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AN UPWELLING-INDUCED RETENTION AREA OFF SENEGAL: A MECHANISM TO LINK UPWELLING AND RETENTION PROCESSES

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In upwelling ecosystems, fish tend to avoid spawning in areas dominated by strong offshore transport and strong wind-mixing. Spawning grounds are usually located downstream of the main upwelling centres and spawning is mostly tuned to avoid the peak of the upwelling season. However, in areas such as Peru, Senegal and Côte d'Ivoire-Ghana, spawning and upwelling occur simultaneously. What are the mechanisms that allow such reproductive strategies to be successful? To attempt to answer this question, some environmental characteristics of the spawning ground of *Sardinella aurita* in the Senegalese upwelling system are investigated. *S. aurita* adults migrate from Mauritania to Senegal in early winter, following the southward extension of upwelling along the coast. Intense spawning in late spring is concentrated south of Cap Vert. There, the surface distribution of several environmental parameters is quite unusual for an upwelling area. Sea surface temperature is minimum over the shelf and increases towards and away from the coast. Chlorophyll distribution peaks nearshore. This unique surface structure is interpreted as the result of a "double cell" structure in the upwelling vertical circulation: a first cell located at the shelf break, the main upwelling cell that brings cold and nutrient-rich subsurface water to the surface, and a second cell located inshore of the shelf break. A nearshore convergence tends to trap and retain phytoplankton and other biological components. In an upwelling system with a double-cell circulation structure, the coastal cell represents a very favourable environment for fish to reproduce: eggs and larvae do not spread offshore, but are retained in the productive and relatively stable coastal waters. Clearly, therefore, upwelling is not always detrimental for larval survival. Rather, upwelling and retention can occur simultaneously and together provide a favourable reproductive habitat.

Coastal upwelling ecosystems are known to be parts of the most productive oceanic regions (Ryther 1969, Cushing 1971). Many of these ecosystems are able to sustain extremely large populations of pelagic fish such as sardine and anchovy, and consequently very important fisheries (Crawford *et al*. 1987, Pauly and Tsukayama 1987, Cury and Roy 1991). Main coastal upwelling ecosystems are characterized by seasonal or permanent, strong, equatorward winds, a contrasted vertical current structure (equatorwards at the surface and polewards at intermediate depths) and a persistent wind-induced drift of surface waters offshore (Wooster and Reid 1963, Brink 1983). Upwelling ecosystems are indeed characterized by a very high rate of primary production, but they are also dispersive environments where particles tend to be swept away from the coast by wind-induced offshore drift. This major characteristic of coastal upwelling ecosystems has strong ecological implications (Bakun 1996).

In a recent synthesis of the major environmental processes affecting fish reproduction, Bakun (1996) identified three major classes of processes that combine to yield favourable reproductive habitat for fish. They are:

(i) enrichment processes (upwelling or mixing);
(ii) concentration processes (convergence, fronts, stratification);
(iii) retention processes, that maintain eggs and larvae in suitable habitats.

Because a coastal upwelling ecosystem is a dispersive environment, adequate conditions to satisfy the requirement of the third element of Bakun's triad (retention) may be not as easy to find as suitable conditions for the first two elements of the triad. The migrations that some of the major populations of small pelagic fish undertake in order to find a suitable reproductive habitat indicate that an upwelling ecosystem can be an adverse habitat for fish to reproduce (Hutchings 1992).

Small pelagic fish such as sardine and anchovy produce tiny pelagic eggs and larvae. Consequently, offshore drift of the surface water will tend to disperse eggs and larvae out of the favourable coastal habitat. However, populations of small pelagic fish have been quite successful: they are well known for being able to develop commercially important biomass in eastern boundary ecosystems. Comparative studies between several upwelling ecosystems indicate that

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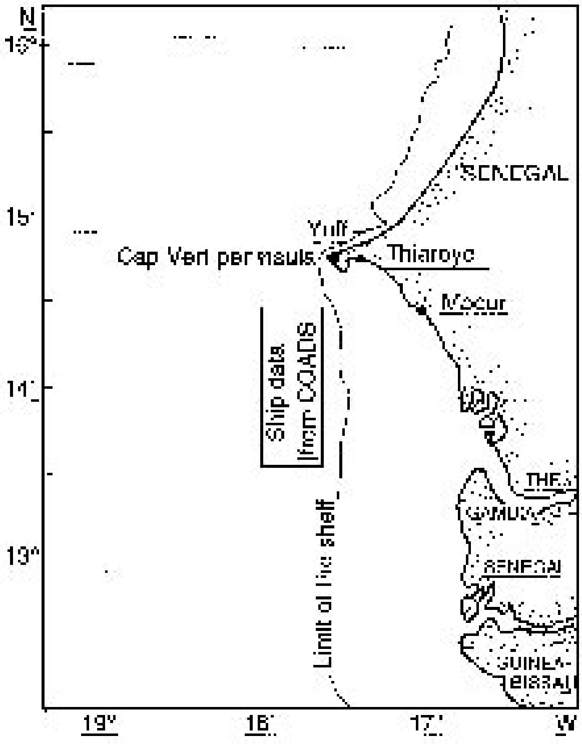

Fig. 1: Map of the Senegalese ecosystem with the location of the two coastal stations where SST is collected on a daily basis and the location of the offshore area for which the mean SST is calculated using the COADS dataset

the reproductive strategies of small pelagics are tuned in order to minimize the detrimental effects of the environment on larval survival (Parrish *et al.* 1983, Roy *et al.* 1992). Sardine, sardinella and anchovy tend to avoid spawning in areas dominated by strong offshore transport and strong wind-mixing (Parrish *et al.* 1983, Roy *et al.* 1989). In the California Current ecosystem, pelagic fish migrate at the time of spawning, sardines avoiding spawning in the upwelling centre. They rather migrate into areas such as the California Bight, where topographical features minimize offshore transport and allow retention of eggs and larvae in the favourable coastal habitat (Bakun and Parrish 1982). The central population of the Moroccan sardine (*Sardina pilchardus*) has adopted a similar reproductive strategy. That sardine population avoids reproducing in the summer upwelling centre off Safi-Essaouira and migrates farther south during winter to an area where upwelling is minimal (Belvèze and Erzini 1983, Belvèze 1991).

In other areas, fish spawn during the upwelling season and sometimes even in places where upwelling is at a local maximum. Spawning of the Peruvian anchoveta *Engraulis ringens* peaks off northern Peru during winter, which is the season of maximum upwelling and offshore transport (Santander 1981, Bakun and Parrish 1982). However, Parrish *et al.* (1983) showed that, when the increase in the depth of the mixed layer off Peru in winter is taken into account, the speed of surface offshore drift is minimal during the spawning peak. They conclude that this pattern may account for the coincidence between the spawning peak of the anchoveta and the season of maximum upwelling. Off Senegal, *Sardinella aurita* spawn simultaneously with upwelling, in an area where upwelling is at a local maximum (Conand 1977, Fréon 1988). Off Côte d'Ivoire and Ghana, upwelling and spawning of *S. aurita* also appear to be in phase. Spawning is concentrated on the eastern side of Cape Palmas and Cape Three Points, where the coastal upwelling is enhanced by the eastward flow of the Guinea Current (ORSTOM/FRU 1976, Bakun 1978, Pezennec and Bard 1992). Off the Sahara, between Cap Bojador and Cap Barbas, *S. pilchardus* spawn in late winter, in an area where upwelling is permanent (F.A.O. 1985).

Such patterns of coincidence between spawning and upwelling are not apparently in accord with the conclusion of Parrish *et al.* (1983), namely that there is a general tendency for small pelagic fish to avoid reproducing in areas or during seasons characterized by potentially crucial offshore surface drift. When upwelling and reproduction are in phase, eggs and larvae will apparently be placed in an environment characterized by maximum offshore drift, making the eggs and larvae highly vulnerable to dispersion out of the coastal habitat. By looking in some detail at some spatial features of the upwelling and at the reproductive strategy of *S. aurita* off Senegal, it may be possible to identify the environmental processes that allow such reproductive strategies to be successful.

REPRODUCTIVE STRATEGY OF *S. AURITA* IN THE SENEGALESE UPWELLING SYSTEM

Off Senegal, upwelling occurs in winter and late spring. It is at its maximum south of Cap Vert, downwind of the peninsula, in a place where the continental shelf extends more than 50 miles offshore (Fig. 1). During summer, weak southerly winds prevail and warm tropical waters extend over the whole shelf, creating a relatively stable and stratified environment (Rébert 1983).

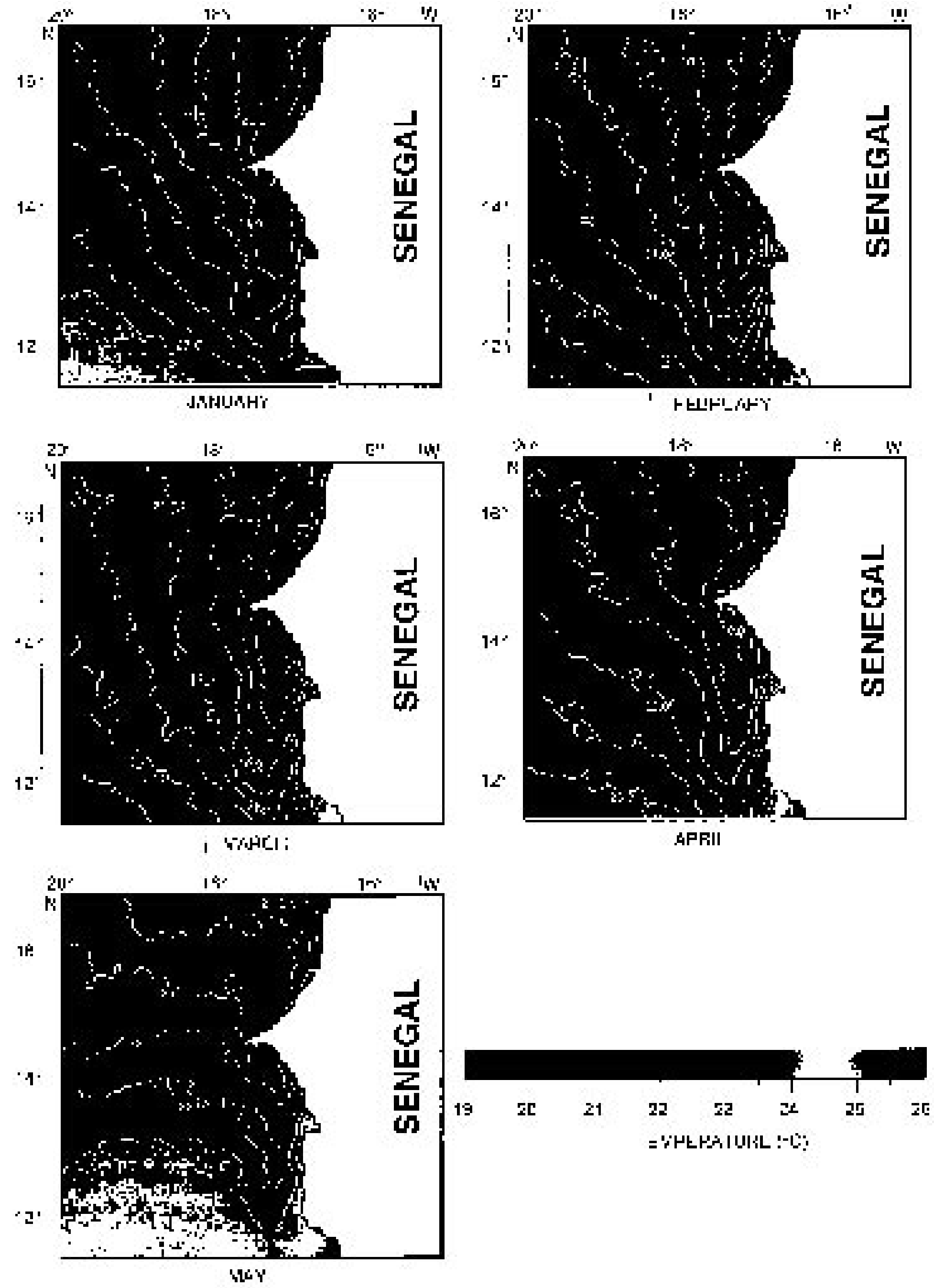

Fig. 2: Mean monthly thermal structure (1984–1993) of the Senegalese upwelling region produced from METEOSTAT infra-red data received at the CRODT in Dakar (see Demarcq and Citeau [1995] for details

S. aurita is an important component of the population of small pelagic fish off Senegal (Barry-Gérard *et al*. 1994). The adults migrate seasonally from Mauritania to Senegal (Boëly and Fréon 1979), a migration related to the southward extension of upwelling in winter and spring. Following Parrish *et al*. (1983), one would expect the spawning season to be out of phase with the upwelling season for the fish to take advantage of the stable summer environment. However, the observed pattern of reproduction of *S. aurita* is different.

The main spawning activity of *S. aurita* is simultaneous with upwelling, from February to June, and it is at its maximum in late spring (Conand 1977, Boëly *et al*. 1982). There is also spawning of young adults in late summer. Spawning is not continuous along the Senegalese coast. There is low-intensity spawning north of Cap Vert and intense spawning in the upwelling core south of Cap Vert in late spring (Fig. 1). Wind-mixing is moderate during the spawning season and has little effect on larval survival (Roy *et al*. 1989). Under such conditions, one would expect feeding conditions for larvae to be adequate and the requirements of the first two elements of Bakun's triad to be met. However, the main spawning season and the spawning ground are characterized by intense wind-induced offshore Ekman transport (Rébert 1983, Roy 1989). According to the third element of Bakun's triad, this would represent an adverse environment in which to reproduce successfully, so negatively influencing recruitment success and the maintenance over time of the reproductive strategy. However, during the past 30 years, catches of *S. aurita* in Senegal show a remarkable pattern: a constant gradual increase in the landings without any signs of recruitment failure (Samba 1994).

Although sardine spawning and upwelling coincide off Senegal, this reproductive strategy is apparently successful. It raises the following question: what retention mechanism is used by *S. aurita* to avoid the loss of reproductive material offshore? A review of the main features of the Senegalese upwelling system may provide some indication of the environmental processes that allow this reproductive strategy to be maintained over time.

SPATIAL STRUCTURE OF THE SENEGALESE COASTAL UPWELLING SYSTEM

Sea surface temperature (SST) collected at two coastal stations (Thiaroye and Mbour, Fig. 1) is used to characterize the seasonal dynamics of upwelling (Roy *et al*. 1985). Monthly means were calculated from daily SST measurements made from 1966 to 1987. The offshore component of Ekman transport is used as an index of upwelling activity (Bakun 1973), an index calculated using three-hourly wind data collected at the Yoff Airport meteorological station. This station is located on the tip of the Cap Vert peninsula, so the wind data are considered to be representative of the wind-forcing over the shelf (Roy 1989). Surface nutrient and chlorophyll data collected during several oceanographic cruises (Deme-Gning *et al*. 1990) are also used in the analysis.

The Senegalese coastal upwelling region is the southern part of the Canary Current ecosystem. Thus, seasonality of upwelling off Senegal is related to the meridional migration of the Azores High. South of Cap Blanc (20°N), trade winds blow from early winter to late spring (December – June). Along the coasts of Mauritania and Senegal, these steady equatorward winds generate strong seasonal coastal upwelling, which removes from the coastal area the warm tropical surface water that extends up to 20°N during summer (Wooster *et al*. 1976, Mittelstaedt 1983, Nykjaer and Van Camp 1994).

The Cap Vert peninsula subdivides the Senegalese ecosystem into two distinct regions. To its north the continental shelf is rather narrow (<20 miles), but to its south the width of the shelf increases, to more than 50 miles offshore at 13°N (Fig. 1). The meridional orientation of the coast favours coastal upwelling when equatorward trade winds start to blow in early winter. The onset of the trade winds in October results in significantly increased offshore Ekman transport and upwelling along the coast and, consequently, a pronounced decrease in SST. Interannual variability in the offshore component of Ekman transport during the upwelling season explains a significant part of the coastal SST variability. There is a negative correlation (r = 0.55) between mean (January–June) coastal SST and the corresponding mean offshore Ekman transport (Roy 1989). Less intense wind-induced offshore Ekman transport weakens the upwelling process and SSTs during the upwelling season tend to be warmer. The counter also applies, so clearly the wind is the dominant factor responsible for upwelling off Senegal.

When there is upwelling, the structures of the surface water on each side of Cap Vert differ (Fig. 2). On the northern side where the shelf is narrow, the surface thermal field has a traditional upwelling-type structure: SST is low at the coast and increases offshore (Fig. 2). On the wider shelf south of the cape, the surface structure of the thermal field is more distinct: the upwelling core is over the shelf, and SST is lowest on the coastal side of the shelf break, increasing in both

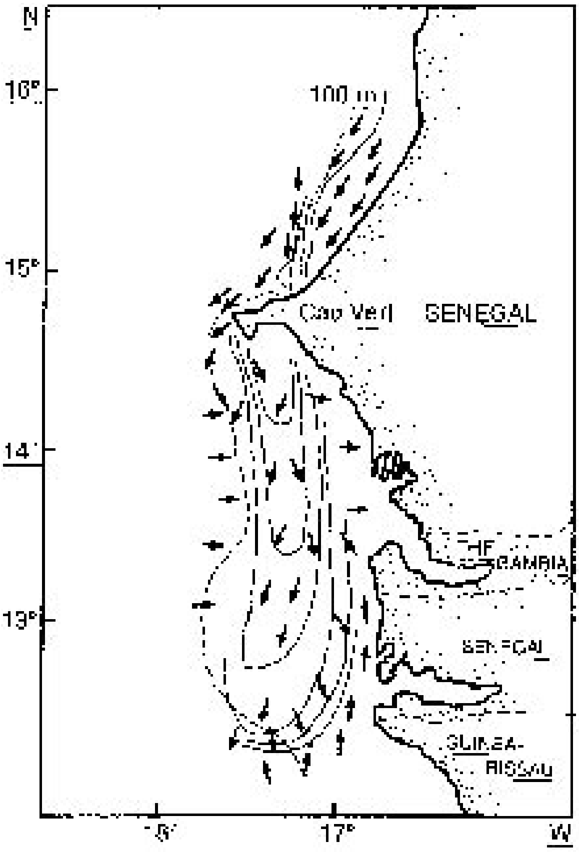

Fig. 3: Orientation of the surface flow over the Senegalese continental shelf during the upwelling season (adapted from Rébert 1983)

offshore and coastal directions (Fig. 2). This displacement of the upwelling core towards the middle of the shelf strongly influences the spatial structure of the surface thermal field south of Cap Vert. A tongue of cold water over the shelf isolates a coastal band of warm water from the offshore area south of 14°20′N, and there is surface divergence associated with the upwelling source over the shelf and convergence nearshore (Fig. 3).

This structure results from the interaction between wind-induced upwelling and the local topography (a wide shelf located downwind of a cape). A strong wind-stress curl south of Cap Vert, resulting from a positive wind-stress gradient in an offshore direction (the windfield shows a local minimum nearshore), may also be an important determinant of this structure.

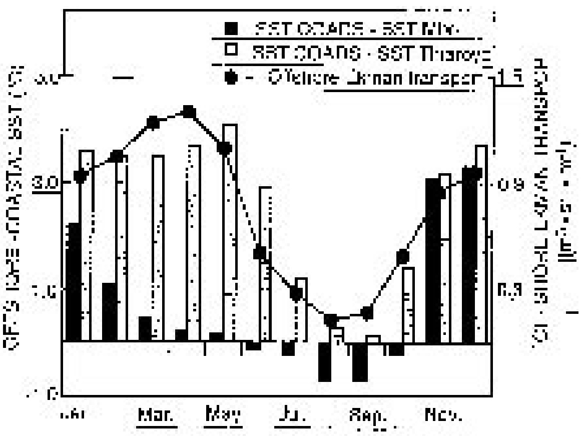

Fig. 4: Mean monthly seasonal cycle of the offshore component of Ekman transport at Yoff, the difference in SST between the offshore area (SST COADS) and Mbour and the difference in SST between the offshore area and Thiaroye

SEASONAL AND INTERANNUAL DYNAMICS OF THE UPWELLING STRUCTURE

The development of a tongue of cold water over the Senegalese continental shelf south of Cap Vert is a recurrent annual phenomenon that occurs during the upwelling season. The seasonal development of this spatial structure is summarized in Figure 2. Generally, the tongue of cold water starts to develop in January, reaches its maximum extension in March and has almost disappeared by June. The relative warming of SST nearshore, resulting from the displacement of the upwelling source towards the shelf break, is highly noticeable from February to May on the METEOSAT SST images (Fig. 2).

The manner in which development of the tongue of cold water influences coastal SST is evaluated by looking at differences in SST between an area located offshore of the continental shelf and that at two coastal stations. One of those two (Thiaroye) is located on the southern edge of the Cap Vert peninsula, in an area where there is maximum cooling resulting from the upwelling. The second (Mbour) is located farther south. For the offshore area (13°30′–14°30′N, 17°40′–18°00′W), the mean monthly SST was extracted from the COADS dataset (Woodruff *et al.* 1987) using the CD-ROM-based version of COADS and the CODE program described in Mendelssohn and Roy (1996).

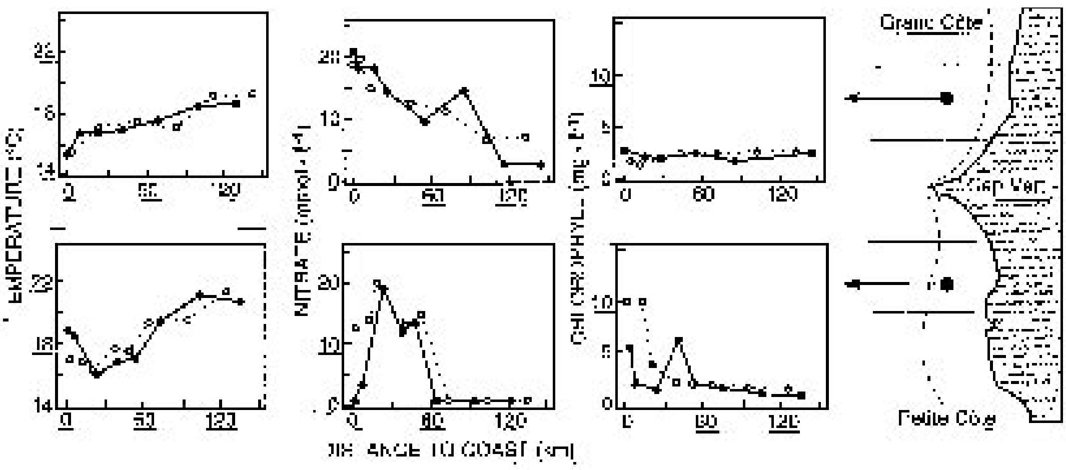

Fig. 5: Surface distribution of SST, nitrate and chlorophyll along four sections (two on each side of Cap Vert) off the Senegalese coast

Upwelling is fully developed from January through May. Offshore Ekman transport reaches its maximum (1.2 m^3·s^{-1}·m^{-1}) in April (Fig. 4), and SST at Thiaroye remains <17.2°C. The difference in SST between the offshore area and Thiaroye is nearly in phase with the onset of wind-induced offshore Ekman transport, it starts to increase in October and remains between 3 and 4°C until June (Fig. 4). On an interannual scale, there is also a positive correlation ($r = 0.52$) between the strength of upwelling and the offshore-coastal difference in SST at Thiaroye during the upwelling season. Thiaroye is located in the upwelling core and SST there is representative of upwelling activity over the shelf.

A totally different situation is observed with the Mbour SST data. Coastal temperatures at Mbour are noticeably colder than the offshore SST in November-December. In January, the offshore-coastal difference in SST suddenly decreases and remains below 1.0°C from March to June (Fig. 4). This is an indication of the effect of coastal warming resulting from the displacement of the upwelling source in the direction of the shelf break. At Mbour, the offshore-coastal difference in SST decreases with the development of the upwelling. This relationship is also valid at an interannual scale: as the upwelling intensity increases, the offshore-coastal SST difference decreases ($r = 0.50$). The seasonal and interannual fluctuations in SST at Mbour are not representative of upwelling activity. Rather, it appears that the SST at Mbour is strongly influenced by the development of a band of warm water nearshore.

Without the spatial information given by the satellite images, the behaviour of the offshore-coastal SST difference at Mbour would have been quite intriguing for a coastal upwelling area where coastal SST would be expected to be colder than offshore SST. At Mbour, the absence of a significant offshore-coastal SST gradient during the upwelling season can be attributed to the displacement of upwelling activity over the shelf south of 14°40′N, and to the occurrence of a band of warm water along the coast. The offshore-coastal SST difference decreases in phase with the intensification of upwelling. The coastal warming south of 14°30′N is positively related to the intensity of the upwelling. As upwelling strengthens, its core moves towards the shelf edge and coastal warming is enhanced by the convergence occurring nearshore. This pattern appears to be valid on both seasonal and interannual scales.

UPWELLING-INDUCED RETENTION RESULTING FROM A TWO-CELL CIRCULATION STRUCTURE

The contrast between the structure of the Senegalese upwelling system on each side of the Cap Vert peninsula is the result of the interaction between the upwelling process and topographical features (an open, narrow shelf on the northern side, a wide shelf downwind of a cape in the south). The surface distribution of nutrients is coherent with the SST distribution (Fig. 5). South of the cape, nitrate concentration is at its maximum over the shelf in the upwelling core,

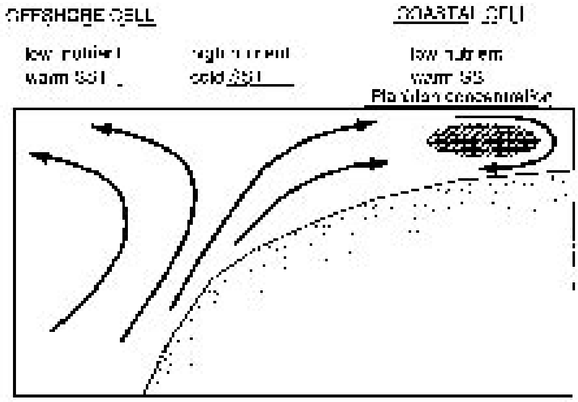

Fig. 6: Sketch view of a double-cell vertical circulation structure in an upwelling area located on a wide shelf, downwind of a cape

decreasing both offshore and in a coastal direction. The distribution of surface chlorophyll is somewhat different (Fig. 5). North of the cape, the surface distribution of chlorophyll is uniform, phytoplankton seeming to be spread homogeneously in an offshore direction. In the south, chlorophyll is at its maximum nearshore, where the plankton distribution appears to be strongly affected by the structure of the upwelling. Physical mechanisms apparently concentrate phytoplankton nearshore. There is a connection between this accumulation of biological material and the location of the coastal band of warm water south of Cap Vert.

The surface distribution of physical and biological parameters suggests that the structure of the vertical circulation is noticeably different in each area. North of Cap Vert, the homogeneous distribution, with little contrast between the coastal and the offshore area, can be interpreted as the traditional upwelling-type situation (a "one-cell structure"). South of the cape, it seems that the observed surface distribution is the result of a "double cell" vertical circulation structure, as presented in Figure 6:

(i) the one cell located on the shelf break is the main upwelling cell that brings cold, nutrient-rich subsurface water to the surface;
(ii) another cell located on the coastal side of the shelf break, where upwelled nutrient-rich subsurface waters have reached the surface and drifted inshore. There is a convergence nearshore and, with such a configuration of the vertical circulation, phytoplankton and other biological components tend to be trapped and retained along the coastal side of the shelf.

The proposed structure is considered to represent a favourable environment for fish to reproduce. In the case of a double-cell upwelling structure, the three elements of Bakun's triad are combined in the coastal cell (enrichment, concentration and retention), so eggs and larvae can be retained in the productive and relatively stable coastal environment. However, there is one important consequence of a double-cell structure of the vertical circulation in an upwelling system. With such a configuration of the vertical circulation, upwelling and retention are positively related and can act simultaneously to provide a favourable reproductive habitat. Off Senegal, this is the structure that is considered to allow *S. aurita* to reproduce successfully during the upwelling season and in the upwelling core.

A simple index can be developed in order to quantify the retention process. The intensity of the thermal gradient between the tongue of cold water over the shelf and the coastal waters can be used as an indicator of the strength of the retention process. SST at Thiaroye is representative of the upwelling intensity and SST at Mbour is strongly influenced by coastal warming resulting from the displacement of upwelling over the shelf. Therefore, a simple "retention index" can be obtained by calculating the SST difference between Mbour and Thiaroye. On a seasonal basis, the intensity of this retention index is almost in phase with the development of upwelling from January to June (Fig. 7). It reaches its maximum in May when the north-south coastal SST gradient reaches >4.0°C. The interannual variability of the retention index during the upwelling season is also positively related to the intensity of the upwelling process (Fig. 7). The timing of reproduction is in accord with the seasonal variability of this retention index: spawning is at its maximum in late spring, when the retention index is also at its maximum.

CONCLUSION

Off Senegal, the surface structure of the thermal field and the surface distribution of some chemical and biological parameters provide evidence of a convergence in the nearshore area. This is interpreted as the result of a double-cell vertical circulation structure over the shelf, generated by the interactions between the upwelling process and the topography. South of Cap Vert and on the coastal side of the upwelling core, the double-cell circulation structure creates an "upwelling-induced retention area" in which particles are trapped over the shelf. With such a configuration of the circulation, upwelling and retention are positively related and provide a favourable reproductive

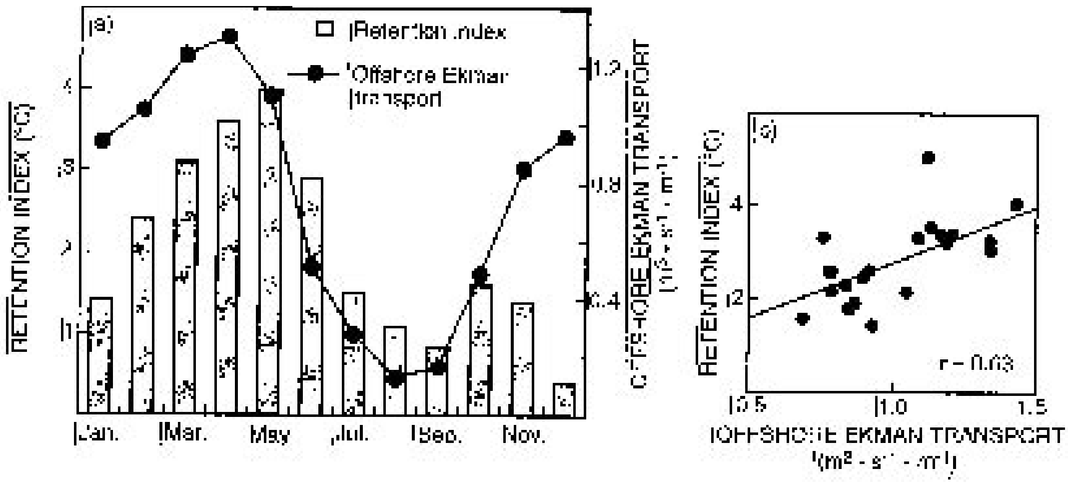

Fig. 7: (a) Mean monthly seasonal cycle of the retention index and of the offshore Ekman transport during the upwelling season off Senegal; (b) the relationship between the retention index and the offshore component of Ekman transport during the upwelling season, 1966–1987

habitat in which the three elements of Bakun's triad (Bakun 1996) are combined. Conditions in this upwelling-induced retention area allow *S. aurita* to reproduce successfully in the upwelling centre south of Cap Vert.

Recruitment data are not available, but several authors have found indications of a positive relationship between upwelling and the abundance of small pelagic fish off Senegal when wind speed remains moderate (Fréon 1988, Cury and Roy 1989). This is in agreement with the positive relationship found between the retention index and the intensity of upwelling: intensification of the retention process should favour larval survival and later recruitment.

The existence of double-cell circulation structures in upwelling areas was first suggested in 1975 by SCOR Working Group 36 (Jacques and Tréguer 1986). The interpretation is derived from some observations made off the Sahara over a wide and open continental shelf. There, it was shown that, under some conditions, the upwelling core moves over the shelf break (Barton *et al.* 1977), resulting in two upwelling cells located each side of the shelf (see Fig. 6 in Walsh 1977). This is slightly different from what is observed off Senegal where the two cells work in opposite directions. There, the offshore cell is an upwelling cell and the coastal cell results in convergence nearshore.

There are also other regions (e.g. Côte d'Ivoire and Ghana, the southern coast of Morocco, Brazil) where spawning and upwelling coincide. In those ecosystems, physical processes, such as shelf-break upwelling (Barton *et al.* 1977) or upwelling plumes (Bakun 1993, Graham and Largier 1997), may allow also a positive coupling between upwelling and retention.

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