Clupeoids Reproductive Strategies in Upwelling Areas: a Tentative Generalization

Yunne-Jai Shin*
Claude Roy**
Philippe Cury***

* ORSTOM
Laboratoire d'Informatique Appliquée
(LIA)
32, avenue Henri Varagnat
93143 Bondy cedex
France

** Centre ORSTOM de Brest
BP 70
29280 Plouzané
France

*** Sea Fisheries Research Institute
Private Bag X2
Rogge Bay 8012
Cape Town
South Africa

ABSTRACT

Using a comparative approach, the reproductive strategies of sardines, anchovies and sardinellas in twelve upwelling areas over the Atlantic, Indian and Pacific Oceans are investigated in relation with major environmental processes affecting recruitment success. The main reproductive habits are identified, in each area and for each species, based on an extensive survey of the literature. From this, the main spawning grounds and the months corresponding to the peaks of the spawning season are identified. The monthly mean values of upwelling intensity and of wind speed are calculated in each spawning grounds using data from the Comprehensive Ocean Atmosphere Dataset (COADS). A comparison, between areas, of the value of these environmental parameters during the peaks of the spawning season is performed. Off Peru, spawning occurs when the intensity of upwelling is maximum (1.8 $m^3/s/m$). Off Morocco, reproduction is out of phase with the upwelling process (upwelling intensity is in the range of 0.2-0.3 $m^3/s/m$). Off Namibia, Chile and California, spawning occurs at intermediate values. It appears that the timing of the reproduction of sardines, sardinella or anchovies occurs over a wide range of upwelling intensity. There is no apparent link between the timing or the intensity of upwelling and the occurrence of the seasonal spawning peaks. A similar analysis is performed using the monthly values of wind speed during the seasonal spawning peaks. It turns out that for sardine and sardinella, reproduction occurs when the monthly values of wind speed are within a narrow window, bounded by 5.3 and 6.1 m/s for ten of the twelve upwelling ecosystems. The two outliers are the sardine populations from the southern Benguela and the Iberian Peninsula. For anchovy, there is apparently little correspondence between the timing of reproduction and wind speed values. These results are discussed in the light of the 'optimal environmental window' concept of P. Cury and C. Roy, and a generalization of the spawning strategies of small pelagic fishes in upwelling areas is presented.

RÉSUMÉ

A travers une approche comparative incluant douze régions d'upwelling des océans Atlantique, Indien et Pacifique, les stratégies de reproduction des sardines, anchois et sardinelles sont étudiées en relation avec les processus environnementaux majeurs affectant le succès du recrutement. Dans chaque région et pour chaque espèce considérée, une revue exhaustive de la littérature permet d'identifier les principales caractéristiques de la dynamique de reproduction. Les principales zones de ponte et les mois correspondant aux pics de la saison de reproduction sont ainsi identifiés. Les moyennes mensuelles de l'intensité de l'upwelling et de la vitesse du vent sont calculées dans chaque zone de ponte à partir de la base de données COADS (Comprehensive Ocean Atmosphere Dataset). Une comparaison des valeurs de ces paramètres environnementaux durant les pics de la saison de reproduction est effectuée entre les différentes zones d'upwelling étudiées. Au large du Pérou, la reproduction a lieu lorsque l'intensité de l'upwelling est maximale (1,8 m^3/s/m). Au large du Maroc, la reproduction est décalée par rapport au processus d'upwelling (l'intensité de l'upwelling se situe dans l'intervalle 0,2-0,3 m^3/s/m). Le long des côtes de la Namibie, du Chili et de la Californie, la ponte a lieu à des valeurs intermédiaires d'upwelling. Il apparaît que le calendrier de la reproduction des sardines, anchois et sardinelles, s'étale sur une large gamme d'intensité d'upwelling. Il n'y a pas de lien apparent entre l'occurrence du processus d'upwelling et celle des pics saisonniers de reproduction. Une analyse similaire est effectuée en utilisant les valeurs moyennes de la vitesse du vent durant les pics saisonniers de reproduction. Il en résulte que pour les sardines et sardinelles, la reproduction a lieu lorsque les moyennes mensuelles de la vitesse du vent sont comprises dans une étroite fourchette de valeurs de 5,3 à 6,1 m^3/s/m pour dix des douze écosystèmes d'upwelling étudiés. Les deux exceptions sont les populations de sardine du sud du Benguela et de la péninsule ibérienne.

Pour l'anchois, il.y a apparemment peu de correspondance entre le calendrier de la reproduction et les valeurs de la vitesse du vent. Les résultats sont discutés à la lumière du concept de la « Fenêtre Environnementale Optimale » de P. Cury et C. Roy, et une généralisation des stratégies de reproduction des petits poissons pélagiques dans les zones d'upwelling est présentée.

INTRODUCTION

Located in the tropical or subtropical zones, coastal upwelling ecosystems represent less than 0,1% of the entire oceanic surface but are part of the most productive oceanic regions and are able to produce between 20 and 30% of the worldwide annual fish catches (Cushing, 1969; Ryther, 1969; Pauly and Tsukayama, 1987). Coastal upwelling ecosystems are mainly colonized by small pelagic fishes such as anchovies, sardines or sardinellas. These fish populations are characterized by important annual fluctuations of their abundance. For instance, after a peak of production in 1970, the Peruvian anchoveta stock collapsed in 1972-1973 (Valvidia, 1978; Pauly and Tsukayama, 1987); similarly, Pacific sardine suddenly disappeared from the fishery in the 1950s (Lasker and MacCall, 1983). Although these populations are usually submitted to strong fishing pressure, these variations of abundance appear mainly due to recruitment failure related to changes in the marine environment (Kawasaki, 1983; Shepherd *et al.*, 1984). Upwelling ecosystems are characterized by a very high rate of primary production. An upwelling ecosystem is also a dispersive environment where particles tend to be swept away from the coastal environment by the wind-induced offshore drift. Persistent equatorward winds also induce a strong and continuous mixing of the surface water column. These are some of the major characteristic of coastal upwelling ecosystems; they can have strong ecological implications.

In a recent synthesis of the major environmental processes affecting fish reproduction, Bakun (1996) identified three major classes of processes that combine to yield favorable reproductive fish habitat. They are: 1) enrichment processes (upwelling or mixing); 2) concentration processes (convergence, fronts, stratification) and 3) retention processes that maintain eggs and larvae in the suitable habitat. Despite the high rate of production, the triad indicates that the offshore flow and the intense wind mixing that characterize upwelling ecosystems can create adverse conditions for larval survival and subsequent recruitment success. The migrations that some of the major small pelagic fish population undertake in order to find suitable reproductive habitat confirm that an upwelling ecosystem can be an adverse habitat for fish to reproduce (Hutchings, 1992; Bakun, 1996). However, small pelagic fish populations are quite successful: they are well known for being able to develop very important biomass in eastern boundary ecosystems. Comparative studies, in several upwelling ecosystems, of the reproductive strategy of fishes helped identify common key environmental processes for small pelagic fish reproductive strategy: 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). Reproductive strategies of small pelagics appear to be tuned to minimize the detrimental effects of the environment on larval survival (Bakun, 1996).

The Optimal Environmental Window concept (OEW; Cury and Roy, 1989) provides a simple model for relating the upwelling process to larval survival and recruitment success. Roy *et al.* (1992) used the OEW to account for the difference between reproductive strategies of small pelagic fishes observed in several areas within the Canary Current upwelling ecosystem. These authors showed that off West Africa, there is no apparent relationship between the upwelling process and reproduction, but rather a striking correspondence between the timing of reproduction and the occurrence of wind speed of about 5-6 m/s. This range of wind speed corresponds to the optimal wind conditions defined by the OEW. We present here an attempt to generalize the results of Roy *et al.* (1992) to other upwelling areas such as the Benguela Current system, the California Current system, the Humboldt Current system and the Malabar coastal upwelling ecosystem off India. These upwelling areas constitute a unique opportunity to develop a comparative approach. They share fundamental characteristics: wind is the driving force of the upwelling process in these areas; they are colonized by closely related species, such as anchovies, sardines and sardinellas (Table 1), which are all small-sized, and have fast growth, a short life span, an early maturation and very high fecundity.

System	Dominant clupeoids
Canary Current	*Sardina pilchardus* *Sardinella aurita* *Sardinella maderensis* *Engraulis encrasicolus*
Benguela Current	*Sardinops ocellatus* *Engraulis capensis*
California Current	*Sardinops caeruleus* *Engraulis mordax*
Humboldt Current	*Sardinops sagax* *Engraulis ringens*
India, Malabar Coast	*Sardinella longiceps* *Sardinella fimbriata*

Table 1: Species of coastal pelagic fishes studied in each upwelling area.

1. BIOLOGICAL AND ENVIRONMENTAL DATA

A review of the literature provides information on the reproductive seasons and locations for each spawning area and each species. Table 2 summarizes the information gained through this review. The identification of the spawning seasons results from a compromise between the information collected. It can be considered as being, in average, valid for the period covering the 1950s to the 1990s. In some cases, data do not extend on a sufficiently long time interval. Then, some particular years are chosen to compare biological information and environmental data (Table 3).

Environmental data are derived from the Comprehensive Ocean Atmosphere Dataset (COADS; Woodruff *et al.*, 1987) using the software and CD-Rom produced for CEOS (Mendelssohn and Roy, 1996; Roy and Mendelssohn, this vol.).

ECOSYSTEMS **Spawning grounds**	**Spawning seasons**												**References**
SARDINES													
CALIFORNIA CURRENT ***Sardinops caeruleus***													
Southern California Bight (30-34°N)			M	$\underline{A}$	$\underline{M}$	$\underline{J}$							Ahlstrom (1960), Rosa and Laevastu (1960), Ahlstrom (1967), Parrish *et al.* (1981, 1983).
Baja California (26-30°N)								$\underline{A}$	$\underline{S}$				Ahlstrom (1967).
CANARY CURRENT ***Sardina pilchardus***													
Spain, Bay of Biscay			$\underline{M}$	$\underline{A}$	$\underline{M}$								Wyatt and Pérez-Gandaras (1989), Sola (1987), Lago de Lanzos *et al.* (1988), Sola *et al.* (1992).
Portugal (37-41°N)	$\underline{J}$	$\underline{F}$	$\underline{M}$								N	$\underline{D}$	Ré (1981), Ré *et al.* (1982), Figueiredo and Miguel Santos (1988), Cunha and Figueiredo (1988), Ré *et al.* (1990).
Morocco (28-30°N and 32-34°N)	$\underline{J}$	$\underline{F}$										$\underline{D}$	Furnestin and Furnestin (1959), Parrish *et al.* (1983). Domanevsky and Barkova (1976), FAO (1985).
Western Sahara (22-26°N)			M	A	M					$\underline{O}$	$\underline{N}$	$\underline{D}$	
HUMBOLDT CURRENT ***Sardinops sagax***													
Peru (6-14°S)	J	F					$\underline{J}$	$\underline{A}$	$\underline{S}$	O			Sharp (1980), Parrish *et al.* (1983), Muck *et al.* (1987). Parrish *et al.* (1983).
Chile, Arica (18-24°S)							$\underline{J}$	$\underline{A}$	$\underline{S}$	O			
BENGUELA CURRENT ***Sardinops ocellatus***													
Walvis Bay (20-24°S)	$\underline{J}$	$\underline{F}$	$\underline{M}$						S	O	N		Matthews (1960), Parrish *et al.* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°S)	$\underline{J}$	$\underline{F}$							$\underline{S}$	O	N	D	De Jager (1960), Rosa and Laevastu (1960). Parrish *et al.* (1983).
SARDINELLAS													
CANARY CURRENT ***Sardinella aurita***													
Mauritania, Banc d'Arguin (18-22°N)							$\underline{J}$	$\underline{A}$	$\underline{S}$				Conand (1977), Boëly *et al.* (1982), Fréon (1988).
Southern Senegal (12-15°N)					$\underline{M}$	$\underline{J}$				O	N		Conand (1977), Boëly *et al.* (1982), Fréon (1988).
INDIA ***Sardinella longiceps***													
Malabar Coast (8-16°N)						J	$\underline{J}$	$\underline{A}$	S				Nair (1959, 1960), Rosa and Laevastu (1960), Antony Raja (1964), Longhurst and Wooster (1990).
ANCHOVIES													
CALIFORNIA CURRENT ***Engraulis mordax***													
Southern California Bight (30-34°N)		$\underline{F}$	$\underline{M}$	$\underline{A}$									Hunter (1977), Lasker and Smith (1977), Smith and Richardson (1977), Smith and Lasker (1978), Parrish *et al.* (1981, 1983, 1986).
Baja California (26-30°N)		F	$\underline{M}$	A	M								Sharp (1980).
Southern Baja California (22-26°N)	J	F	M	A									Parrish *et al.* (1983).
CANARY CURRENT ***Engraulis encrasicolus***													
Morocco (28-30°N and 32-34°N)						$\underline{J}$	$\underline{J}$	$\underline{A}$					Furnestin and Furnestin (1959).
HUMBOLDT CURRENT ***Engraulis ringens***													
Peru (6-14°S)		F	M					$\underline{A}$	$\underline{S}$	$\underline{O}$			Valvidia (1978), Sharp (1980), Cushing (1982), Parrish *et al.* (1983), Alheit *et al.* (1984), Pauly and Soriano (1987), Muck (1989), Senocak *et al.* (1989).
Chile, Arica (18-24°S)							J	$\underline{A}$	S	O			Parrish *et al.* (1983).
BENGUELA CURRENT ***Engraulis capensis***													
Walvis Bay (20-24°S)	$\underline{J}$	$\underline{F}$	$\underline{M}$									$\underline{D}$	Parrish *et al.* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°E)	$\underline{J}$	F							S	$\underline{O}$	$\underline{N}$	$\underline{D}$	Shelton and Hutchings (1982), Parrish *et al.* (1983), Hutchings (1992), Waldron *et al.* (1992).

Table 2: Spawning seasons of sardines, sardinellas and anchovies in upwelling areas. The months corresponding to the peaks of reproduction are underlined.

SARDINES		ANCHOVIES	
Baja California	1952-1959	Southern Baja California	1970-1990
Spain	1980-1990	Walvis Bay	1970-1990
Portugal	1970-1990	Agulhas Bank	1970-1990
Chile, Arica	1970-1990	–	–

Table 3: Years considered in the study of biological and climatological data, by species.

Monthly time series of scalar wind speed and wind-stress, from 1950 to 1990, were constructed in each spawning areas (Table 2). A Coastal Upwelling Index (CUI) was calculated from the wind stress data following Bakun (1973). This index of the strength of the upwelling process is the offshore component of the wind induced Ekman transport. From the monthly time-series of scalar wind speed and CUI, a mean monthly cycle was calculated.

In most cases spawning grounds and nursery grounds have a similar location. This is not the case for the spawning areas located on the Agulhas Bank (Benguela) and in the Bay of Biscay (Spain). In these two areas, spawning occurs outside the upwelling area and eggs, once spawned, are removed from the spawning grounds and carried by coastal jets to the nursery grounds located in the upwelling (Shelton and Hutchings, 1982; Cabanas *et al.*, 1989). Consequently, for these two examples, environmental data corresponding to the nursery grounds are considered: the Galician Coast (Spain: 42-44°N) and the area surrounding St Helena Bay (Benguela: 30-34°S).

2. RESULTS

The duration of the upwelling season varies from one ecosystem to the other (Fig. 1): it is a year-round process off Peru and South Africa but limited to spring and summer off California and Morocco. There is no apparent relationship between the timing of reproduction and the upwelling process (Fig. 2): for instance, off Morocco, sardine reproduces outside the upwelling season; on the contrary, in the California Bight or off Peru, spawning occurs when the upwelling is active.

Following Bakun and Parrish (1982) and Parrish *et al.* (1983), we try to characterize the environmental conditions prevailing during the spawning season by using CUI and wind speed. These two environmental parameters are used as proxy-variables to estimate the strength of several environmental processes such as mixing by the wind, enrichment by the upwelling and offshore drift by the wind induced Ekman transport. These wind related processes are thought to be the key environmental processes to be considered when addressing the effect of the environment on fish population in upwelling areas (Lasker, 1975; Parrish *et al.*, 1981; Cury and Roy, 1989; Bakun, 1996). Since the observed spawning habits reflect the net adaptive response to a history of annual successes or failure in reproduction, one may expect that spawning habits would be seasonally and geographically tuned in order to provide a compromise between the environmental processes affecting recruitment success (Bakun *et al.*, 1991).

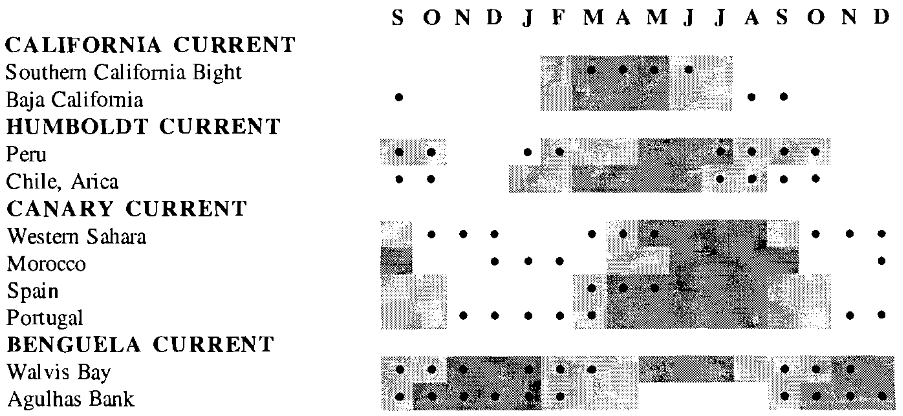

Fig. 1: Temporal relationships between sardines reproduction seasons and upwelling seasons. Spawning periods are represented by black points, upwelling seasons are in light grey, and upwelling peaks in dark grey (references for upwelling seasons : Cushing, 1971; Chesney and Alonso-Noval, 1989).

The mean monthly values of the two parameters during the sardine peak spawning season in each ecosystem are selected and plotted against each other (Fig. 2). Each ecosystem is characterized by different CUI values, either high or low. Two groups can be clearly distinguished. A first one corresponding to the sardine population off California, Morocco, Western Sahara, Peru, Chile and Namibia; for this group the wind speed values reported during the spawning seasons are clustered within a narrow band of wind speed, between 5 and 6 m/s. The second group corresponds to the Iberian Peninsula (Spain, Portugal) and the Agulhas Bank; in these ecosystems, the sardine populations do not follow the same pattern, wind values reported during the spawning season reach 7 to 9 m/s.

We follow the same procedure for the anchovy and sardinella populations. For anchovy, there is no clear pattern of correspondence between spawning and wind speed. Reproduction occurs within a wide wind range: data points are scattered between wind speed values of 5 and 8 m/s (Fig. 3). For the West African and Indian sardinella populations, spawning appears to be restricted to a range of wind speed between 5 and 6.8 m/s (Fig. 4). However, one should note that the number of data points for sardinella is rather limited.

3. DISCUSSION

Through the study of clupeoid reproductive strategies, two categories of ecosystems can be identified:

- Ecosystems of low latitudes: the main upwelling ecosystems of the world are part of this group: California, West Africa (Morocco, Sahara, Mauritania, Senegal), Peru, northern Chile, Namibia and India (Malabar Coast).
- Ecosystems of mid latitudes: the southern Benguela (South Africa) and the Iberian Peninsula (Spain and Portugal).

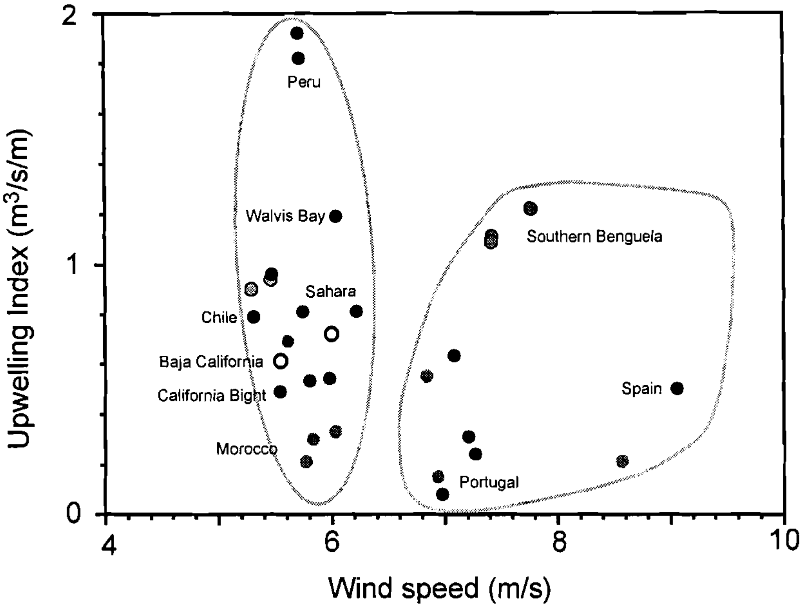

Fig. 2: Plots of spawning peaks of sardines against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

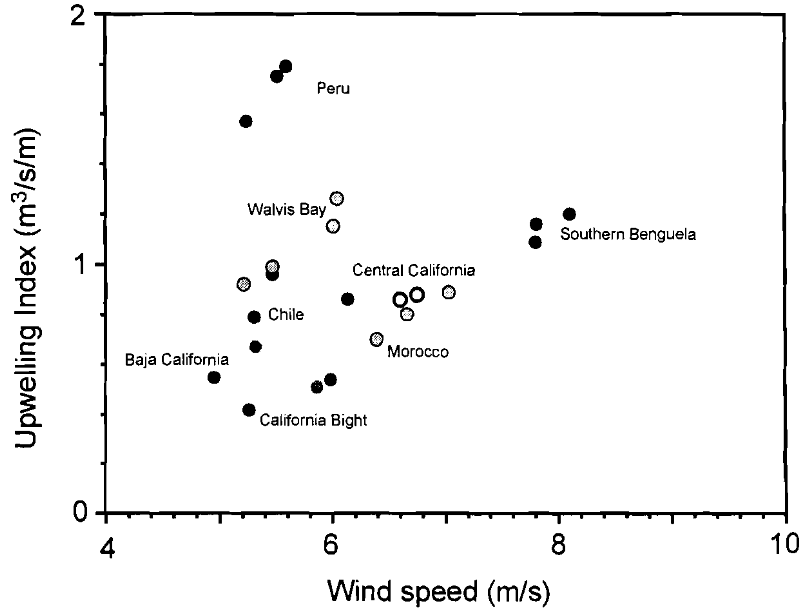

Fig. 3: Plots of spawning peaks of anchovies against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

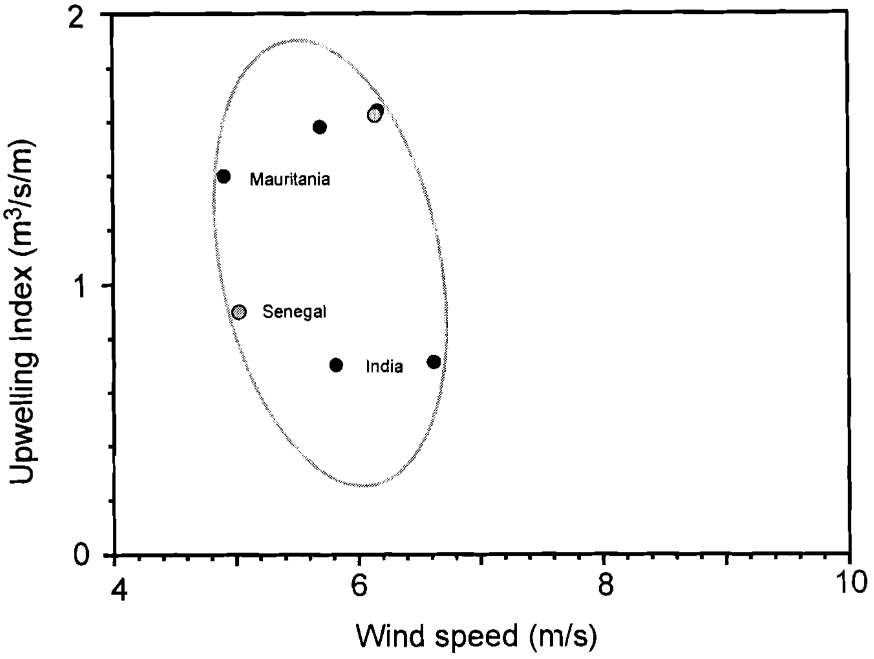

Fig. 4: Plot of spawning peaks of sardinella against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

3.1. Low latitude ecosystems

In these ecosystems, a generalization of Roy *et al.'s* (1992) results is possible for the sardines and sardinella population. The timing of reproduction for these two species coincides with the occurrence of 5-6 m/s winds. This range of wind speed values is in accordance with the 'Optimal Environmental Window' defined by Cury and Roy (1989). There is no apparent relationship between spawning and upwelling intensity. Spawning occurs sometimes during the upwelling season and sometimes outside the upwelling season.

The coincidence between spawning and the optimal wind range defined by the OEW suggests that reproductive strategies are strongly influenced by the seasonal fluctuations of the wind regime. Reproductive strategies appear to be seasonally tuned in order to coincide with the wind value that maximizes recruitment success. The wind value corresponding to the seasonal occurrence of the spawning peaks is constant over a wide range of latitude: from 5°N for Peru to 33°N for Morocco. This apparent constancy of the 'ideal' wind intensity around which the spawning activity of sardines and sardinella is maximum and is remarkable in view of the strong latitudinal dependence of some of the key environmental processes and scales that can be expected to be involved (Bakun *et al.*, 1991; Bakun, 1996). The magnitude of the enrichment by the upwelling and of the offshore drift by the wind-induced Ekman transport are both related to the intensity of the wind, but are also latitude-dependent processes. Wind generated turbulent mixing is estimated to be proportional to the third power of the wind speed, and is a process independent of latitude. The apparent constancy of the optimal wind intensity over several ecosystems located at different latitudes, can therefore be interpreted as an indication of the dominance of wind mixing in the seasonal adjustment of small pelagic fish reproductive strategy in upwelling areas. This may leave the choice of an adequate spawning location as an available means for dealing with limiting factors such as offshore transport and enrichment.

The duration and the intensity of the upwelling process appears to have a limited effect on the timing of the reproduction. However, offshore Ekman transport can be detrimental for larval survival and the fate of a fish population. Fish may have to select an adequate location for spawning in order to avoid the detrimental effect of wind-induced offshore drift. In these mid-latitude ecosystems, the spawning grounds are located in bays or in coastal indentations, downstream of intense upwelling centres (Parrish *et al.*, 1983; Roy *et al.*, 1989). Off Walvis Bay, the upwelled waters coming from the Lüderitz upwelling centre, are carried away by the main current, diffuse in the bay and supply the nursery with nutrients. The advection of cold waters in the bay induces at the same time the formation of convection cells, reducing larval offshore drift (Bakun, 1996). Furthermore, the larvae are sheltered from strong mixing by the wind. The width of the continental shelf is also an important characteristic. A wide continental shelf enables the formation of retention eddies (Brink, 1983; Nelson and Hutchings, 1987). As the retention process applies also to plankton, a wide continental shelf may allow a better coupling between primary and secondary productions. The inshore side of upwelling plumes also provide adequate locations for larvae retention (Graham and Largier, 1997; Roy, in press).

3.2. Mid-latitudes ecosystems

There are two ecosystems for which the seasonal spawning is not related to the occurrence of the optimal wind value defined by the OEW (Fig. 2). These ecosystems are the Iberian Peninsula and the southern Benguela. In these ecosystems, reproduction occurs during time period characterized by an intense wind regime. One also notes that the spawning grounds and nursery grounds are spatially distinct. In these two areas, the configuration of the coastline is quite similar with a North-South coast where the upwelling develops and an East-West coast located poleward and up-wind of the upwelling area. This configuration of the coast provides a unique opportunity for the fish populations to avoid the reproductive difficulties inherent in an exposed upwelling coast (Bakun, 1996). In both cases, the spawning grounds are located outside the upwelling coast and rather concentrate poleward along the East-West oriented coast (the Agulhas Bank off South Africa and the Bay of Biscay off Spain).

Eggs laid in the Bay of Biscay are carried by a coastal jet towards the Galician Coast, in the North-West of Spain (Cabanas *et al.*, 1989). Unlike most cases, eggs are thus laid upward the upwelling centres as regards to the main surface circulation. As spawning occurs outside the upwelling zone (Garcia *et al.*, 1991), early larval stages are not subjected to the detrimental effects of dispersion linked to Ekman transport. Furthermore, they probably take advantage of the spring bloom. This seasonal primary production peak indeed favors larval survival. After being transported along the Galician Coast, they can take advantage of the upper layers enrichment by the upwelling process. Moreover, at this stage of development, larvae are more mobile; therefore, their survival is supposed to depend less on concentration (pursuit and attack behavior) and retention processes (horizontal and vertical displacement).

The reproductive strategies of sardine and anchovy in the southern Benguela follow a similar pattern. Sardine and anchovy eggs are laid on the Agulhas Bank, upward the upwelling centre, and are then carried by a coastal jet toward the west coast upwelling area, North of Cape Columbine (Largier *et al.*, 1992). Shelton and Hutchings (1982) have estimated that the time for the eggs to be transported to west coast upwelling is in order of days. Along the west coast, St Helena Bay is thought to be an important nursery ground. It is a place where biological production can benefit from the input of nutrient by the upwelling. The upwelling plume that develops down-wind Cape Colombine creates a physical barrier allowing retention to occur within St Helena Bay (Graham and Largier, 1997). This area constitutes a place a priori favorable for a nursery ground.

In these two ecosystems, the question of the evolutionary advantage of developing such a strategy, i.e. to spawn outside the upwelling area during time period characterized by intense wind induced mixing remains an open question. In both places, the spawning grounds seem to be characterized by a strong vertical stratification which may counteract the detrimental effect of wind mixing. Over the Agulhas Bank, warm waters advected from the Indian Ocean by the Agulhas Current overlie cooler and dense water from the Atlantic (Shannon, 1985). This allows to form a protected stable layer where fish can successfully reproduce under energetic wind conditions (Parrish *et al.*, 1983). Egg development is also strongly affected by temperature. The cold temperature encountered along the west coast upwelling may also be an important element in favor of spawning in the warm waters off the Agulhas Bank. In the Bay of Biscay, spawning occurred in spring and is in phase with the annual planktonic bloom, this might be an important element favoring larvae survival within the Bay.

CONCLUSION

The timing of sardine and sardinella spawning in low latitude upwelling ecosystems appears to be linked with the occurrence of wind speed within a range of 5 to 6 m/s. There is no apparent relationship between spawning and upwelling intensity. Thus, it was possible to extend Roy *et al.'s* (1992) results to the major low latitude upwelling ecosystems of the world. This optimal wind range is in accordance with the OEW (Cury and Roy, 1989) which defines 5-6 m/s wind as being the optimal condition for small pelagic fish recruitment success in upwelling areas. The constancy over a wide range of latitude of the optimal wind range is an indication of the dominance of wind mixing in the adjustment of small pelagic fish reproductive strategy to seasonal upwellings. This may leave the choice of an adequate spawning location as an available means for dealing with limiting factors such as offshore transport and enrichment.

There are two outliers for which the spawning is not related to the occurrence of the optimal wind value. These ecosystems are the Iberian Peninsula and the southern Benguela. In these areas, spawning grounds and nursery grounds are also spatially distinct. They both share similar topographical characteristics with a North-South oriented coast where the upwelling develops (the nursery grounds) and an East-West oriented coast located poleward and up-wind of the upwelling area (the spawning grounds). This configuration of the coast provides a unique opportunity for fish population to avoid the reproductive difficulties inherent in an exposed upwelling coast.

Anchovy reproductive strategy appears to be quite distinct from sardine and sardinella strategies. There is no apparent relationship between the upwelling indices or the wind intensity and the timing of anchovy spawning. This remains an open question.

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