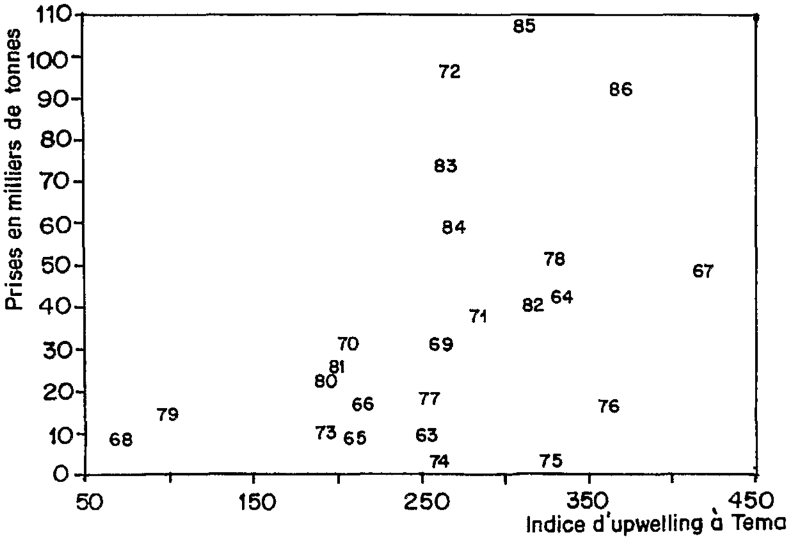


Figure 2 : Relationships between the annual yield (Y) of *Sardinella aurita* in Ghana and Côte d'Ivoire (1964-1985) and (a) : an index of upwelling intensity (U) at Tema, (b) : the Bandama and Comoé rivers flows (F). The regression are (a) Y(t) = 162U - 5430 (r=0.44) and (b) Y(t) = - 50.3 D(m3/s) + 56700, (r=0.45). From Binet *et al.*, (1991).

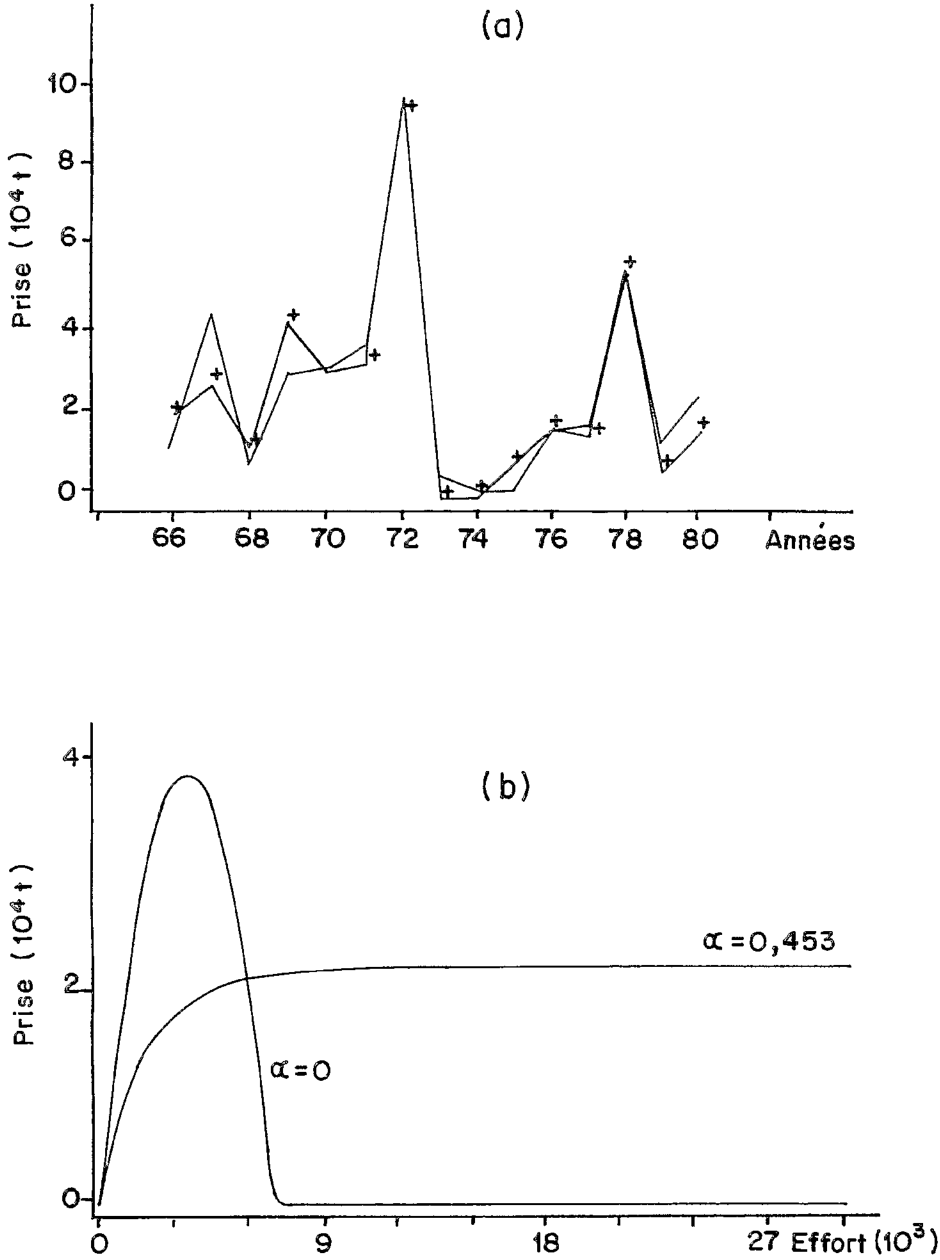


Figure 3 : Global production model with unaccessible part of biomass (Laloe, 1988). a) Observed and fitted catches, with model M1. b) Equilibrium Catch-Effort relationship when biomass is totally accessible (a=0) or not (a=0.453), with model M2.

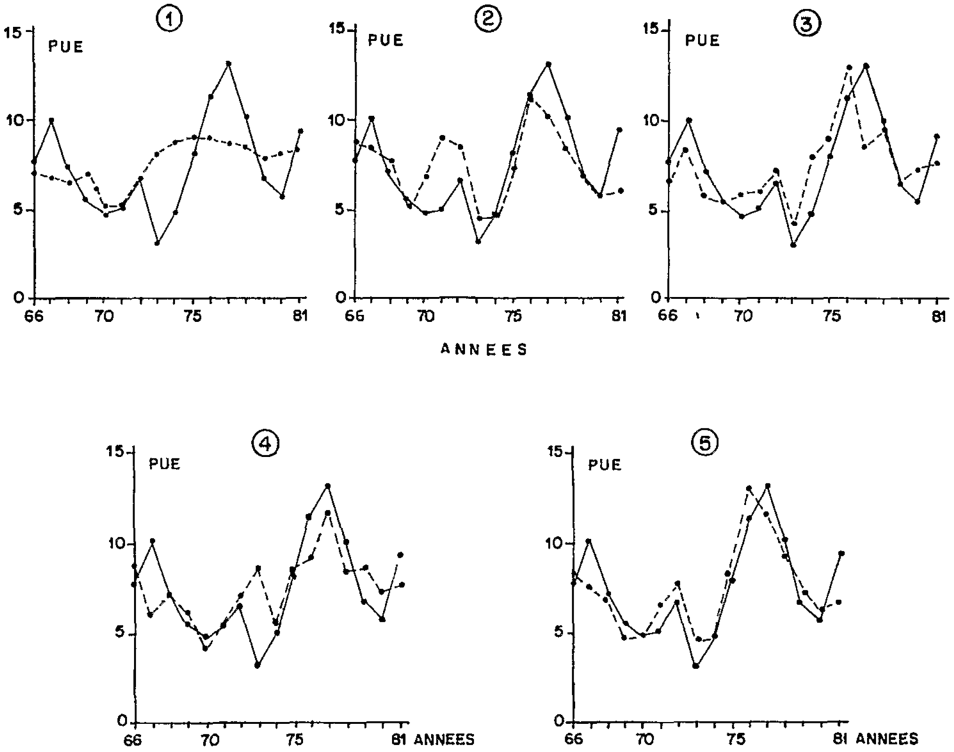


Figure 4 : A production model using fishing effort and upwelling indices (Cury and Roy, 1987). CPUE for all the pelagic species, from 1966 to 1981, observed values (solid line) and predicted values (dashed line), with the following parameters : 1) effort only; 2) upwelling indices, year i and i-1 only; 3) effort and upwelling index, year i; 4) effort and upwelling index, year i-1; 5) effort and upwelling indices, year i and i-1.

Fig. 5 a

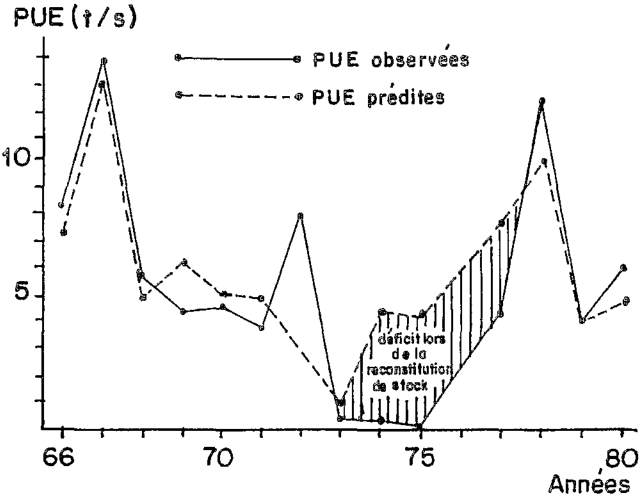


Fig. 5 b

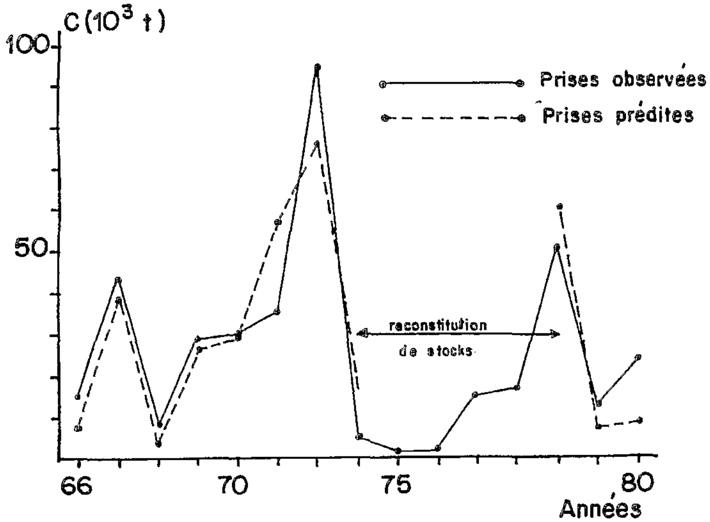


Figure 5 : Production model using fishing effort and environmental indices (Fréon, 1991). (a) : Observed and modeled CPUE of the Ivorian purse seiners using upwelling indices for abundance and catchability of *Sardinella aurita*. Adjustement without the years 1974 and 1975. (b) : Observed and modeled *S. aurita* catch of the Ivorian and Ghanaian fisheries using upwelling index and river flow to account for abundance and catchability, respectively. 1974-1978 : recovering period following the 1972 overfishing.

Biomass obtained by acoustic surveys

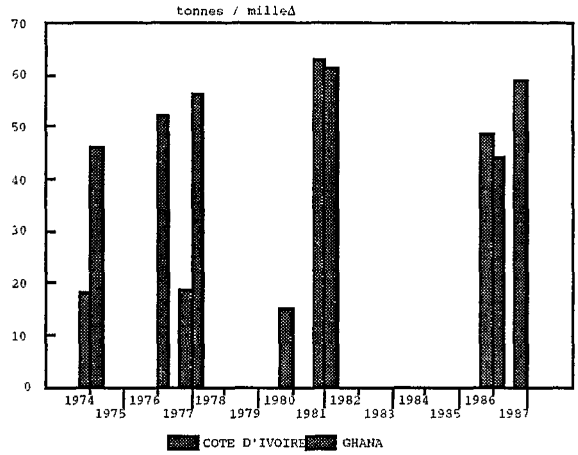


Figure 6 : Density of pelagic fish estimated by acoustic surveys (t/mille^2) over the Ghana and Côte d'Ivoire shelf in 1976, 77, 80, 81, 86 and 87. For 1981, the average for two cruises is given; *Balistes carolinensis* amounted 25-83 % of this biomass. During subsequent surveys *Sardinella aurita* represented 10 to 38 %, From Marchal (1993) and Binet and Marchal (1992).

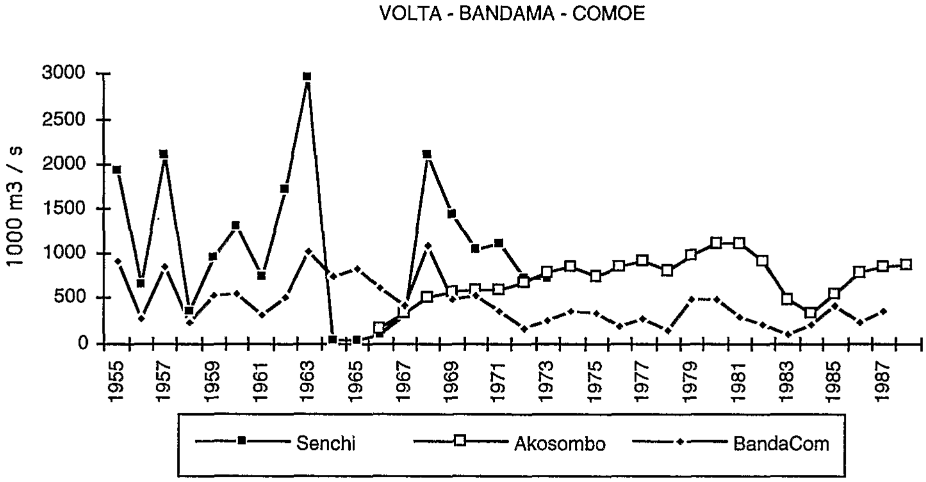


Figure 7 : Annual flows (1955-1988) in m^3/s for the Bandama, Comoé and Volta rivers. Data of Bandama, Comoé and Volta at Senchi from ORSTOM and DRES Côte d'Ivoire, data for the Volta river at Akosombo from the Volta River Authority (Arma, pers. comm.).

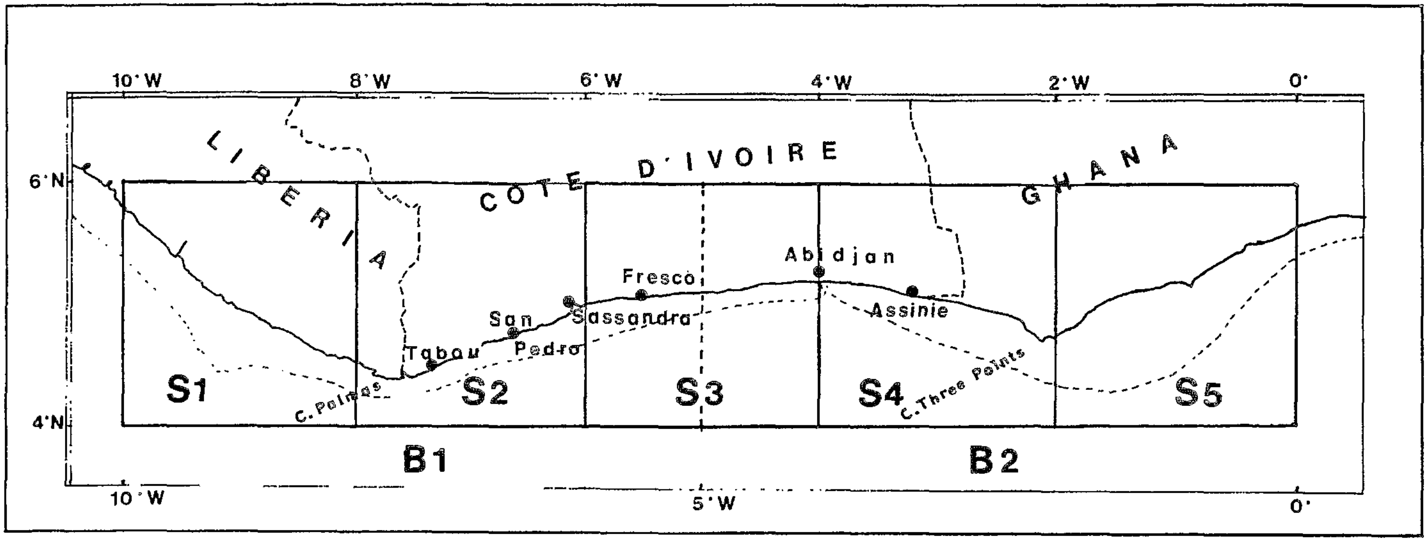
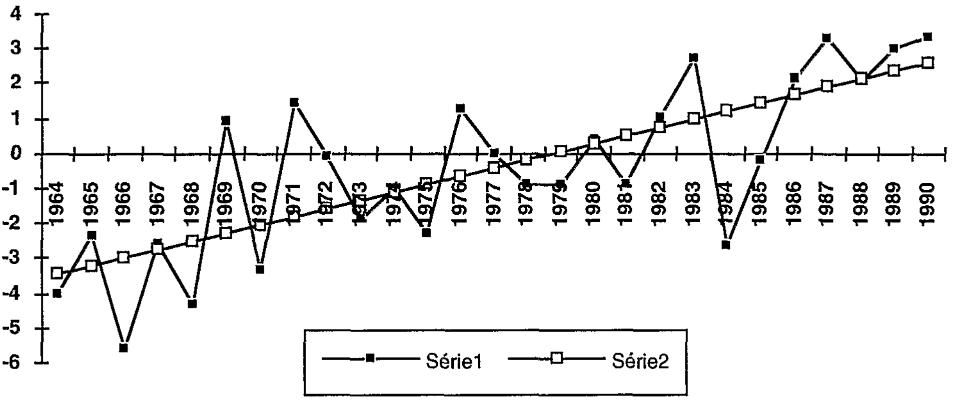
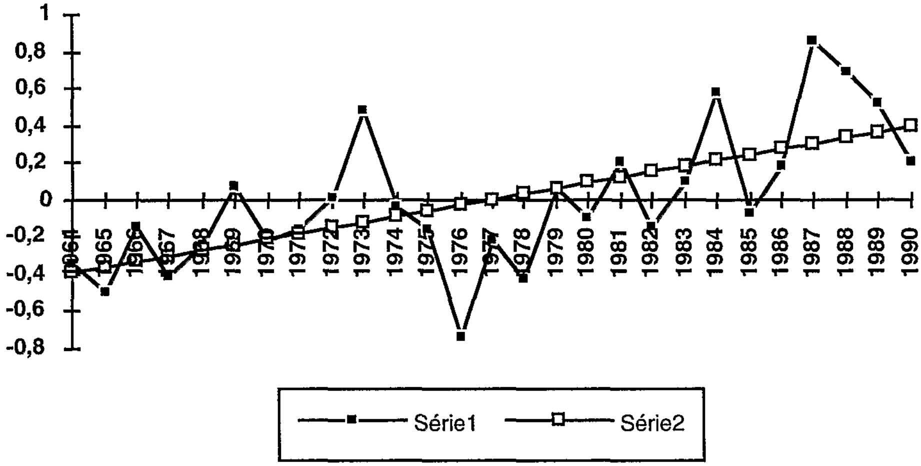


Figure 8 : Map of the northern part of the Gulf of Guinea, indicating the positions of coastal stations along the Ivorian gulf and the 2° x 2° (S1 to S5) grids used in the processing of ships observations.



a - Wind Stress Modulus Anomaly (mΔ/sΔ)
0° - 10° W



b - SST Anomaly (°C) - 0°-10° W

Figure 9 : Annual anomalies of : (a) wind stress modulus m2/s2; and (b) SST (°C) averaged between 0° and 10°W (S1 to S5) from ships data (1964-1990). Dashed lines represent adjusting functions. From Binet and Servain (1993).

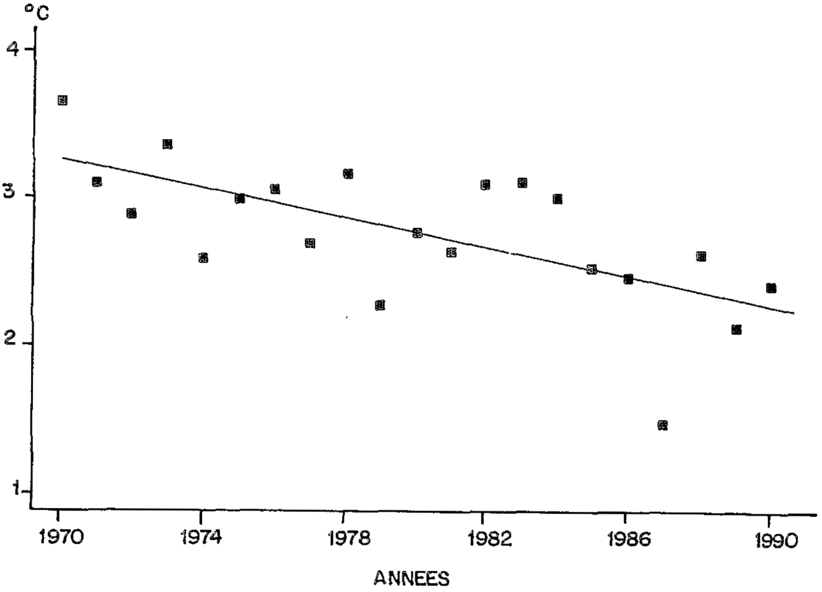


Figure 10 : Annual differences (1970-1990) between SST in January-March (little cold season) and in July-September (great cold season), from the merchant ship data set in the Ivorian region (8°-2° West, 4°-6°N). From Pezennec and Bard (1992).

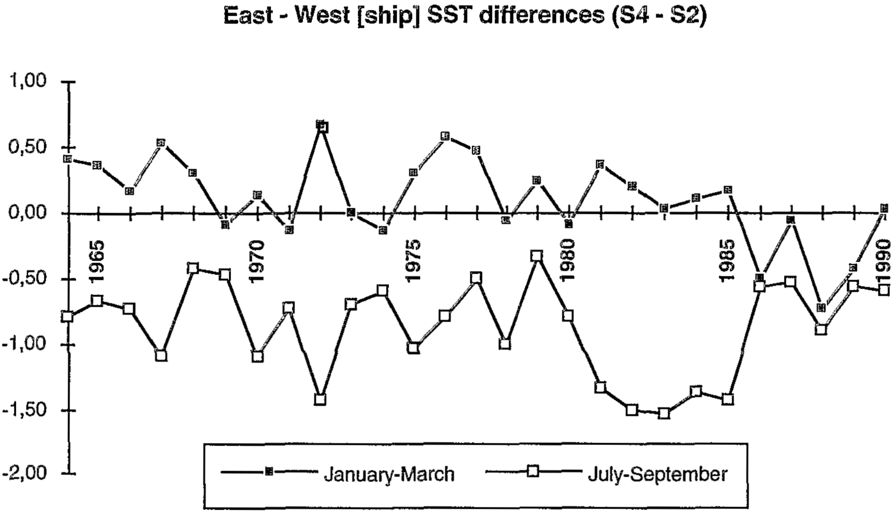
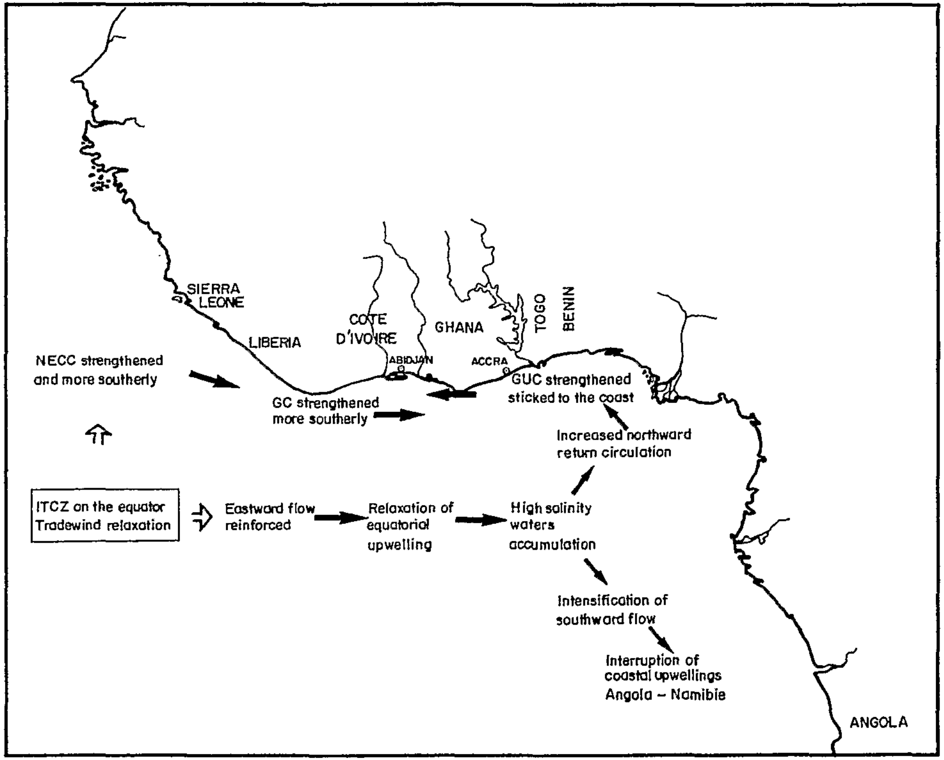


Figure 11 : Annual differences (1964-1990) between eastern and western sea surface temperature in the Ivorian gulf: SST (4°-2°W) - SST (8°-6°W), for January-March and July-September. The usual SST zonal gradient is inverted during the great cold seasons 1981-1985 and during the little cold seasons 1986-1989. From Binet and Servain (1993).

Figure 12 : Outlines of the changes in the circulation of the tropical Atlantic, due to the Inter-Tropical Convergence Zone (ITCZ) move towards the equator in 1984. NECC : North Equatorial Counter Current, GC : Guinea Current, GUC : Guinea Under Current. Italics : supposed changes. From Binet and Marchal (1992).



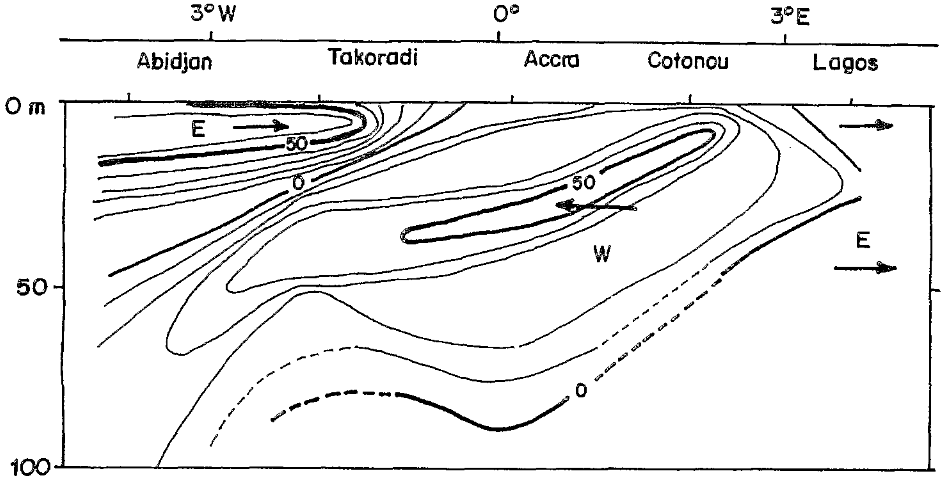


Figure 13 : Longitudinal section of the zonal components of the circulation off the Côte d'Ivoire to the Nigeria; 0-100 m profiles on the continental shelf at 10 to 23 nautical miles from the shore, May 1972. The zonal velocities are indicated in cm/s; each contour line corresponds to a 10 cm/s variation. E and W indicate the eastward and westward flow, respectively. The 0-contour is the shear layer separating the Guinea Current (GC) from the Guinea Under Current (GUC). From Lemasson and Rebert, (1973).

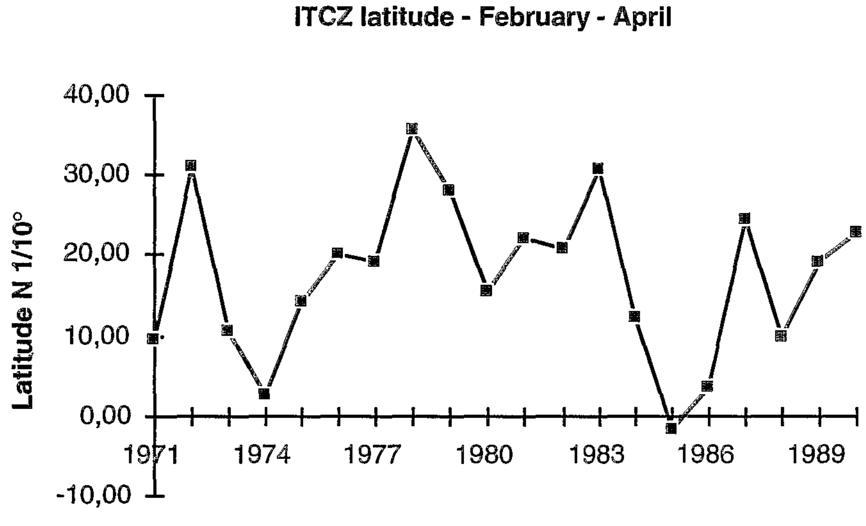


Figure 14 : Annual changes (1971-1990) of the mean ITCZ latitude in February-April, in 1/10 degrees
latitude N. Data from remote sensing observations (UTIS-Dakar and Citeau pers. comm.).

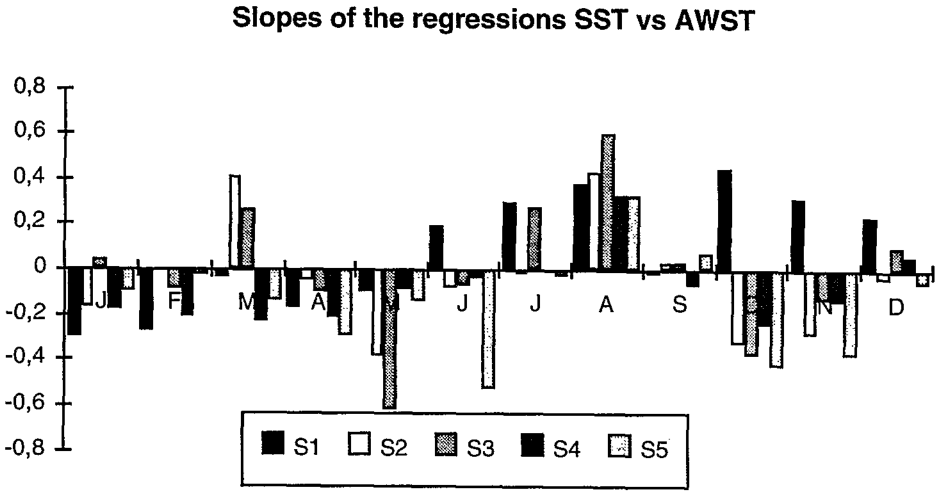


Figure 15 : Regression coefficients of SST vs Alongshore Wind Stress, for every month and squares 1 to 5. 12th differencing each monthly series has been done prior to analysis to remove autocorrelations. Negative values indicate likely wind-induced upwellings. The interannual variations of the surface waters coolings in the long cold season are unrelated to the wind stress, meanwhile weak upwelling trends occur during the rest of the year, except in S1. Longitude ranges of the geographical squares S1 : 10°-8°W, S2 : 8°-6°W, S3 : 6°-4°W, S4 : 4°-2°W, S5 : 2°W-0° (See Figure 8). From Binet and Servain, (1993).