Introduction

The Gulf of Guinea ecosystem extends from the Bissagos Islands to Cape Lopez (Fig. 1). Its shelf waters are shared between subsystems; one is characterized by thermal stability of waters, the other by instability. In the first subsystem, nutrient input depends on land drainage, river flood, and turbulent diffusion through a stable pycnocline; in the second subsystem, periodic rising of mid-depth water raises nutrients to the euphotic layer (Binet, 1983a). This seasonal

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**Figure 1.** Surface circulation in the eastern tropical Atlantic. NECC: North Equatorial Counter Current; GC: Guinea Current; SEC: South Equatorial Current. Hatched belt along the coast: Seasonal upwelling and *Sardinella aurita* fishery area.
Large Manne Ecosystem of the Gulf of Guinea

upwelling only concerns the part of the coast between Cape Palmas and Cotonou, from approximately 8°W to 2°E. The processes regulating the functioning of these two subsystems are quite different. The Gulf of Guinea upwelling ecosystem differs from eastern boundary current systems because of its proximity to the equator and its seasonal functioning.

Living resources of the Gulf of Guinea have supported increasing fishing effort since the end of the 1950s. Significant changes have occurred in the weight and taxonomic composition of landings since the start of this industrial fishery (Fig. 2). The most abundant pelagic species are Sardinella aurita, S. maderensis, Engraulis encrasicolus, Brachydeuterus auritus, and, in certain years, Scomber japonicus. During the last 2 decades, the most striking events were the dramatic increase of the trigger fish (Balistes carolinensis) during the 1970s, recently followed by a severe decrease (Caverivière, 1982, 1991), and the 1973 collapse of the Sardinella aurita fishery, followed by a recovery and unprecedented sustained landings during the 1980s (Binet et al., 1991). Population dynamics alone do not explain these changes; thus, wise management of living resources requires, in addition, an understanding of the climatic forcings on the ecosystem to determine the level of fishing effort appropriate to these changing patterns.

Meteorology and Oceanography

The Inter-Tropical Convergence Zone (ITCZ) is the doldrums area separating northern and southern trade winds. It is a zone of instability, generating rains. On the northern coast of the Gulf of Guinea, this frontal zone separates dry, continental, heavy air masses from wet, maritime, lighter, southern trade wind air masses. Latitudinal migration of the ITCZ generates seasons over the tropical Atlantic Ocean and African land masses.

The Tropical Surface Waters (TSW) with high temperatures and varying salinity overlie a density discontinuity layer at the thermocline. Below this layer lies the South Atlantic Central Water (SACW) (Longhurst, 1962). The salinity of the TSW is lowered by input from rivers, especially during the wet monsoon. The first rains occur in June, when the ITCZ crosses the shoreline to begin its northward ascent. The short coastal rivers are in spate. The second, and most important flooding season, extends from September to November, when the ITCZ migrates southward and the floods of the great Sudanian rivers reach the sea (Fig. 3). Large amounts of warm water of low salinity (Guinean waters) originate also from the Bight of Biafra and off the Guinea coast (Berrit, 1961, 1962a, 1962b, 1966). These Guinean waters limit the seasonal upwelling area on one side at the front of Cape Palmas and on the other side in the Cotonou-Lagos region.

Off the Côte d'Ivoire and Ghana, the TSW are seasonally driven away by an upwelling. The underlying SACW takes their place from the end of June to late September. Does this cooling result from a true Ekman-type, wind-driven
upwelling, as Verstraete (1970) proposed? More recently, Colin (1988) defends this opinion, which has been criticized by Bakun (1978). Is the rise of the thermocline caused by the geostrophic adjustment of the Guinea Current (GC) (Ingham, 1970) or by the passage of an internal coastal trapped wave (Picaut, 1983)? Downstream eddies created in the GC can also have a part in this cooling (Marchal and Picaut, 1977). The answer may be composite and is unclear. Nevertheless, it is a biologist’s concern because in a wind-driven upwelling the advective offshore transport, caused by wind stress, drives plankton away from the nutrient spring. In this case, upwelling intensification raises the nutrient input to the euphotic layer. But meanwhile, it also increases the loss of plankton from the coastal ecosystem.

An interesting feature of wind-driven upwellings is that the same Ekman offshore transport requires a weaker wind in lower rather than higher latitudes. Consequently, the same nutrient supply may be reached at a lower turbulence rate. Thus, in this near-equator upwelling, the primary production bloom can follow cool events with a shorter lag than in a subtropical region, such as the Canary Current (Roy, 1991).

The GC is an eastward, superficial flow that is fed by the North Equatorial Counter Current (NECC) off the Liberian coast (Fig. 1). The GC is not very deep—on average, it extends from the surface to 15 m near the coast and 25 m offshore. It overlays the Guinea Under Current (GUC) flowing westward. The GUC originates from the Bight of Biafra, as a return branch of the Equatorial Under Current (EUC) (Fig. 4). In the Bight of Biafra, the GUC may often be observed at the surface (Longhurst, 1964). As it runs westward, the GUC progresses under the GC. Some inversions of the surface flow (i.e., westward circulation) occur from time to time; the percentage occurrences of these reversals decrease from the Niger River to Cape Three Points (Longhurst, 1962). In 1972, Lemasson and Rébert (1973a) located the dive of the GUC under the GC off the Ghana coast (Fig. 5).

![Figure 4. Subsurface circulation in the eastern tropical Atlantic. EUC: Equatorial Under Current; GUC: Guinea Under Current; BUC: Benguela Under Current. Dotted region is the area of the subsurface salinity maximum (>36 x 10^{-3}) located around 50 m depth in May 1984 (from Piton and Wacongne, 1985).]
Plankton

Seasonal variations

Dandonneau (1971), Reyssac and Roux (1972), Bainbridge (1972), and Binet (1977, 1978, 1979, 1983b) showed that the taxonomic composition of phytoplankton and zooplankton was strongly related to the different hydrological seasons. Multivariate analyses show the coincidence between species assemblages and hydrological seasons: stability or upwelling, coastal rains, or flood season (Fig. 6). Thus, during every season, the specificity of nutrient supply, of vertical stratification or mixing, and perhaps coastal stream patterns, generate different states of the ecosystem.

Primary production is stimulated by the nutrient input carried to the surface of the sea by the runoff of the first rains over the land (June), then by the major upwelling, and finally by the flood of the larger rivers (September-October). Thus, the number of phytoplanktonic cells is at a peak during the months from June to September (Fig. 7). The depletion of external nutrients then leads to a progressive decrease in phytoplankton biomass. The production then depends only on regenerated nutrients, except during the minor upwelling.

Figure 5. Longitudinal section of the zonal components of circulation off the Ivory Coast to Nigeria; 0–100 m profile 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 eastward and westward flows, respectively. The 0-contour is the shear layer separating the Guinea Current (GC) from the Guinea Under Current (GUC) (from Lemasson and Rebért, 1973a).

Figure 6. Principal components analysis of mean fortnightly abundances of zooplankton taxa during a composite year: projections of the average fortnights (points 1 to 24) in the factorial plane II, III (from Binet, 1977). The position of the points in the factorial space depends on the taxonomic composition of the corresponding fortnights; the nearer the points, the more similar the taxonomic compositions. The vicinity of points belonging to the same hydrological set show the similarity between hydrological and ecological seasons: (a) great cool season (July to September); (b) littoral cool season (January to mid-February); (c) great warm season (March to May); (d) little warm season (mid-November to mid-December); (e) first flood season (June); (f) second flood season (October to mid-November). (See Figure 3).
season (January to March), when small-intensity, short-lived upwellings take place—especially on the eastern sides of Cape Palmas and Cape Three Points—in the wake these headlands create in the GC (Dandonneau, 1973).

The zooplankton biomass follows the same seasonal pattern (Fig. 7). The number of copepods is also correlated with the upwelling cooling, but with a 2-week lag time (Binet, 1976).

**Relationships between upwellings and river flows**

A detailed analysis of the relationships between upwellings and river flows shows that the biomass of zooplankton is not linearly correlated to the input of deep-origin nutrients in the euphotic layer. At a coastal station near Abidjan, the correlation found between the upwelling intensity and the increase of zooplankton biomass is not valid for the months of August, September, and October, namely, the maximum cooling period (Binet, 1976). The upwellings benefit the zooplankton biomass especially when they break a period of thermal stability; but during the main cold season, after some weeks of continuous upwelling, the zooplankton biomass is no longer related to upwelling intensity.

Two explanations may be proposed. One possibility is that the input of deep-origin nutrients is linked to some turbulence that delays the phytoplankton growth and destroys patches of zooplankton. That would be the case in a wind-driven upwelling, but Cury and Roy (1989) do not accept this hypothesis for Côte d'Ivoire and Ghana. The second possibility is that nutrients may become a limiting factor. In upwellings, the growth of large diatoms consumes heavy quantities of silica, the regeneration of which is rather long. The flood from rivers enters the sea during these months and can alter the silica deficiency. Indeed, the biomass of zooplankton is correlated with the inflow of fresh water, especially during these 3 months (Binet, 1976, 1983b).

Finally, it appears that the planktonic biomass production depends on nutrient input from deep water or from the rain runoff from land. However, the relationship between the physical factors accountable for this enrichment and the planktonic production cannot be linear, except in the short range. In a wind-driven upwelling, the turbulence or deficiency of a given element slows down biological growth. In river plumes, the speed of the stream

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**Figure 7.** Average seasonal variation in abundance of phytoplankton (number of cells/l, log scale) and zooplankton (settled volumes in ml/m$^3$). Averages calculated from data collected during the period 1969–1975 (data from Dandonneau and Binet, unpublished).
and the opacity of water caused by suspended materials inhibits primary production in the proximate lagoons and river mouths. To be optimal with respect to other factors, the transfer of organic matter along the food web needs a long residence time of grazers near their forage. An algal cell takes on the order of hours to divide, but the reproductive cycle of copepods, even in tropical waters, needs about 2 weeks to be achieved.

Zooplankton retention behavior

The quasi-coincidence of phytoplankton and zooplankton seasonal maxima must be pointed out. It may be explained by a behavioral particularity of some copepods. Many zooplankton species migrate between surface and sub-surface waters. Diel migration is the most well known of these vertical movements. The progressive sinking of the core of a species distribution as it is growing older (i.e., ontogenetic migration) is another interesting vertical movement. As a matter of fact, *Calanoides carinatus*, the most abundant copepod species in the upwelling season, spends the first stages of its life in surface waters and then dwells in deeper layers (Binet and Suisse de Sainte Claire, 1975). The sinking of this population means a change from an eastward- to a westward-moving one; thus, horizontal advection of the total population is reduced (Fig. 8). This species and others exhibiting the same vertical migration pattern considerably reduce the numerical loss they would be subject to if they were to spend all of their lifetime in the same current layer. In addition, this behavior allows a more favorable transfer from primary to secondary production because the secondary consumers remain in the vicinity of the upwelling phytoplankton bloom.

The shallowness of the undercurrent and this pattern of migration are probably the reasons why phytoplankton and zooplankton seasonal cycles are in phase in the Guinea upwelling LME, an occurrence that is not observed in other eastern boundary current ecosystems. In the Canary Current, the undercurrent is very deep (500 to 1000 m) and the Ekman offshore transport is very fast. Thus, larger zooplankton are found off the shelf and the biomass peak lags several weeks behind that of plankton (Binet, 1988).

Pelagic tunicates and Cladocera are interesting exceptions. By their opportunistic strategy, they can harvest a plankton bloom and reproduce quickly by scissiparity or parthenogenesis, resulting in crowding populations. They live at the surface and their multiplicative forms can be found in great numbers in the vicinity of upwellings in the Canary Current (Furnestin, 1957) and in the GC (Binet, 1977). When the period and location of food abundance is past, they generate resting forms.

Long-Term Environmental Changes

The drought

The Sahelian countries have been suffering from a severe drought for the past 2 decades. The mean annual flow of the great Ivorian rivers has been reduced to half the volume of the 1950s–1960s. The most important changes have occurred during the flooding season. Short coastal rivers did not undergo this calamity, because their basins received sufficient water during the first monsoon rains. Rivers of Ghana suffered the same flow reduction. The case of the Volta was aggravated by the erecting of a dam and the filling of Volta Lake. In Côte d’Ivoire, two dams on the Bandama were built.
during the last 2 decades. When the filling was achieved, these dams regulated the flow, especially during the floods, thereby decreasing the load of particles in downstream waters.

Figure 9 shows the marked reduction in discharge from the Bandama and Comoé Ivorian Rivers since 1972. They have not recovered their former values, despite some amelioration in recent years.

As described previously, floods have a favorable effect on planktonic production; thus, biomass may decrease as a direct result of reduced river flow. Indeed, after 1972, plankton biomass maxima at the end of the cool season have not reached the values observed between 1969 and 1971 (Fig. 10).

The upwelling

In the usually stratified coastal waters, the temperature decrease at 0 or 10 m depth is a good index of upwelling intensity. Annual indices for Tema (Ghana) and Abidjan (Côte d’Ivoire) show strong interannual variations but no significant long-term trend. Nevertheless, coastal monitoring at several shore stations shows interesting changes in the zonal gradient of sea-surface temperature (Arfi et al., 1991).

From 1969 to 1980, the spatial pattern of surface temperature variations agreed with the concept of two upwellings, the cores of which would be on the eastern sides of Cape Palmas and Cape Three Points. The temperature dropped abruptly on the downstream side of each cape, then increased progressively eastward as the waters were carried by the GC (Morlière and Rébert, 1972).

In 1982, the decrease in temperature was almost the same along the coast. From 1983 to 1986 the pattern was reversed: The coldest waters were found in the western side of Cape Three Points. In 1987, upwelling was weak at all stations (Herbland and Marchal, 1991).

The sea-surface temperature (SST) observed by merchant ships in the area between the two capes (Servain and Lukas, 1990) shows a slight increasing trend after 1976 (Fig. 11).

The currents

The eastward-flowing NECC crosses a part of the Atlantic Ocean against the tradewind direction (Fig. 1). This flow migrates between a northern (summer and fall) and a southern (winter and spring) latitude, parallel to the movement of the ITCZ, and is controlled by changes in the curl of the wind stress. The seasonal variation of the NECC is part of the equa-
torial response to seasonal wind-forcing (Richardson and Reverdin, 1987). According to Philander (1986, p. 238): “Interannual variations in the Atlantic Ocean can be viewed as perturbations to the seasonal cycle. In 1984, the seasonal migration of the ITCZ took it further south than normal and it remained in a southerly position longer than normal.”

We suppose that an interannual change in the migration pattern of the ITCZ will induce a similar deviation in the latitude of the NECC.

During the 1970s, the ITCZ remained usually northward of 2° or 3°N in winter and spring at the most southerly latitude of its seasonal migration. During 1984, 1985, and 1986, the ITCZ moved southward as far as the equator (Citeau et al., 1989). As Lamb (1978) observed previously, a southward shift of the ITCZ occurs during an Atlantic El Niño (warm event).

Figure 10. Coastal environmental variations, 1969–1980. From the top: monthly flow of the Badama and Comoé rivers; settled volume of zooplankton at the coastal station at Abidjan; and temperature at 10 m the same station. Zooplankton settled volume: monthly averages of recorded zooplankton volumes (Large dots and solid lines). Predicted volumes of zooplankton using river-flow and sea-temperature multilinear regressions (Small dots) (from Binet, 1983b).
Atlantic El Niños occurred in 1968 and in 1984 (Hisard, 1988). The trade winds were reduced, the NECC intensified, and its axis shifted southward. Finally, anomalous southerly positions of the ITCZ and NECC might be related, especially during Atlantic El Niños.

Because the NECC directly feeds the GC, 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 (Fig. 12).

On the other hand, high-salinity waters (>36 per mil) of the EUC are usually upwelled along the equatorial divergence, and, in the subsurface waters of the Guinea Gulf, the high-salinity water belt is very narrow. However, in 1984 the relaxation of trade winds was followed by a weakening of the equatorial upwelling. The high-salinity waters of the EUC were not upwelled to the surface, and they spread in the Gulf of Guinea (Fig. 4).

This unusually important eastward transport of surface and subsurface waters reversed the sea-surface slope along the equator during the boreal winter, 1983–1984 (Hisard et al., 1986). A strong rise in sea level occurred along the African coast (Katz et al., 1986). A strengthening of the poleward (southward and westward) return-circulation may be expected from this unusual accumulation of water. Indeed, some of this water flowed southward along the African coast and suppressed coastal upwelling as far south as Angola and Namibia (Philander, 1986). A rather similar change is likely north of the equator, and the westward GUC should be intensified. Because of its increased velocity, the GUC undergoes higher Coriolis force, thus it should shift northward, closer to the coast, and sink under the GC to the west of the usual longitude. Indeed, high-salinity waters were observed along the coasts of Benin and Togo (Ploton, 1987).

Upstream surface and subsurface circulation anomalies should change the regular pattern over the shelf (Figs. 5 and 12). The eastward surface flow (GC) will shift to the south and the westward flow (GUC) will remain near

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**Figure 11.** Sea-surface temperature anomalies for 1964–1990 from ship of opportunity data in the area 2°W–8°W, 4°N to the coast (from Servain and Lukas, 1990). Thin line: monthly anomalies (°C); Heavy line: filtered anomalies >12 months.

**Figure 12.** Diagram of the Ivory Coast and Ghana shelf illustrating hypothesized changes in the current pattern (arrows) and their consequences on *Sardinella* populations (circles). Hatched: situation prevailing in the 1960s and 1970s; White: situation in the 1980s. The oblique surfaces show the shear planes between two currents for 1972 (solid line) and 1984 (dotted line). CP: Cape Palmas; ABJ: Abidjan; C3P: Cape Three Points; AC: Accra; GC: Guinea Current; GUC: Guinea Under Current. The spawning areas of *Sardinella aurita* (circles) are situated eastward of Cape Palmas and Cape Three Points (see Fig. 14). In the 1960s–1970s, the Ghanaian population was larger than the Ivorian, but during the next decade, the new current pattern led to a rapid maturation of the Ivory Coast population.
the surface until it plunges under the GC, westward of the usual sinking region.

Measurements of superficial currents off Abidjan, Côte d'Ivoire (Table 1), made by Lemasson and Rébert (1973b) and Colin (1988), indicate westward transport in 7% and 9% of the observations during "normal" years (1969 and 1970, respectively), versus 23% and 35% during years of southward ITCZ shift (1968 and 1984, respectively). This supports the hypothesis of an increase in westward transport along the shelf, associated with a southward shift of the ITCZ. Similarly, the change observed in the coastal temperature zonal gradient sustains the idea of a shoreward and westward displacement of the GUC.

The Sardinella fishery

Two Sardinella species constitute the majority of the pelagic fishery of the coastal upwelling (Fig. 2). Until 1980, most of the catch from Ivorian purse seiners was comprised of Sardinella maderensis. Since that time, Sardinella aurita has ranked first in Côte d'Ivoire landings.

The main Sardinella aurita fishery was centered in Ghanaian waters during the 1960s and 1970s. Only a small part of the catch came from the Ivorian coast. That fishery took place during the major upwelling season (boreal summer) and fluctuated widely from year to year (Marchal, 1966, 1993), probably as a result of the influence of environmental factors, on one hand, and from stock abundance changes, on the other.

Influence of upwelling

Increased upwelling should improve plankton productivity and, consequently, increase the forage for plankton feeders, thus improving their survival rate in the early life stages. The fortnightly catch per unit effort (CPUE) for Sardinella spp. proved to be correlated to the upwelling intensity of the preceding fortnight (Mendelsohn and Cury, 1987). This time lag corresponds to the mean life span of copepods, as if upwelled nutrients enhanced phytoplankton and zooplankton growth.

Based on these hypotheses, Cury and Roy (1987) modeled the annual Sardinella CPUE to assess the effects of upwelling intensity on fishing effort (the same year) and on recruitment (the next year). Their model worked for the years prior to 1981. It accounts for the total of both Sardinella species landings in Côte d'Ivoire only; but if we consider S. aurita separately, the sudden increase in landings in 1972 and the subsequent collapse remain unexplained. Bakun (1978) had observed that heavy rains were associated with poor Sardinella catches along this coast, and Binet (1982) hypothesized that the 1972 overfishing was favored by the drought. S. aurita is a stenohaline fish, avoiding turbid and low-salinity waters. During the dry year (1972), the salinity of coastal waters was not lowered by rivers, and juveniles frequented the coastline. Their proximity to the coast led to overfishing of juveniles, notably by canoe fishermen from Ghana. The stock suffered a 5-year collapse, but it had completely recovered by 1978. Fréon (1988) simulated these variations in a global production model in which two climatic variables—upwelling intensity and river flow—were incorporated to improve the fit of stock abundance and the catchability coefficient, respectively.

From the beginning of the 1980s, the Sardinella aurita fishery patterns changed again completely (Figs. 13 and 14):

- About half of the yield was caught on western Côte d'Ivoire, and not only in Ghana, as in past decades.
- The fishing season extended over the entire year, rather than being limited to the upwelling season only.
- The landings were high (over 100,000 metric tonnes [mt] in 1985) and were sustained over several consecutive years, even following a collapse in 1973 after a 90,000-mt catch.

Table 1. Occurrences of Guinea Current (eastward) and Guinea Under Current (westward) in surface observations of Lemasson and Rébert (1973b) and Colin (1988).

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Changes in the spatial distribution of pelagic biomass

Comparisons among acoustic surveys conducted in different years confirm that the change in the regional fishery pattern is not only caused by changes in fishermen's habits, but also results from a new geographical distribution of pelagic stocks.

Echo-integration surveys over the shelf (Marchal and Picaut, 1977) indicated the fol-
lowing fish biomass densities in 1974: Cape Palmas to Abidjan, 17.8 mt/nm²; Abidjan to Cape Three Points, 20.3 mt/nm²; Cape Three Points to Volta River mouth, 53.3 mt/nm². Because of the difference in the width of the continental shelf, the estimated fish biomass is greater eastward of Three Points (225,000 mt) than between the two capes (82,000 mt).

This pattern of biomass distribution was consistent until 1980. From 1980 to 1990, several acoustic surveys carried out in this area show a sudden increase in the fish density on the Ivorian shelf with equivalent values on both sides of Cape Three Points (Marchal, 1993).

One or two populations?

Because the preceding models cannot account for these changes, it seemed necessary to take a new look at stock and population localization.

Until recently, it was believed that a single stock supported the whole yield of the fishery. Based on tagging experiments, a population spawning in the vicinity of Cape Three Points during the major upwelling season has been identified. Its larvae are very abundant off Tema during July, August, and September (FRU et al., 1976). Nevertheless, evidence from plankton sampled on surveys conducted between Cape Palmas and Cape Three Points from 1969 to 1972 indicated the likelihood of a second population (Marchal, 1991). The samples contained many larvae of *Sardinella aurita* that were found eastward of Cape Palmas during the minor upwelling (especially in March).

In addition, the lengths of *S. aurita* caught near Cape Palmas are notably greater than those in the Three Points area. Finally, the growth rates of these two groups also seem different (Pezennec et al., 1993).

Thus, *Sardinella aurita* from this ecosystem may belong to two different populations (Fig. 14). The cores of these two populations are situated in the eddies created in the surface current downstream (i.e., eastward) of Cape Palmas and Cape Three Points. The two populations differ in their spawning times and locations. The fish of Cape Palmas grow faster and larger than those of Cape Three Points. They also differ in their seasonal availability, although the geographical ranges of adult distributions overlap slightly.

The changes in total landings for the last 3 decades may be understood as changes in the abundance and harvest of the two populations. The Ghanaian population of *S. aurita* was flourishing and supported the yield of the fishery in the 1960s; but in 1972, the drought caused an exceptional availability to coastal fishermen, which resulted in overfishing and a 5-year collapse, followed by a subsequent recovery, which presently yields variable catches.

In the beginning of the 1980s, an oceanographic event occurred that may have favored the increase of the Ivorian population. The fishery now harvests this population at the same time of year as formerly.

Improved retention of larvae by a shift of the currents

According to Sinclair’s hypothesis (1988) on marine population regulation (member/vagrant), we think that the abundance of a population is partly controlled by the advective processes occurring before recruitment, as has been seen in copepods, where the vertical distribution of pelagic larvae ranging over two currents minimizes advective losses. Thus, a change in the current system may be responsible for the sudden increase in the Ivorian population.

The Ghanaian population spawns over the shelf, mainly between Cape Three Points and Tema (i.e., near the usual boundary of the two currents). Migration of larvae between these two layers ensures the retention of early stages over the shelf. Empirical results suggest that the strength of recruitment may be dependent on the food supply only, that is, on the upwelling intensity.

During the previous 2 decades, the larvae of the Ghanaian population distributed in the two currents were retained in this area and yielded good year classes. In the same time period, the larvae hatched in the western Ivory Coast were advected eastward by the GC; thus, Ivorian population recruitment was very poor.

Since the beginning of the 1980s, a possible change in the current pattern occurred

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**Figure 13.** Catches of *Sardinella aurita* from the Ivory Coast and Ghana (in thousand tons) (from Pezennec et al., 1993).
Figure 14. The map shows fishery divisions along Côte d'Ivoire and Ghana. Black dots correspond to the barycenters of the two populations of *Sardinella aurita*. The graphs show changes in the seasonal and regional patterns of Ivorian fisheries between 1970 and 1971 (before the collapse) and between 1983 and 1987 (during maximum yields) (from Binet et al., 1991).
that may have reversed the abundance of the two populations. The shear surface between the two currents shifted westward, leaving the Ivoirian and Ghanaian populations in reversed advective processes. The Ivory Coast population is now at the boundary of the two currents, and the advective losses of its larvae are minimized, whereas the Ghanaian population larvae may add to the recruitment of the other population.

Conclusions: Implications for Management

The northern coast of the Gulf of Guinea, cooled by a seasonal upwelling, may be considered a subsystem of the Gulf of Guinea LME. Hydrology and circulation features, nutrient enrichment processes, plankton features, benthos, and fish species assemblages make it a different regime from its neighbors, who are situated in thermally stable regions. One commercial stock of the pelagic fish species Sardinella aurita, likely comprised of two populations, ranges all along the coast and is bounded by the zonal extent of the upwelling.

The management of coastal pelagic resources has never been easy. Their sudden increases or collapses seem to escape the classic rules of population dynamics. On one hand, it is difficult to correctly assess the fishing effort, because of the overdispersed distribution of fishes (schooling behavior) and the fact that rarity sometimes increases the catchability (contrary to randomly distributed species). On the other hand, availability and recruitment of these species seem very sensitive to environmental changes. Thus, approximate management rules may be proposed, provided that environmental changes remain in a narrow range. These alterations are probably linked to distant climatic anomalies, such as the ITCZ southward displacement during Atlantic El Niños. Improving ecological forecasts in the Gulf of Guinea requires a better understanding of oceanographic processes (what is the mechanism of the coastal upwelling?) and of remote ocean-atmosphere interactions (what determines the position and the flow of great oceanic currents?).

It is not clear how long the Ivoir Coast population of Sardinella aurita will flourish. Perhaps the current system has already reversed to the prior situation and the high catches will quickly fall!

Acknowledgments

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References

Caveri+re, A.
Fisheries Research Unit (FRU), Tema; Centre de Recherche Oceanographique (CRO), Abidjan; ORSTOM. 1976. Rapport du groupe de travail sur la sardelle (S. aurita) des côtes ivoiro-ghanéennes. 26 June–3 July, Abidjan. Ed. by ORSTOM.


