PNDR

Rapport de synthèse
Octobre 1998

Thème général :
La dynamique du recrutement dans les zones côtières d'upwelling.

Projets réalisés à l'ORSTOM avec le soutien de l'action incitative PNDR-GLOBEC.

Rapport rédigé par C. Roy
avec la collaboration de P. Cury et H. Demarcq

INTRODUCTION

De 1995 à 1998, quatre projets dont le thème central était la dynamique du recrutement dans les zones d'upwelling côtiers ont été réalisés à l'ORSTOM dans le cadre de l'action incitative PNDR-GLOBEC. Le noyau de l'équipe est constitué de trois chercheurs de l'ORSTOM (P. Cury-écologiste, H. Demarcq-biologiste et C. Roy-océanographe physicien); des étudiants (V. Faure, P. Penven et Y.J.Shin) et des chercheurs des pays partenaires de l'ORSTOM ont contribué à la réalisation de ces projets. Les quatre composantes ont été coordonnées par P. Cury en 1995 et ensuite, de 1996 à 1998, par C. Roy.

Ces projets ont abordé, à travers quatre thèmes de recherche qui sont rappelés dans le paragraphe suivant, différents aspects de la dynamique du recrutement. Ils avaient en commun : 1)-un domaine : les principales zones d'upwelling côtiers et 2)-des espèces cibles (sardine, sardinelles et anchois) proches. Les deux premiers thèmes se sont basés sur une approche comparative, entre espèces et entre régions, pour tenter de généraliser certains traits particuliers de la dynamique du recrutement. Le troisième thème a tout d'abord été focalisé sur un écosystème (le Sénégal) pour tenter de montrer l'importance de certains processus spatiaux pour le déterminisme des stratégies de reproduction et la variabilité du recrutement. Dans une deuxième phase, un modèle hydrodynamique a été développé pour quantifier les processus de rétention dans la principale nursery de poissons pélagiques de l'écosystème du Benguela. Le quatrième thème avait pour objectif une étude de la variabilité à court terme de la dynamique de la ponte des sardinelles au Sénégal, en relation avec la dynamique de l'upwelling.

Des bases de données et des outils ont été développés pour soutenir ces actions de recherche. Une base de données de température de surface couvrant l'ensemble de l'upwelling sénégalais, de 1981 à 1995 a été mise en place à partir des données IR du satellite METEOSAT. Ces données ont été rendues disponibles aux membres de l'équipe. Différents outils de quantification de l'upwelling ont été développés et rassemblés dans un logiciel intitulé CUSSI. Enfin un modèle hydrodynamique 3D a été mis en place pour étudier les interactions entre l'upwelling et la topographie (effet de cap).

Ces projets ont contribué au programme Climate and Eastern Ocean Systems (CEOS) et plusieurs articles ont été publiés dans l'ouvrage édité par l'ORSTOM à l'issue de CEOS (Durand et al., 1998). Une collaboration étroite a été établie avec le programme international GLOBLEC-SPACC (Small Pelagic fishes And Climate Change), l'équipe ORSTOM-PNDR a participé activement à l'élaboration de ce programme et à la définition des thèmes des différents groupes de travail qui ont été mis en place [1].

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[1] Hunter J.R. and J. Alheit (eds.). International GLOBEC Small Pelagic Fishes And Climate Change program. Report of the first planning meeting, La Paz Mexico, June 20-24 1994. GLOBEC report n°8, 72pp.
Hunter J. et J. Alheit (eds). 1997. International GLOBEC Small Pelagic Fishes and Climaet Change program. Implementation plan. GLOBEC Report 11, 1-36p

1. RAPPEL DES THEMES PROPOSES

THEME 1: DYNAMIQUE DE L'EXPLOITATION DES POPULATIONS DE POISSONS PELAGIQUES DES ZONES D'UPWELLING MONDIALES : INCIDENCE DE LA VARIABILITE DU RECRUTEMENT.

Les espèces pélagiques côtières, telles les sardines, les anchois, les maquereaux sont en majorité capturées dans les zones d'upwelling et représentent environ 50 % des captures mondiales de poissons marins. L'exploitation a débuté au début du siècle et les statistiques de pêche fiables sont disponibles depuis les années cinquante dans les différents systèmes d'upwelling mondiaux (Afrique de l'ouest, Afrique du sud, Californie, Pérou, Chili, Cote d'Ivoire, Ghana, Inde...). Aujourd'hui ces ressources sont intensément exploitées et connues pour leur instabilité. La variabilité du recrutement, liée principalement aux fluctuations de l'environnement, affecte donc de façon notable la dynamique des pêcheries: nombreux sont les exemples de pêches pléthoriques qui ont connu des effondrements de stocks brutaux et parfois durables. Les questionnements scientifiques ont surtout tenté de définir les causes de la variabilité du recrutement. Dans ce thème nous abordons deux facettes. La première est celle des conséquences de la variabilité du recrutement sur la dynamique des pêcheries. La deuxième est celle de la productivité des grands systèmes d'upwelling au travers de la production pélagique et du recrutement des poissons pélagiques (une des interrogations majeures étant les raisons de l'importante productivité de l'écosystème péruvien).

THEME 2: LES STRATEGIES DE REPRODUCTION DANS LES UPWELLINGS COTIERS : TENTATIVE DE GENERALISATION.

En Afrique de l'Ouest, un modèle unique permet d'interpréter de manière cohérente, en fonction des caractéristiques environnementales, les différentes stratégies de reproduction des espèces pélagiques côtières. Ce modèle peut être résumé de la manière suivante : le calendrier de la reproduction des populations de clupéidés est établi de manière à faire coïncider les saisons de reproduction avec les périodes pendant lesquelles la vitesse du vent est voisine de $6 m.s^{-1}$, indépendamment de la présence ou non d'un upwelling. Les quatre grands écosystèmes d'upwelling (Courant des Canaries, du Benguela, de Californie et du Humboldt) forment un ensemble aux caractéristiques écologiques comparables; on peut émettre l'hypothèse que quelques processus clés, communs aux différents systèmes, contrôlent l'ensemble de la dynamique. La question posée concerne la possibilité de généraliser le modèle établi en Afrique à l'ensemble des écosystèmes d'upwelling.

THEME 3: DYNAMIQUE D'UNE ZONE DE RETENTION DANS UN UPWELLING COTIER

Pour se reproduire, les espèces pélagiques côtières (sardines, anchois, sardinelles) produisent un grand nombre d'œufs et de larves pélagiques. Dans des milieux aussi dispersifs que les upwellings, une telle stratégie de reproduction est éminemment risquée. En effet, la probabilité est grande de voir les œufs et les larves entraînés au large en dehors de l'habitat côtier. Cela peut conduire à une dispersion des individus en dehors des zones favorables à leur développement et affecter la cohésion de la population. Pour assurer le succès de la reproduction, on observe de manière générale que les adultes quittent les zones productives que sont les zones d'upwelling intense pour se reproduire dans des zones moins dispersives. Cependant, dans certaines régions (Pérou, Sénégal, Sahara, Afrique du Sud), la reproduction se concentre dans des zones où la résurgence présente un maximum local et où l'advection est intense. Malgré des conditions *a priori* défavorables à la reproduction, ces populations sont pérennes : elles sont exploitées depuis de nombreuses années et parfois à des niveaux soutenus. Ces populations ont vraisemblablement tiré profit de particularités locales permettant aux larves de rester piégées dans la zone côtière et ainsi d'assurer le succès de la reproduction.

L'objectif de ce thème de recherche, est, dans une première phase, d'identifier les processus physiques permettant de générer des structures favorables à la rétention des œufs et des larves dans la zone côtière. La deuxième phase consiste à développer un modèle hydrodynamique 3D pour étudier la dynamique de ces processus et quantifier l'intensité de la rétention.

THEME 4: VARIABILITE DE L'UPWELLING COTIER ET DYNAMIQUE DES PONTES DE DEUX ESPECES DE SARDINELLES

Ce thème vise à explorer l'hypothèse d'un déterminisme à court terme entre les fluctuations de l'upwelling côtier au Sénégal et le déclenchement de pontes de la sardinelle ronde (*Sardinella aurita*) et de la sardinelle plate (*Sardinella maderensis*), sous l'influence de conditions environnementales momentanément favorables (successions enrichissement-réchauffement par exemple).

Les chances de succès de ces pontes et leur participation au recrutement devront être estimées à travers les données existantes. Les questions posées sont les suivantes:

-Existe-t-il une relation déterministe en zone d'upwelling côtier entre un stimulus environnemental et le déclenchement d'une ponte au sein d'une population pélagique côtière (ou d'une fraction de celle-ci) à partir de l'exemple de *Sardinella aurita* au Sénégal?

-Quelle est l'échelle (ou les échelles) de temps où une réponse peut être observée (une semaine, un mois, une saison) ?

-Dans quelle mesure la dynamique de l'upwelling (en terme d'intensité et de turbulence induite notamment) permet-elle ou pas de favoriser l'avenir de ces pontes ?

-Si l'intensité des pontes et la survie larvaire s'avèrent largement dépendantes de la dynamique de l'upwelling et de ses effets induits, un indice de recrutement peut-il être estimé qualitativement par cette seule dynamique ?

- Cet indice a-t-il un effet mesurable en terme d'évolution démographique ?

2-RESULTATS OBTENUS

2.1-THEME 1: DYNAMIQUE DE L'EXPLOITATION DES POPULATIONS DE POISSONS PELAGIQUES DES ZONES D'UPWELLING MONDIALES : INCIDENCE DE LA VARIABILITE DU RECRUTEMENT.

(Rédaction P. Cury et C. Roy).

Les résultats de cette action de recherche ont été présentés au Symposium Benguela Ecology Programe de décembre 1996 et rassemblées dans deux articles publiés en 1998 et dans un rapport de DEA

Faure V. et P. Cury, 1998. Pelagic fisheries and environmental constraints in upwelling areas: how much is possible. In: Durand M.H., P. Cury, R. Mendelssohn, C. Roy, A. Bakun et D. Pauly (eds). Global versus local changes in upwelling systems. Editions Orstom Paris. p391-407.

Cury P., Roy C et V. Faure. 1998. Pelagic fisheries and environmental constraints in upwelling areas: the Peruvian puzzle. *In:* Benguela Dynamics. Pillar, S. C., Moloney, C., Payne, A. I. L. and F. A. Shillington (Eds). South African Journal of Marine Science 19.

Faure V. 1995. Caractérisation et comparaison des variabilités de l'environnement et des populations de poissons pélagiques des zones d'upwelling mondiales. Rapport DEA Univ Montpellier II. 37p.

La productivité halieutique en relation avec les variables environnementales est analysée pour onze zones d'upwelling. Pour chacune de ces régions, la surface du plateau continental a été calculée (tab. 1). Deux indices de productivité sont estimés à partir des statistiques de captures disponibles depuis le début des pêcheries (tab.1); elles sont assimilées à la productivité en poisson d'un écosystème

	Upwelling areas	**Time period considered**	**Maximum pelagic fish catch (10^{3}tons)**	**Surface of the shelf (10^{3}km2)**	**Maximum productivity per unit of surface (tons/km2)**
1	California	1924-1991	609	101	6.0
2	Chile	1966-1993	3708	62	59.3
3	Spain and Portugal	1937-1989	368	59	6.2
4	Morocco	1950-1991	362	118	3.1
5	Senegal	1964-1991	194	32	5.9
6	Côte d'Ivoire-Ghana	1966-1993	270	54	5.0
7	Namibia	1966-1992	1561	90	17.3
8	South-Africa	1950-1992	623	178	3.5
9	India	1948-1988	448	70	6.4
10	Peru	1958-1993	12286	86	142.0

Tab. 1 : Captures maximales de poissons pélagiques, surface du plateau continental et captures maximales par unité de surface pour les dix zones d'upwelling et les trois principales espèces pélagiques (sardine, sardinelles etanchois) considérés (d'apres Cury et al., 1998).

Cinq variables environnementales sont considérées pour chaque zone d'upwelling : indice d'upwelling côtier et vitesse du vent, température de surface de la mer, surface et longueur du plateau continental (tab. 1 et 2).

	Upwelling areas	**Coastal Upwelling index** $m^3/s/m$	**Wind mixing index** m^3/s^3
1	California	0.36	654
2	Chile	0.93	345
3	Spain and Portugal	0.36	627
4	Morocco	0.66	305
5	Senegal	0.59	150
6	Côte d'Ivoire-Ghana	1.04	103
7	Namibia	1.28	517
8	South-Africa	0.31	770
9	India	0.44	239
10	Peru	1.20	224

Tab. 2 : Indice d'upwelling et indice de mélange dans les dix zones d'upwelling considérées. considérés (d'apres Cury et al., 1998).

Il existe une disparité importante entre la productivité des dix écosystèmes. Le Chili et surtout le Pérou sont deux écosystèmes dans lesquels la productivité dépasse largement les valeurs observées ailleurs (tab. 1). La taille des écosystèmes, estimée à partir de la surface du plateau continental, ne permet pas d'expliquer la disparité observée entre les productivités en poissons pélagiques des différentes régions (fig. 1). La productivité par unité de surface du Pérou reste extrêmement élevée, comparée à celles des autres écosystèmes d'upwelling.

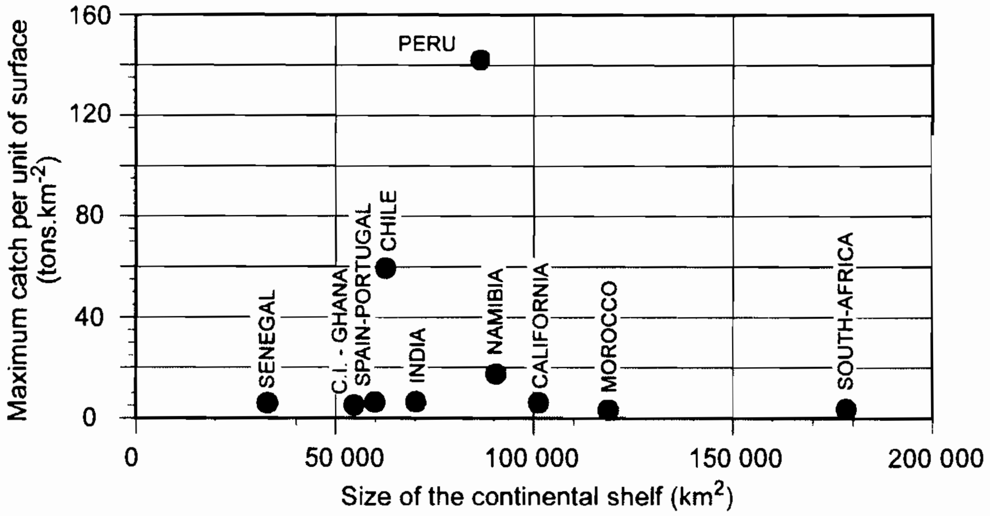

Figure 1: Capture maximale par unité de surface (tonnes/km2) pour les dix zones d'upwelling considérées (d'après Cury et al., 1998).

L'étape suivante pour tenter d'expliquer ces disparités et surtout de tenter de comprendre pourquoi l'upwelling du Pérou est si productif, fut de comparer les conditions environnementales dans ces différentes régions. Une méthode régressive non paramétrique révèle qu'une combinaison de plusieurs facteurs environnementaux est en effet nécessaire pour qu'une forte productivité soit réalisable. Les conditions optimales sont les suivantes (fig. 2): un fort indice d'upwelling (proche de 1.3 $m^3/s^1/m^1$), un indice de mélange par le vent modéré (proche de 250 m^3/s^3). Pour cette analyse, les données du Pérou ne furent pas prises en compte.

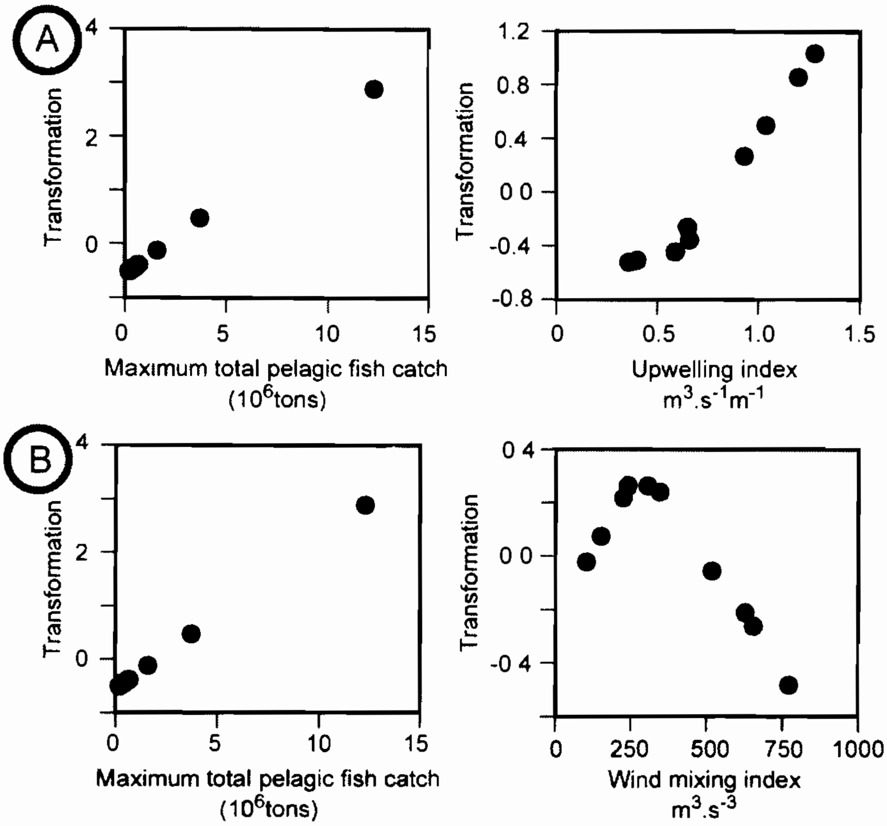

Figure 2: Transformations empiriques optimales données par l'algorithme ACE avec pour variable dépendante l'indice de productivité (captures maximales) et, comme variable indépendante: A)-l'indice d'upwelling et B)-l'indice de mélange par le vent. Dans cette exemple, les données du Pérou ont été exclues (d'après Cury et al., 1998).

Pour chaque écosystème, il est maintenant possible d'identifier le ou les facteurs environnementaux qui limitent la productivité en poisson (le recrutement). Au Chili et en Namibie, l'indice d'upwelling est favorable mais la production en poisson serait limité par un mélange par le vent trop important. En Afrique du Sud, Espagne et Californie, un mélange par le vent important et un faible indice d'upwelling contribue à limiter la production en poisson. Ces résultats permettent également de faire un diagnostic des changements consécutifs aux événements climatiques futurs.

L'écosystème Péruvien s'avère être le seul qui regroupe l'ensemble des conditions environnementales optimales. La forte productivité de l'écosystème péruvien serait donc le résultat d'un upwelling intense associé à un mélange par le vent modéré.

2.2-THEME 2: LES STRATEGIES DE REPRODUCTION DANS LES UPWELLINGS COTIERS : TENTATIVE DE GENERALISATION

(Rédaction : C. Roy et P. Cury)

Les résultats de cette action de recherche ont été publiés dans un article paru en 1998 et dans un rapport de DAA:

Shin Y.J., C. Roy et P. Cury. 1998. Clupeoids reproductive strategies in upwelling areas : a tentative generalization. *In* Durand M.H., Cury P., Mendelssohn R., Roy C., Bakun A. and D. Pauly. 1998. Global versus local changes in upwelling systems. Orstom, Paris, 409-422.

Shin Y.J. 1995. Stratégies de reproduction des Clupéoidés des zones d'upwelling côtier: tentative de généralisation. Rapport DAA. ENSA Rennes.68p.

Une approche comparative est utilisée pour étudier la dynamique temporelle des stratégies de reproduction des Clupéidés dans les écosystèmes d'upwelling, en relation avec des processus environnementaux supposés affecter la survie larvaire.

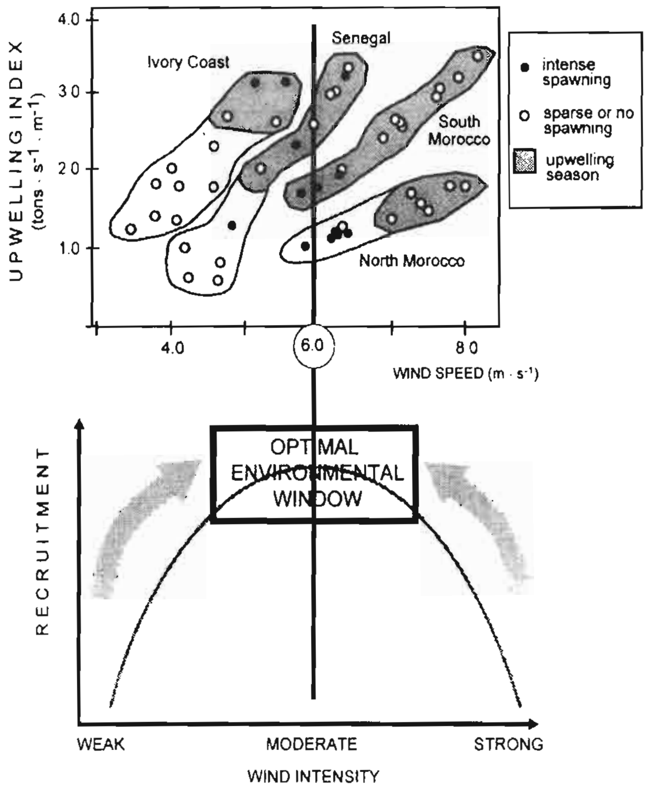

Figure 3: La reproduction des populations de sardines et sardinelles d'Afrique de l'Ouest en relation avec la vitesse du vent et l'intensité des upwellings. Pour chacune des populations, les valeurs mensuelles de la climatologie de l'indice d'upwelling sont tracées en fonction de la climatologie mensuelle de la vitesse du vent; les périodes d'upwelling correspondent aux zones hachurées. Les périodes de reproduction intense sont identifiées par les points noirs. On note: 1) qu'il n'y a pas de relation entre l'activité des upwellings et la ponte; 2) que l'activité de reproduction se regroupe dans chacune des zones, autour de vitesses de vent voisines de 6m/s qui est la valeur optimale du vent mise en évidence par la FEO. (D'après Roy et al., 1992).

En Afrique de l'Ouest, l'intensité du vent est un des déterminants la dynamique temporelle de la reproduction (fig. 3). Dans cette région, il n'y a pas de relation entre l'intensité de l'upwelling et la ponte; l'activité de reproduction est associée à l'apparition de vitesses de vent voisines de 6m/s (fig. 3). Quand le vent ne dépasse pas 6m/s pendant la saison d'upwelling, upwelling et reproduction peuvent s'établir simultanément (Sénégal, Côte d'Ivoire); les caractéristiques topographiques (baies, plateau large) sont alors mises à profit pour limiter l'advection des œufs et larves vers le large. Dans d'autres régions (Maroc, Sahara), la vitesse du vent dépasse $6 m.s^{-1}$ pendant la période d'upwelling, le calendrier de la reproduction se décale pour s'établir au cours d'une période de vent plus faible de manière à limiter les effets néfastes induits par un vent trop fort. L'objectif de ce thème de recherche était de généraliser à l'ensemble des écosystèmes d'upwelling, le schéma établi en Afrique de l'Ouest (Roy et al., 1992).

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 entre les différentes zones d'upwelling étudiées durant les pics de la saison de reproduction est effectuée. Au large du Pérou, la reproduction a lieu lorsque l'intensité de l'upwelling est maximale ($1.8\ m^3.s^{-1}.m^{-1}$). Au large du Maroc, la reproduction est décalée par rapport au processus d'upwelling (l'intensité de l'upwelling se situe dans l'intervalle $0.2\text{-}0.3\ m^3.s^{-1}.m^{-1}$). Le long des côtes de la Namibie, du Chili et de la Californie, la ponte a lieu pour 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 $6.1\ m^3.s^{-1}.m^{-1}$ pour dix des douze écosystèmes d'upwelling étudiés. Les deux exceptions sont les populations de sardine du sud du Benguela et de la péninsule ibérique. Pour l'anchois, il y a apparemment peu de correspondance entre le calendrier de la reproduction et les valeurs de la vitesse du vent.

Pour les sardines et les sardinelles, une généralisation du schéma obtenu en Afrique de l'Ouest est possible. Pour ces deux espèces, les conditions environnementales rencontrées lors de la ponte correspondent aux conditions optimales pour le succès du recrutement définie par la "Fenêtre Environnementale Optimale". Les deux écosystèmes (Afrique du Sud et Espagne) où la ponte se produit dans conditions de vent fort possèdent des caractéristiques topographiques identiques: une côte orientée nord-sud où se développe l'upwelling et une côte orientée est-ouest où a lieu la ponte.

Le déterminisme du calendrier de la ponte des anchois est différent de celui des deux autres espèces. Il ne semble pas exister de relation entre les fluctuations saisonnières de l'environnement et l'activité de reproduction.

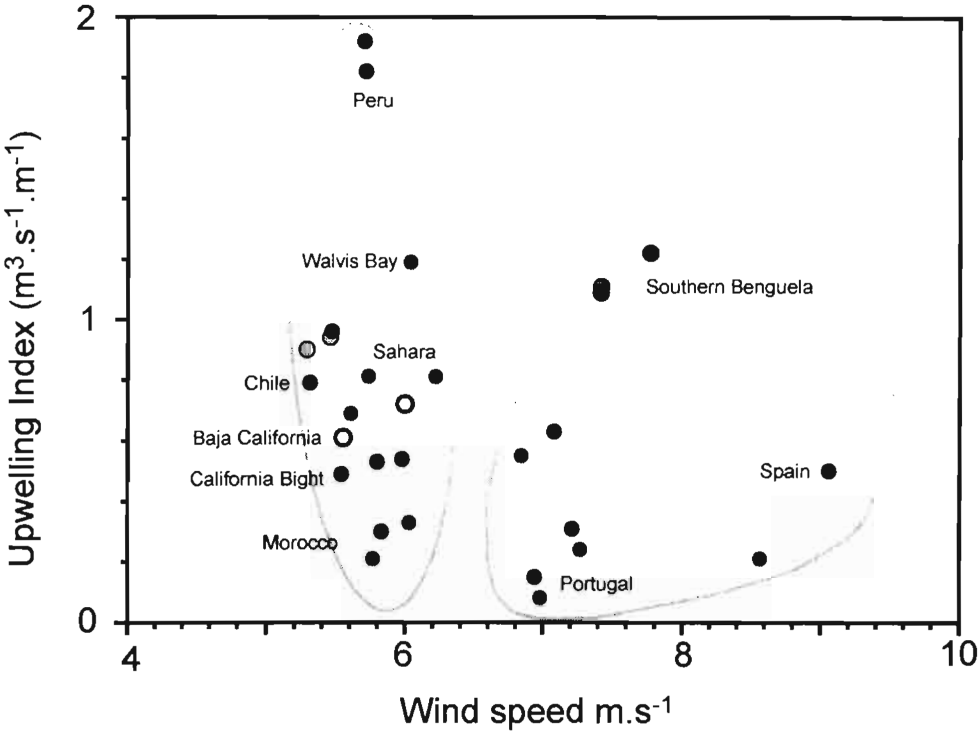

Figure 4 : Intensité de l'upwelling et vitesse du vent au cours des pics saisonniers de ponte des populations de sardine dans les principaux écosystèmes d'upwelling (d'après Shin et al. 1998).

2.3-THEME 3: DYNAMIQUE D'UNE ZONE DE RETENTION DANS UN UPWELLING COTIER (Rédaction: C. Roy et P. Penven)

Cette action de recherche s'est déroulée en deux phases successives. Dans un premier temps, les travaux se sont concentrés sur l'upwelling du Sénégal afin d'identifier des structures de rétention à partir d'images satellites. Dans la deuxième phase un modèle hydrodynamique a été développé sur un site présentant des caractéristiques similaires à celles du Sénégal : la partie sud de l'écosystème du Benguela.

Les résultats de la première phase de cette action de recherche ont été présentés au Symposium Benguela Ecology Programe de décembre 1996 et rassemblés dans un article publié en 1998 :

> Roy C., 1998. Upwelling-induced retention area: a mechanism to link upwelling and retention processes. *In:* Benguela Dynamics. Pillar, S. C., Moloney, C., Payne, A. I. L. and F. A. Shillington (Eds). South African Journal of Marine Science 19.

Ils ont également été publiés, dans une version abrégée dans PNR information, dans un document de la FAO et ils ont fait l'objet d'un rapport de DEA:

Roy C., 1996. Upwellings et zones de rétention. In T. DoChi and D.A. Keifer eds. Report of the workshop on the coastal perlagic ressources of the upwelling system of Northwest Africa : research and prediction. FI:TCP/MOR/4556(A). Field document 1. FAO Rome.

Roy C., 1996. Upwelling et zones de rétention. PNDR informations, 25, p1-9.

Olivier F.1996. Dynamique d'une zone de rétention dans upwelling côtier: l'exemple de la petite côte au Sénégal. Mémoire de DEA. Laboratoire de Physique des Océans-Université de Bretagne Occidentale. 72p.

Les résultats de la deuxième phase seront présentés lors du symposium PNDR de décembre prochain.

2.3.1-Phase 1 : identification des processus de rétention.

Au Sénégal, une importante population de sardinelles (*Sardinella aurita*) a colonisé le milieu et est exploitée par les pêcheries locales. Cette population présente une stratégie de reproduction singulière qui ne correspond pas au schéma proposé par Parrish *et al.* (1983). L'upwelling sénégalais s'établit à partir du mois de décembre et reste dans sa phase active jusqu'au mois de juin. En suivant le schéma traditionnel, on pourrait s'attendre à rencontrer une saison de ponte décalée par rapport à la saison d'upwelling. Une ponte secondaire concernant les jeunes adultes est observée au coeur de l'été et en automne, cependant l'essentiel de l'activité reproductrice des adultes se situent en mai-juin pendant la saison d'upwelling. Bien que les niveaux de turbulence induits par le vent restent dans une gamme de valeurs compatibles avec la survie des larves, le processus d'upwelling devrait inévitablement conduire à une dérive des larves en direction du large; cet effet néfaste pour le maintien des larves dans l'habitat côtier et leur survie devrait conduire à un niveau de recrutement faible, difficilement compatible avec la persistance sur le long terme d'une telle stratégie de reproduction. La question posée est la suivante : Quels sont les mécanismes qui permettent à la population de sardinelle du Sénégal de maintenir une telle stratégie ?

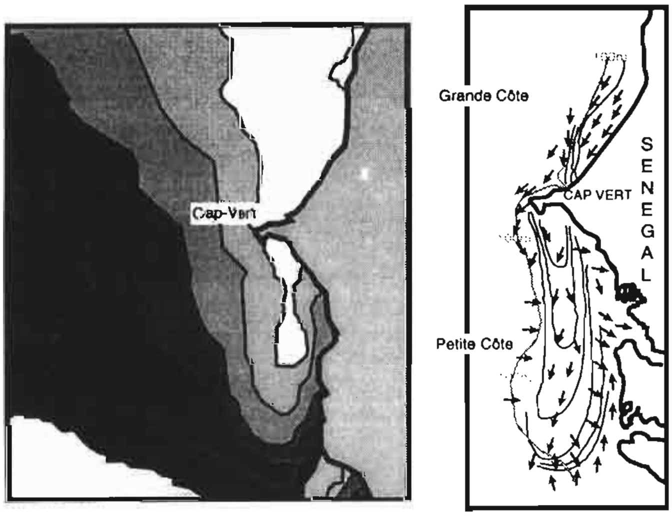

Figure 5 :Champ thermique de surface en février d'après les images METEOSAT (moyenne 1983-1989, source : UTIS/ISRA-ORSTOM) et courant de surface en saison d'upwelling (d'après Roy, 1998).

L'activité de reproduction des sardinelles est inégalement répartie le long du littoral; plutôt atténuée dans la région située au Nord du Cap-Vert ("Grande Côte"), l'activité reproductrice se concentre au Sud du cap ("Petite Côte"), dans une zone où le plateau continental s'élargit pour atteindre près de 30 milles dans sa partie la plus étendue.

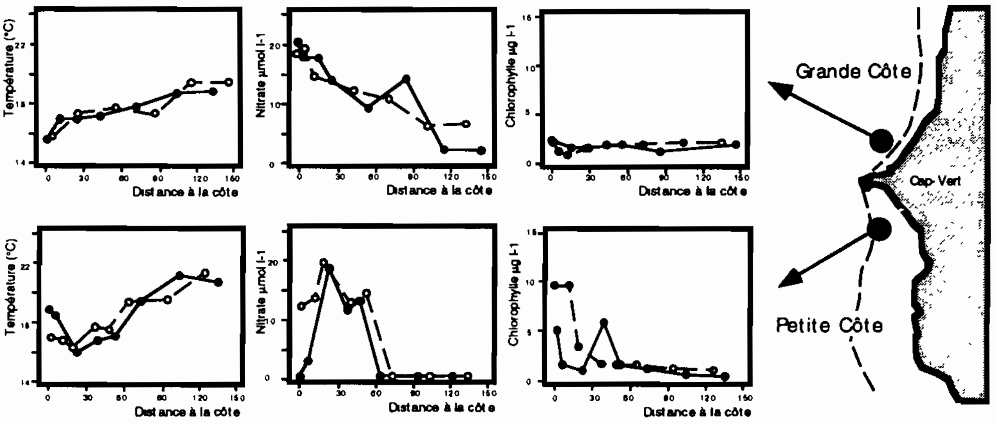

Figure 6 : distribution en surface de la température, des nitrates et de la chlorophylle le long de radiales situées de part et d'autre de la presqu'île du Cap-Vert (d'après Roy, 1998).

En période d'upwelling, le champ thermique superficiel présente dans cette zone une structure particulière (fig. 5): alors qu'au Nord du Cap-Vert on observe le schéma classique d'un upwelling côtier avec un minimum thermique à la côte et un gradient régulier (positif) en direction du large, au sud du cap, on rencontre une langue d'eau froide isolée sur le plateau, avec un minimum thermique au niveau du talus continental et un maximum relatif dans la zone littorale. Les sels nutritifs et la chlorophylle présentent aussi une distribution contrastée qui reproduit la structure mise en évidence par la distribution spatiale de la température de surface (fig. 6). Les fortes concentrations de chlorophylle observées dans la bordure côtière constituent un élément remarquable. Cette accumulation du phytoplancton dans la zone littorale peut être interprétée comme étant le résultat de processus de concentration. Des interactions entre la topographie (un plateau large situé sous le vent d'un cap) et le processus d'upwelling sont à l'origine de la formation des structures rencontrées sur la Petite Côte.

Les différences constatées dans la distribution spatiale de paramètres physico-chimiques entre les régions situées de part et d'autre du Cap-Vert sont la clé pour comprendre le déterminisme de la reproduction des sardinelles (*S. aurita*) au Sénégal. La présence dans la bordure côtière au sud du Cap-Vert d'un maximum relatif de la température de surface et d'un maximum de chlorophylle sont les indices de l'existence d'une structure de circulation à double cellule sur le plateau (fig. 7):

-une première cellule, située à l'aplomb du talus continental, constitue la cellule de remontée principale alimentant la résurgence;

-une seconde cellule, située dans la zone littorale à la périphérie de la première, permet à une bande d'eau côtière d'être confinée et isolée du large; dans cette cellule les conditions optimales sont réunies pour le développement d'une production planctonique : relative stabilité, alimentation en sels nutritifs, etc. Un tel habitat est particulièrement favorable au développement larvaire.

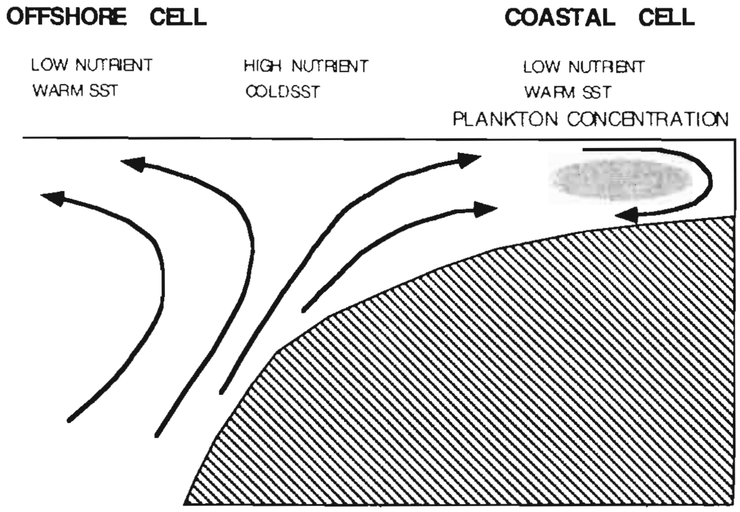

Figure 7 : représentation schématique de la circulation verticale sur la Petite Côte illustrant le mécanisme de rétention dans la bordure côtière. (d'après Roy, 1998)

Sur la Petite Côte, le processus d'upwelling associé à des caractéristiques topographiques particulières est le mécanisme permettant l'établissement d'une zone de rétention dans laquelle les conditions favorables à la reproduction sont réunies (concentration, rétention et enrichissement). Au nord du cap, la structure unicellulaire de l'upwelling entraîne des échanges continus avec le large, situation défavorable à la survie larvaire. Au sud du cap, en dehors de la période d'upwelling, la cellule littorale disparaît, et il n'existe plus de "barrière" limitant les échanges entre la côte et le large.

Au Sénégal, l'upwelling est à l'origine de la formation d'une zone de rétention littorale, favorable au développement des œufs et larves. C'est une situation originale dans le sens ou les processus d'upwelling et de rétention sont reliés positivement. La situation décrite au Sénégal n'est pas unique. Dans d’autres écosystèmes (Afrique du Sud, Pérou, sud-Maroc, Brésil, etc.), la reproduction de certaines populations de poissons et le processus d’upwelling se déroulent, comme sur la Petite Côte, de manière concomitante. Un trait commun à l'ensemble de ces régions semble cependant émerger: elles se situent dans des zones où le plateau continental s’élargit.

2.3.2-Phase 2 : modélisation des processus de rétention.

Pour la deuxième phase de cette action de recherche, des contraintes logistiques et le développement d'un programme de coopération[2] avec l'Université de Cape-Town, le Sea Fisheries Research Institute et l'ORSTOM nous ont conduit à choisir la région de la Baie de Sainte Hélène (partie sud de l'écosystème du Benguela) pour implanter le modèle 3D (fig. 8). Cette région possède des caractéristiques topographiques similaires à celle du Sénégal; c'est aussi une des principales zones de nurscry de la région.

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[2] Ce projet (VIBES) est t un programme de recherche appliquée destiné à l'obtention de nouveaux outils et d'informations pour l'évaluation et la gestion régionale des ressources pélagiques côtières de l'écosystème du Benguela. L'objectif principal de VIBES est d'étudier sur le long-terme et à différentes échelles d'observation, les changements intervenus dans les pêcheries, le recrutement et leurs processus spatiaux en relation avec l'environnement et l'abondance des poissons adultes.

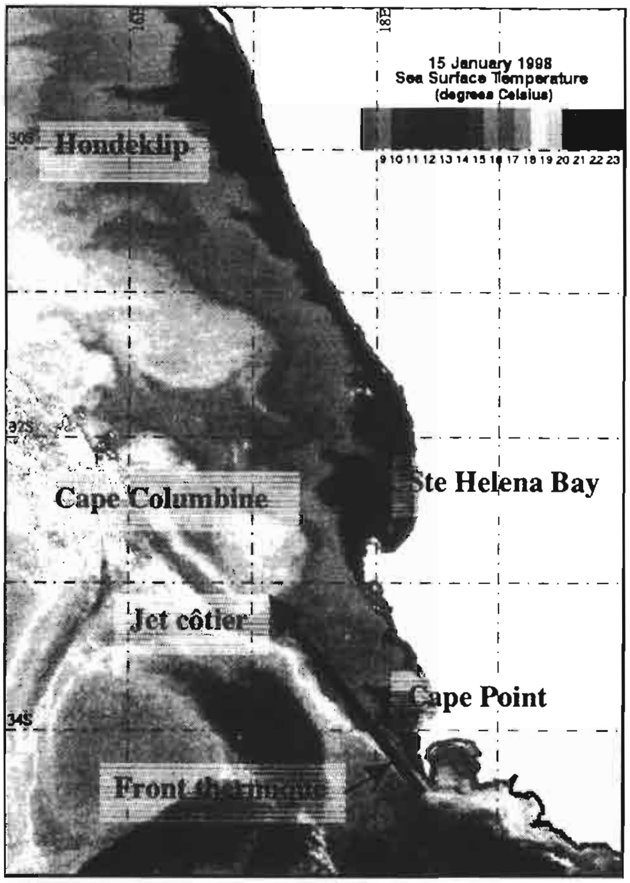

Figure 8. Carte de la température de surface (images AVHRR/NOAA du 16/01/1998) dans la partie sud du courant du Benguela (image communiquée par S. Week – UCT)

Dans la partie sud du Benguela, la baie de Ste Hélène, est le principal accident topographique le long de cette côte. Dans cette zone, la présence d'un cap, d'une baie et d'un plateau large modifient profondément la structure de l'upwelling: il se forme une plume d'eau froide, décollée de la côte et s'étendant vers le nord sur une distance d'environ 80km (fig. 8). En direction du large, la zone frontale marquant limite de l'extension de l'upwelling est caractérisée par des filaments et des tourbillons, structures classiques observées dans les autres régions d'upwelling.

La ponte des sardines et des anchois a lieu essentiellement au printemps et en été, quand l' upwelling est actif. Le mélange turbulent induit par le vent et le transport d'Ekman des eaux côtières vers le large créent un environnement défavorable à la reproduction sur la côte Atlantique. Les sardines et anchois migrent vers le banc des Aiguilles pour se reproduire où des eaux chaudes transportées par le courant des Aiguilles créent un environnement stable et fortement stratifié (Parrish et al., 1983).

Les œufs et larves sont rapidement transportés vers le nord par un jet côtier (fig. 9). Après quelques jours, ils atteignent la région d'upwelling de la côte ouest (Hutching, 1992). Les distributions de taille obtenues lors des campagnes montrent que les jeunes larves se trouvent alors au niveau du front de l'upwelling et les larves plus âgées (1-2 mois) se concentrent à la côte. Quelques mois après la ponte, au début du printemps, les jeunes recrues se concentrent dans la baie de Ste Hélène où une part importante des captures annuelles est alors réalisée sur des individus âgés de moins d'un an. Les mécanismes permettant, au niveau de la côte ouest, la "migration" des larves vers la zone côtière et leur rétention restent encore mal connus. Les faibles capacités de déplacement de ces jeunes individus ne permettent pas d'envisager une telle migration (entre 80 et 150 km suivant la saison). Des processus physiques (filaments, pulsations de l'upwelling, plume d'upwelling...) ainsi que des aspects comportementaux des larves (migrations verticales) ont alors un rôle majeur. Le modèle 3D est développé dans le but d'étudier ces mécanismes permettant la concentration et la rétention des larves dans la bordure côtière.

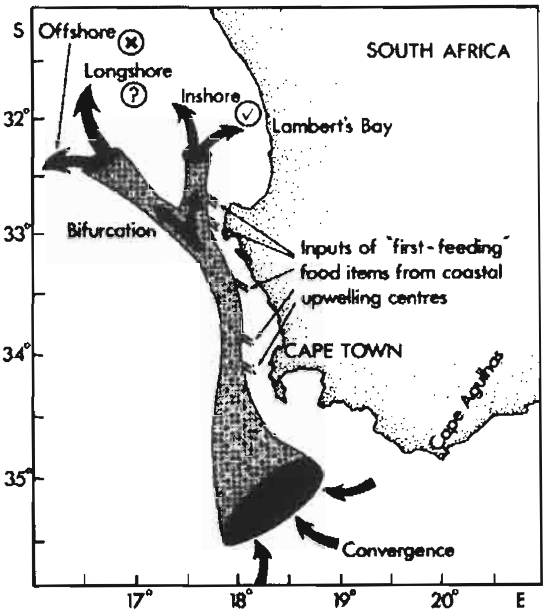

Figure 9: Un modèle conceptuel du transport des œufs et larves du Banc des Aiguilles vers la côte ouest illustrant le rôle joué par l'advection. (D'après Hutching, 1992).

Le domaine pris en compte par le modèle s'étend de 34°S à 31°S et de la côte à 16°30'E, c'est un compromis permettant de conserver une résolution fine et des performances acceptables avec les moyens de calculs disponibles localement (fig. 10).

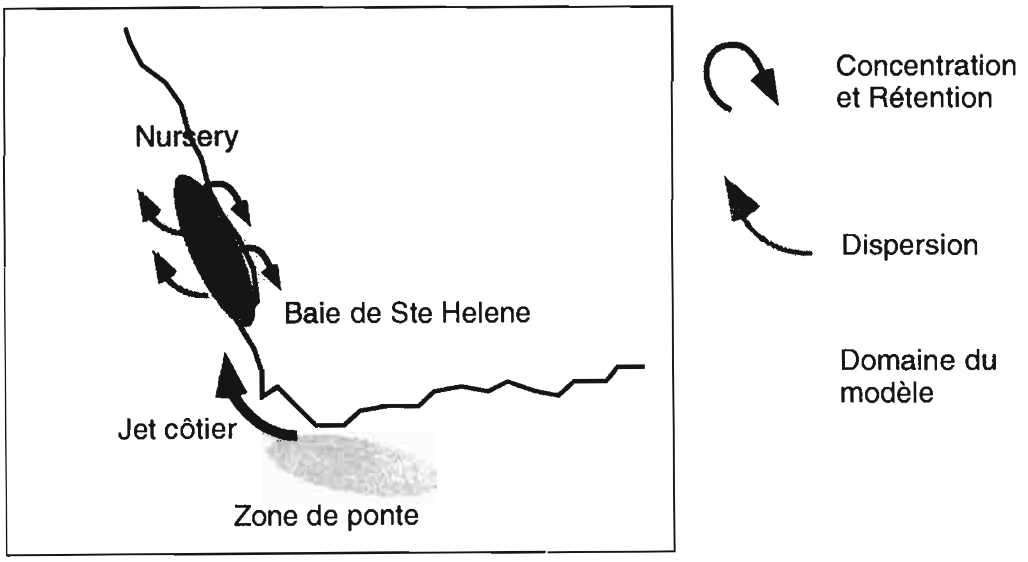

Figure 10: Domaine à prendre en compte par la modélisation des processus environnementaux affectant le recrutement dans la partie sud du Benguela.

L'implantation du modèle a démarrée en octobre 1997 au Laboratoire de Physique des Océans (Université de Bretagne Occidentale-Brest) par un étudiant de thèse(P. Penven) supervisé par Pr. A. Colin de Verdière. Ce modèle est basé sur le code 3D SCRUM développé à Rutgers University. Ce code est particulièrement adapté pour résoudre les équations de la dynamique des fluides géophysiques dans la zone côtière englobant le plateau continental et le talus (Haidvogel et al., 1991). Pour le cheminement de notre démarche, nous avons fait le choix de séparer les différents processus physiques ayant un rôle au niveau de la rétention. Cela nous a conduit à étudier tout d'abord les mouvements horizontaux pour ensuite aborder les phénomènes verticaux. Les résultats présentés ici portent uniquement sur les mouvements d'ensemble des colonnes d'eau, ce que l'on appelle la circulation barotrope.

Pour résoudre les processus à l'échelle de quelques dizaine de km, un pas de grille de 5km a été choisi. La grille du modèle est régulière, de taille variant de 300 à 900 km suivant les expériences réalisées. Pour la prise en compte des conditions aux limites, nous avons opté pour un canal périodique où tout élément sortant d'un coté rentre de l'autre et vice-versa. Ceci garantit une bonne stabilité du modèle aux frontières. Une bathymétrie analytique a été développée afin de décrire la configuration générale de la côte et du plateau (fig. 11).

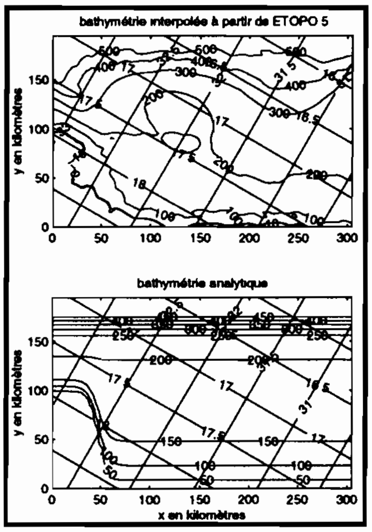

Figure 11: Comparaison entre les bathymétries réaliste et analytique.

Pour quantifier les processus de rétention, nous avons développé un traceur barotrope qui permet une mesure quantitative des phénomènes de recirculation. Ce traceur est inspiré de ceux mesurant le temps écoulé depuis le plongeon d'une masse d'eau de surface dans les modèles à grande échelle.

Plusieurs expériences numériques ont été réalisées afin de tester le modèle, de le valider et d'évaluer sa sensibilité suivant différents types de configuration (influence de la friction du fond, de la taille du bassin, ...).

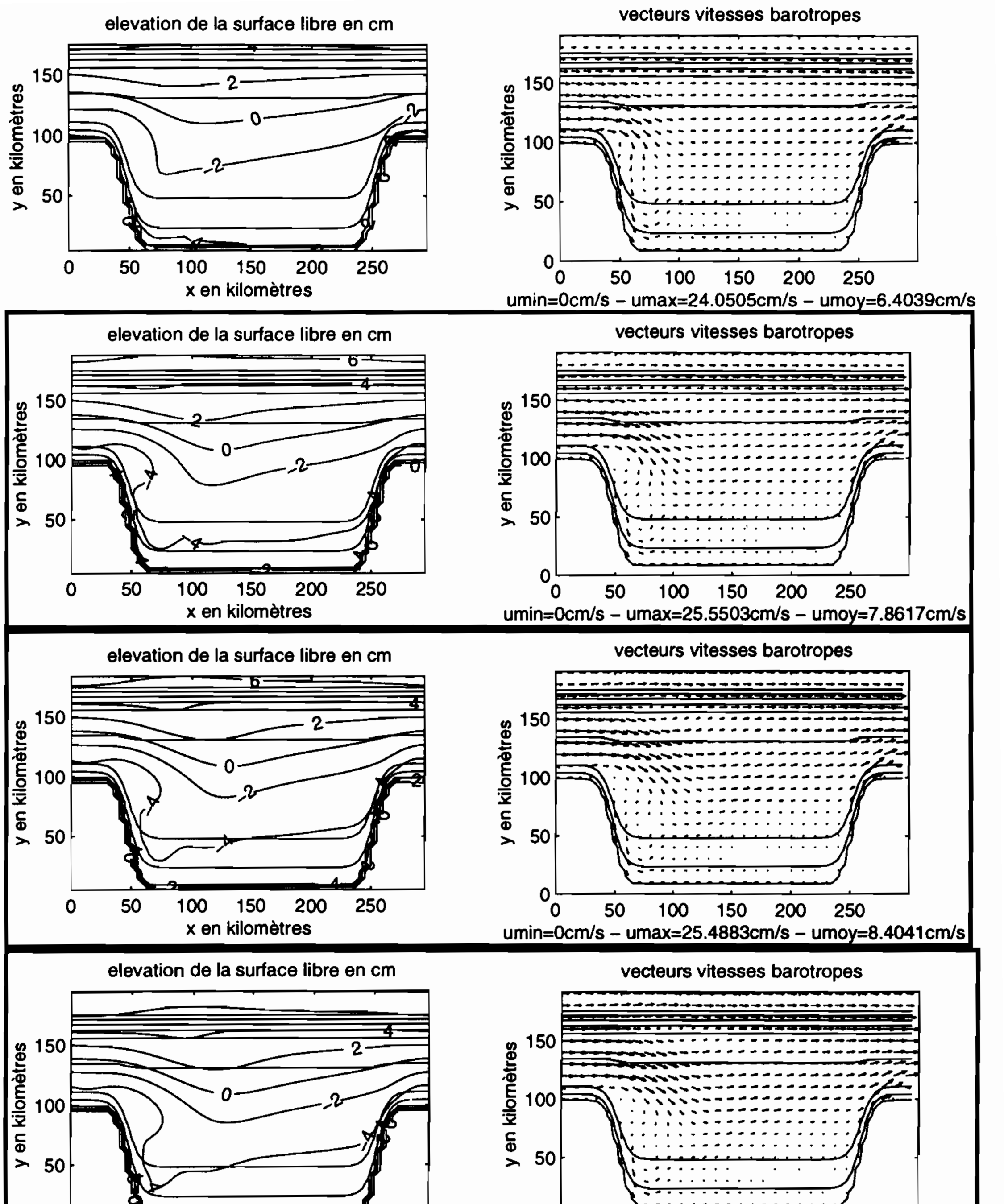

Figure 12: Champ de vitesses et élévation de la surface libre pour les jours 10, 20, 30 et 50. La solution varie peu après le jour 30. Un tourbillon s'est formé en aval du cap.

Les résultats obtenus lors d'une expérience de référence sont présentés sur la figure 12. Plusieurs phénomènes intéressants apparaissent :

- La solution devient quasi-stationnaire à partir du trentième jour.
- Dès le jour 10, un tourbillon cyclonique se forme au niveau du coin gauche du cap (x=50 km , y=100 km). C'est le phénomène de recirculation que nous voulons analyser. Les vitesses en son centre sont quasiment nulles.

- Les vitesses sont aussi très faibles sur la partie droite du plateau (x entre 150 km et 250 km et y < 75 km). Ceci semble dû à l'influence du cap de droite, cela peut perturber le réalisme de la solution. Il faudra donc lancer d'autres expériences en faisant varier la taille du bassin (surtout selon x) pour observer l'impact de cette longueur sur les processus de recirculation.
- Les vitesses sur le talus paraissent peu influencées par la topographie. Elles subissent tout de même une perturbation caractérisée par une courbe anticyclonique et un affaiblissement des vitesses au large du cap (x=100 km y=150 km). Ceci est associé à la circulation extérieure au cyclone. On peut supposer que ce phénomène est dû à la compression des colonnes d'eau lors du franchissement du talus.

Durant les trente premiers jours, le cyclone croît jusqu'à atteindre une extension maximale d'une cinquantaine de kilomètres.

A partir de ces simulations, une analyse diagnostique a été réalisée. Ensuite, des simulations ont été lancées afin d'évaluer la variabilité de la rétention en fonction des conditions de forçage par le vent. Pour cela, nous avons lancé une dizaine d'expériences en faisant varier la tension de vent de 0.2e-4 à 2.0e-4 m^2/s^2 et en faisant varier la taille du bassin. La variabilité de l'age des masses d'eaux en fonction de la tension du vent dans un domaine situé au large et dans le domaine côtier du modèle est présentée sur la figure 13.

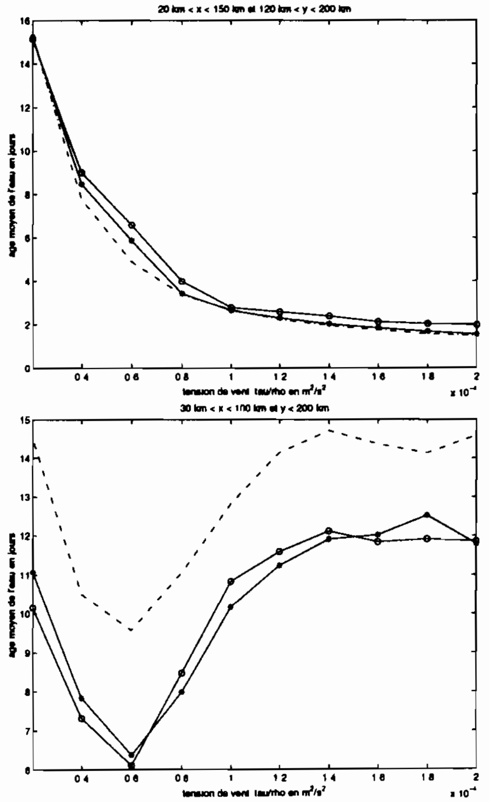

Figure 13: Age moyen des masses d'eaux 1) dans un domaine situé au large et 2) dans le domaine côtier près du cap. Les résultats obtenus en faisant varier la taille du bassin sont aussi présentés : bassin simple (-), bassin double (*) et bassin triple(o).

L'interprétation est la suivante :

- Pour $\frac{\tau}{\rho} < 0.6*10^{-4}$ m^2/s^2 , l'age moyen diminue suivant une loi inverse de la tension de vent: la recirculation associée au tourbillon n'est pas encore suffisamment importante. Le cyclone est plus petit que l'extension du cap vers le large, il n'a donc pas d'influence sur l'âge moyen de l'eau.
- Pour un vent plus fort, l'age moyen augmente. Le tourbillon est plus grand que le cap mais reste compris dans la zone de moyenne.
- L'age moyen atteint un maximum pour $\frac{\tau}{\rho} = 1.4*10^{-4}$ m^2/s^2 puis stagne ou diminue.

Ceci semble lié au choix de la zone de calcul de la moyenne. En effet, ce plafond est atteint quand l'extension du cyclone dépasse cette zone. Ensuite, quand le vent s'accroît la l'age moyen des masses d'eaux stagne ou diminue.

Un indice de rétention est ensuite obtenu en faisant la différence entre l'age des masses d'eaux dans la zone côtière et l'age au large (fig. 14). Cet indice montre que la rétention dans la zone côtière, sous le vent du cap, s'accroît avec vent jusqu'à des valeurs de tension de vent de l'ordre de 1.5 m2/s2., se stabilise ensuite pour des valeurs comprises entre 1.5 et 1.8 m2/s2 et décroît pour des valeurs supérieures à 1.8 m2/s2. La relation entre intensité de la rétention et intensité du vent est donc non-linéaire, la rétention atteint une valeur limite pour des tensions de vent de l'ordre de 1.8 m2/s2. Ce résultat suggère que des upwellings faibles à modérés ont, en terme de rétention, un effet bénéfique sur la survie larvaire en limitant les pertes par advection en direction du large

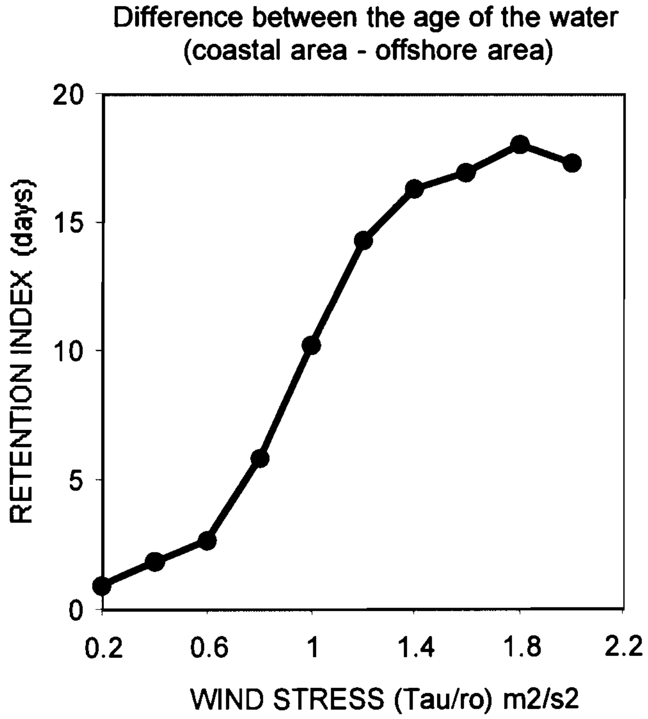

Figure 14: Variation de l'indice de rétention en fonction de la pseudo tension du vent.

Il est sans doute prématuré d'extrapoler ce résultat obtenu à l'aide d'un simple modèle barotrope aux situations réellement observées sur le terrain. On peut cependant remarquer que la relation non-linéaire entre la rétention et le vent est en accord avec le schéma de la "Fenêtre Environnementale Optimale" (Cury et Roy, 1989) et les relations existant entre des données de recrutement et de vent dans les écosystèmes d'upwelling. Ce résultat est encourageant pour la suite de ce travail, l'étape prochaine étant la prise en compte de la composante barocline dans le modèle, étape qui permettra de se rapprocher du réel.

2.4-THEME 4: VARIABILITE DE L'UPWELLING COTIER ET DYNAMIQUE DES PONTES DE DEUX ESPECES DE SARDINELLES (Rédaction: H. Demarcq)

Les résultats de la première phase de cette action de recherche ont été rassemblés dans un article publié en 1998 :

Demarcq H. 1998. Spatial and temporal dynamic of the upwelling off Senegal and Mauritania: local change and trend. *In* Durand M.H., Cury P., Mendelssohn R., Roy C., Bakun A. and D. Pauly. 1998. Global versus local changes in upwelling systems. Orstom, Paris, 149-165.

Ils ont également fait l'objet des publications et rapports suivants:

Anneville O., 1996. Quantification de l'upwelling côtier sénégalo-mauritanien à partir de l'information satellitale. Rapport de stage. Université de Perpignan .39 pp.

Demarcq H., Cury P. et C. Roy. 1997. La dynamique spatiale de l'upwelling sénégalo-mauritanien de 1984 à 1994 à l'aide de la télédétection. Géo Observateur, 7, p79-102.

Cette étude repose sur une utilisation avancée de l'information satellitale comme indicatrice de l'environnement, par l'intermédiaire d'indices spécifiques caractérisant l'évolution spatio-temporelle de l'upwelling côtier Ouest africain, de la Mauritanie au Sénégal. Deux exemples sont traités, au Sénégal et en Mauritanie, pour illustrer l'utilisation de ces indices sur les mécanismes intervenant dans la limitation du recrutement de trois espèces.

Un logiciel spécifique d'utilisation de ces données satellitales a été développé. Il permet la visualisation et la gestion simple de longues séries temporelles de "cartes" de paramètres, tels que la température de surface de la mer (TSM) pour générer des séries d'indices environnementaux directement utilisables pour de telles études.

2.4.1-Les données satellitales: traitements spécifiques et extraction d'indices.

Les paramètres identifiables et mesurables à partir des champs de TSM satellitaux (figure 15) sont essentiellement un minimum côtier local de TSM et un gradient maximal de TSM, situé plus au large. Les critères de détections sont invariants sur la série et la détection automatique.

Le minimum de TSM correspond au lieu de remontée maximal de l'eau issue de l'upwelling et dépend fortement de la bathymétrie locale. Sa détection fournit également un indice de présence/absence objectif de l'upwelling. Le gradient maximal délimite l'extension zonale de l'upwelling. Il dépend de l'intensité de l'upwelling et de la direction du vent et des courants.

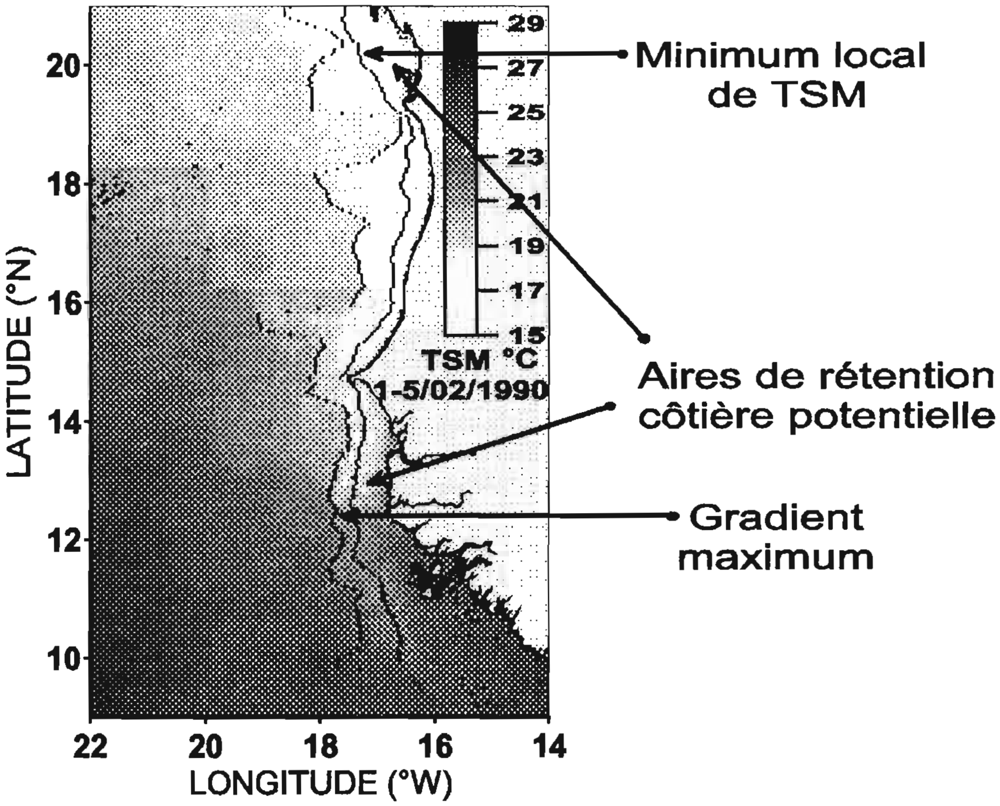

Figure 15. Calcul du gradient E-W de TSM et détermination automatique d'un minimum local de TSM et du gradient maximum vers le large

Un indice d'intensité de l'upwelling est proposé (Demarcq, 1998). Il est basé sur le rapport entre : 1)la différence entre le minimum de TSM (TSMmin) et une référence "chaude" (TSMmax), calculée à chaque latitude et 2) la différence entre la référence "chaude" et la valeur initiale de la température de l'eau upwellée (TSMup), soit 14°au Sénégal. L'indice peut s'exprimer suivant la formule :

Indice d'upwelling côtier = (TSMmax –TSMmin)/(TSMmax-TSMup)

Un indice original de rétention côtière est également calculé en chaque point de côte par l'intégrale des TSM entre TSMmin et la côte. Il est ainsi proportionnel à la distance de TSMmin à la côte ainsi qu'à la différence de maximale de TSM. Grâce à la régularité d'échantillonnage, les discontinuités spatio-temporelles sont bien mises en évidence, ce permet de réaliser un découpage spatial en entités écologiques homogènes et de manière objective. Cet indice intègre les effets spatiaux complexes liés à la topographie et permet de mettre en évidence d'importantes variations régionales de la configuration de l'upwelling (figure 16).

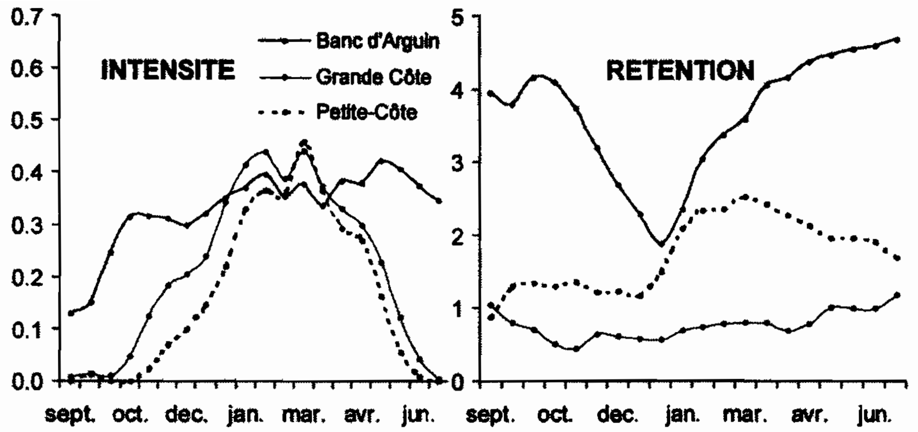

Figure 16. Dynamique Saisonnière moyenne des indices d'upwelling et de rétention côtière calculés à partir de la donnée satellitale de 1984 à 1996 sur deux zones de rétention forte (Banc d'Arguin et Petite Côte sénégalaise) et une zone de rétention faible (Grande Côte sénégalaise).

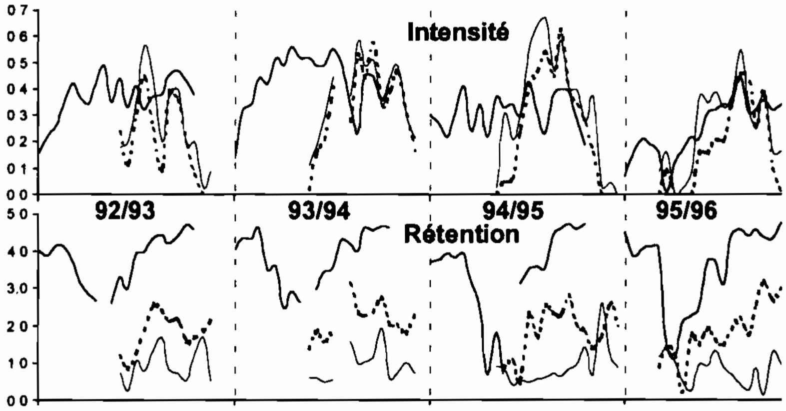

Figure 17. Exemple de variabilité interannuelle des indices d'intensité et de rétention côtière sur 4 années, de 1992 à 1996 pour les mêmes trois régions écologiques de la figure 2.

L'ensemble de la série (1984-96) montre nettement une succession de type années froides/ années chaudes. La variabilité interannuelle des deux indices (figure 17) est très forte, aussi bien en terme d'intensité que de décalage saisonniers, particulièrement dans les zones à topographie complexe (Banc d'Arguin et petite côte Sénégalaise).

Les données utilisées ainsi que les indices présentés sont utilisables à travers **CUSSI** (Coastal Upwelling Structures derived from Satellite images) un logiciel de gestion, de visualisation et d'extractions d'indices environnementaux à partir de séries chronologiques d'images de variables géophysiques, (telle que la TSM). Ce logiciel, écrit en Java et donc multi-plateforme permet de gérer des séries temporelles volumineuses, quelque soit le pas de temps.

2.4.2-Variabilité des pontes des sardinelles au Sénégal.

L'hypothèse d'un déterminisme entre la dynamique de l'upwelling et le déclenchement des pontes est exploré. La pêche de ces deux espèces représente environ 300 000 tonnes, soit 70 à 80% des captures nationales de la pêche artisanale.

Le milieu physique a été caractérisé à partir des trois indices environnementaux précédemment décrits. Les données biologiques utilisées pour les deux espèces sont le rapport gonado-somatique (RGS), représentatif de l'activité de ponte et le facteur de condition (FC).

Les fluctuations d'abondances sont importantes et très caractéristiques des fluctuations généralement rencontrées dans les zones d'upwelling côtier pour les espèces pélagiques côtières, ressources naturellement "instables". Les valeurs moyennes de RGS des années à upwelling faible et à upwelling fort montraient déjà une nette dépendance de l'intensité saisonnière moyenne de l'upwelling (Roy et al., 1989). L'évolution détaillée (pas de temps de 15 jours) des RGS et FC a été examinée pour les deux espèces de 1988 à 1990.

Les évolutions temporelles des deux variables (figure 18) montrent à la fois une forte corrélation significative entre les deux espèces (r=.68), ce qui n'est pas le cas pour l'évolution des RGS. De plus, les relations RGS/environnement montrent que les deux espèces ne répondent pas de la même manière à la dynamique saisonnière, *S. aurita* pouvant présenter des périodes de pontes avec un très faible saisonnalité alors que les épisodes de pontes de *S. maderensis* sont très dépendants de la saisonnalité de l'upwelling.

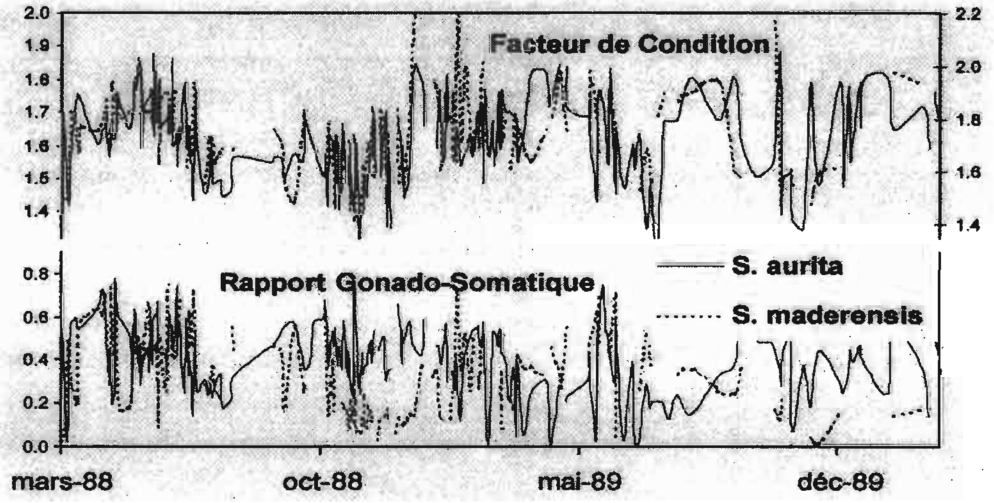

Figure 18. Evolution des RGS et FC de *S. aurita* et *S. maderensis* de mars 1988 à mars 1989

Les fortes fluctuations de l'indice suggèrent qu'il existe bien une dépendance avec les facteurs environnementaux à plusieurs niveaux, depuis la saison jusqu'à la quinzaine pour les deux espèces, mais avec une sensibilité à l'environnement très différente.

Le paramètre le plus adéquat pour mettre en évidence ces dépendances est l'indice d'upwelling et en deuxième lieu la rétention côtière associée dont la dynamique semble moins liée à celle des pontes dans cette région.

Bien que réagissant de manière plus sensible aux fluctuations de l'environnement, *Sardinella aurita* permet de tirer parti de fluctuations importantes, contrairement à d'autres espèces à priori concurrentes mais qui colonisent des régions d'upwelling soumises à de moindres fluctuations saisonnières.

2.4.3-La variabilité du recrutement du poulpe en Mauritanie.

A l'aide des mêmes indices environnementaux, les relations entre l'environnement et le recrutement du Poulpe (Octopus *vulgaris)* ont été étudiées en Mauritanie (région du Banc d'Arguin) sur la période 1985-1994. La Mauritanie possède une pêcherie de poulpe parmi les plus importantes (52 900 tonnes en 1976, 20 000 tonnes en 1996). La zone d'étude est celle du banc d'Arguin, de 19 à 21° de latitude Nord, zone très peu profonde, de ponte et de nourisserie pour de nombreuses espèces pélagiques comme les sardinelles.

Le stade pélagique planctonique du poulpe dure un a deux mois après l'éclosion avant le stade benthique. La faible espérance de vie, la croissance rapide, la forte mortalité juvénile et l'absence de recouvrement temporel entre deux générations annuelles expliquent le fort impact de l'environnement, ainsi que les très fortes fluctuations d'abondance observées.

Après corrélation croisée des séries, les relations recrutement/environnement sont principalement étudiées par le modèle GAM, pour explorer la forme des relations entre recrutement et environnement.

Les variations du recrutement font état d'une forte variabilité (Figure 5). Les indices de recrutement annuel varient de 22.3% (saison 1991/92) à 40 % (en 1988/89), soit un facteur de deux sur la période d'étude.

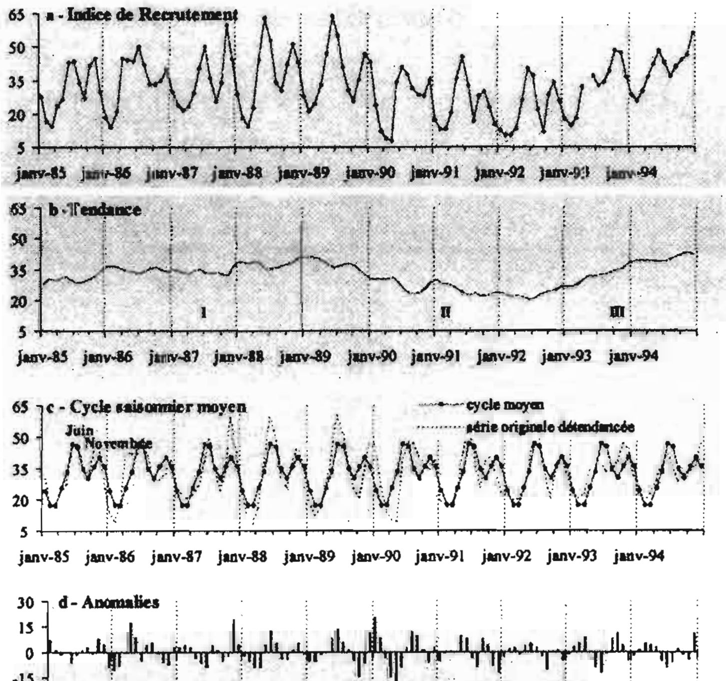

Figure 19 : Décomposition de l'indice de recrutement mensuel du poulpe en Mauritanie

La décomposition saisonnière de l'indice mensuel de recrutement (figure 19) montre clairement deux maximums. Les individus pêchés en novembre sont vraisemblablement issus de la génération de printemps et inversement, ce qui est compatible avec les vitesses de croissances estimées du poulpe. Les écarts résiduels (figure 19) correspondent le plus souvent à une anomalie de l'intensité des pics saisonniers, parfois à un décalage temporel (cas de l'année 1990).

L'upwelling présente souvent un net décalage saisonnier (trois ans sur 10). Comme pour les autres paramètres, la saisonnalité de la rétention est très forte, avec un minimum non synchrone avec celui de l'intensité de l'upwelling, du fait que le banc d'Arguin est saisonnièrement envahi par de l'eau froide du large, ce qui fait chuter l'indice de rétention.

Les corrélations croisées entre les séries montrent un décalage moyen significatif de -6 entre environnement et recrutement. Les pics de recrutement d'automne et d'été sont donc significativement reliés aux conditions de l'upwelling respectivement en mai-juin et décembre-janvier, périodes supposées d'abondance planctonique maximale des larves de poulpe.

Les indices environnementaux sont donc divisés en deux périodes, de printemps (mai-juin) et d'automne (novembre à janvier) en vue de tenir compte de ces constatations dans les analyses qui suivent.

L'approche non linéaire (ACE) entre l'indice de recrutement d'automne et chaque variable environnementale fait état de deux relations importantes :

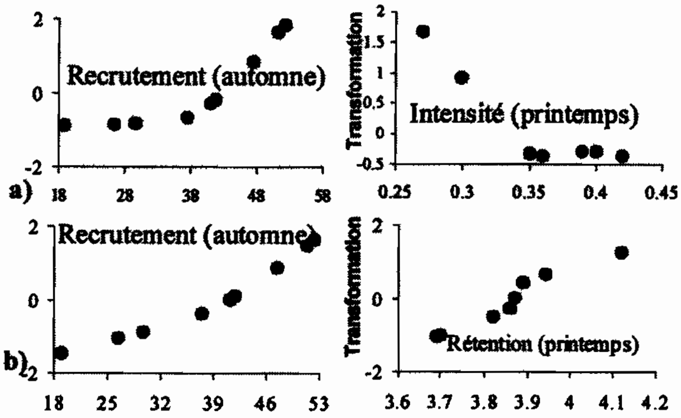

Figure 20. Transformations optimales fournies par l'algorithme ACE pour les relations :
T_1(recrutement) = T_2(Intensité) r^2 =0.50 a)
T_1(recrutement) = T_2(Rétention) r^2 =0.72 b)

Les transformations (figure 20) montrent que les indices d'intensité de l'upwelling et de rétention côtière de printemps sont corrélés respectivement négativement et positivement à l'indice de recrutement d'automne avec des contributions respectives au recrutement de 50% et de 72% en terme de variance expliquée, pour seulement 12% à la turbulence.

L'indice original de rétention côtière calculé à partir de la donnée satellitale apparaît comme un facteur clé dans la triade environnementale Intensité/Rétention/turbulence, confirmant des théories répandues (Sinclair, 1988). Il est majoritairement structurant dans la zone Nord mauritanienne qui se présente comme nettement inhibée par l'upwelling, suivant le concept de fenêtre environnementale optimale (Cury et Roy, 1989).

Une forte analogie peut être suggérée entre le poulpe et les poissons pélagiques côtiers qui sont tous deux contraints d'adapter leur stratégie reproductive à la dynamique saisonnière de l'upwelling côtier ainsi qu'aux opportunités topographiques locales qui constituent autant de chances de minimiser leurs pertes aux stades les plus sensibles de leur cycle de vie.

Le banc d'Arguin permet de passer outre cette sévère limitation, en optimisant la délicate balance nécessaire à la réussite de la survie en zone d'upwelling côtier. Les notions de concentration et de rétention, difficiles à quantifier peuvent avantageusement être abordées par l'imagerie satellitale qui fournit une part importante de réponse.

Les régions Nord mauritanienne et Sud sénégalaise sont deux très bons exemples de balance entre les trois termes enrichissement/concentration/rétention proposés par Bakun (1996). La rétention côtière apparaît comme le facteur prépondérant du déterminisme du recrutement dans la zone du banc d'Arguin (alors que l'indice d'upwelling et la turbulence ont un effet faible et négatif), à l'inverse de la région de la petite côte sénégalaise (zone d'upwelling modéré) où les facteurs enrichissement et rétention sont tous deux corrélés positivement à la plupart des mécanismes biologiques intervenant dans la réussite du recrutement.

On constate également importance des facteurs topographiques qui permettent à une côte soumise à un upwelling côtier de maximiser les processus de rétention et de tirer ainsi parti d'un upwelling côtier de manière optimale, en minimisant les effets néfastes d'une trop forte dispersion.

De telles études montrent l'intérêt de pouvoir disposer de séries environnementales sur les paramètres clé en région d'upwelling afin de pouvoir mettre en évidence les relations fonctionnelles entre l'environnement et les paramètres biologiques de la ressource à des échelles spatio-temporelles où l'action de l'environnement a un poids réellement important.

Les atouts de la donnée satellitale dans le cadre de telles études sont :

- son abondance dans certaines zones marines comme les régions d'upwellings côtiers (en raison de conditions atmosphériques favorables)
- la résolution spatio-temporelle atteinte (quelques jours et quelques kilomètres), souvent plus proche des échelles de transfert d'énergie entre le milieu physique et les premiers stades de la production biologique
- la régularité spatio-temporelle d'échantillonnage, permettant une excellente évaluation de la dynamique des processus spatio-temporels (migrations par exemple)

CONCLUSION

Ces quatre thèmes de recherche ont exploré la dynamique du recrutement des espèces pélagiques côtières à différentes échelles et suivant différentes approches. Les thèmes 1 et 2 ont privilégié des approches comparatives entre les principaux écosystèmes d'upwelling mondiaux et les espèces les plus abondantes. Les thèmes 3 et 4 ont abordé l'étude des processus environnementaux qui contrôlent le recrutement dans deux écosystèmes: l'upwelling du Sénégal et la partie sud du Benguela. Des outils de quantification (CUSSI et un modèle hydrodynamique 3D) et des bases de données ont été développés.

Le thème 1 a permis d'identifier les paramètres de l'environnement qui limitent l'abondance des populations dans ces écosystèmes. La taille des plateaux continentaux ainsi que la température ne sont pas apparus comme des éléments essentiels. L'intensité des upwellings et le brassage par le vent sont apparus comme étant les contraintes environnementales majeures. Une méthode régressive non paramétrique révèle qu'une combinaison de plusieurs facteurs environnementaux est nécessaire pour qu'une forte productivité soit réalisable. Les conditions optimales sont les suivantes : un fort indice d'upwelling (proche de 1.3 $m^3/s^1/m^1$), un vent modéré (proche de 5-6 m/s). L'écosystème péruvien, qui est au niveau mondial l'écosystème d'upwelling le plus productif en terme de ressource pélagique, s'avère être le seul écosystème dans lequel ces conditions optimales sont regroupées. Ces éléments permettent également de faire un diagnostic des changements consécutifs aux événements climatiques futurs.

Dans le thème 2, une approche comparative est utilisée pour étudier la dynamique temporelle des stratégies de reproduction des Clupéidés dans différentes zones d'upwelling, en relation avec des processus environnementaux supposés affecter la survie larvaire. Le schéma précédemment établi en Afrique de l'Ouest a pu être généralisé pour les sardines et les sardinelles à l'ensemble des écosystèmes d'upwelling. Ce modèle montre que, quelque soit l'écosystème considéré: 1) le calendrier de la reproduction s'établit indépendamment de la présence ou non d'un upwelling. 2) la ponte coïncide avec des vitesses de vent comprises dans une étroite fourchette de valeurs de 5.3 à 6.1 $m^3.s^{-1}.m^{-1}$. Cette gamme de vitesses de vent correspond aux conditions optimales pour le succès du recrutement définies par la Fenêtre Environnementale Optimale (Cury et Roy, 1989). Pour l'anchois, le déterminisme du calendrier de la ponte est différent de celui des deux autres espèces. Il ne semble pas exister de relation entre les fluctuations saisonnières de l'environnement et l'activité de reproduction.

Au cours de la première phase du thème 3, des structures spatiales permettant d'assurer la rétention des larves dans la zone côtière d'un upwelling ont été identifiées. Elles sont le résultat de l'interaction entre le processus d'upwelling et la topographie. En présence de telles structures, il existe un couplage positif entre les processus d'upwelling et de rétention. En prenant comme exemple l'écosystème d'upwelling du Sénégal, une quantification de la rétention à partir d'images satellites et de données issues des stations côtières a été réalisée. L'intensité de la rétention est maximale à la fin du printemps et minimale en été et au début de l'automne. Le pic saisonnier de la ponte se produit en mai-juin quand l'intensité de la rétention est maximale. Ce couplage entre le calendrier de la ponte des sardinelles et l'intensité de la rétention souligne l'importance de ces structures pour le succès de la ponte et le recrutement. Dans la seconde phase, un modèle hydrodynamique 3D a été mis en place sur un site de la partie sud du Benguela. Ce site est la principale zone de nursery des sardines et des anchois de la région. Des simulations ont été réalisées avec une version barotrope du modèle en faisant varier les conditions de forçage par le vent. Afin de quantifier les processus de rétention, un traceur barotrope a été développé, il permet une mesure quantitative des phénomènes de recirculation. Cet indice montre que la rétention dans la zone côtière s'accroît avec le vent jusqu'à des valeurs de pseudo tension de vent de l'ordre de 1.5 m^2/s^2, se stabilise ensuite pour des valeurs comprises entre 1.5 et 1.8 m^2/s^2 et décroît pour des valeurs supérieures à 1.8 m^2/s^2. La relation entre intensité de la rétention et intensité du vent est donc non-linéaire, la rétention atteint une valeur limite pour des tensions de vent de l'ordre de 1.8 m^2/s^2. Ce résultat suggère que des upwellings faibles à modérés ont, en terme de rétention, un effet bénéfique sur la survie larvaire en limitant les pertes par advection en direction du large. Cette relation entre la rétention et le vent est en accord avec le schéma de la "Fenêtre Environnementale Optimale" et les relations existant entre des données de recrutement et de vent dans les écosystèmes d'upwelling. Le développement du modèle se poursuit et une version barocline (prise en compte de la stratification verticale) sera mise en place début 1999.

Une base de données satellites et des outils de quantification de certains processus spatiaux, à partir d'images satellites, ont été développés pour le thème 4. Des séries temporelles de l'intensité de l'upwelling et de la rétention le long des côtes du Sénégal et de la Mauritanie ont été construites. Ces indices ont permis d'explorer les relations entre la dynamique de la ponte des sardinelles et celle de l'upwelling. Dans la zone du Banc d'Arguin, la rétention côtière apparaît comme un des facteurs prépondérants du déterminisme du recrutement de la population de poulpe exploitée en Mauritanie.

Ces quatre projets ont exploré la dynamique de recrutement dans les zones d'upwelling. Les thèmes 1 et 2 se sont appuyés sur des approches comparatives entre les principaux écosystèmes d'upwelling. Les principaux facteurs limitant la production des espèces pélagiques côtières dans les upwellings ont été identifiés dans le thème 1. Dans le thème 2, il a été possible de généraliser un modèle mettant en relation le calendrier de la ponte des sardines avec l'environnement. Ces résultats mettent en évidence l'importance du vent comme facteur limitant du recrutement, ils viennent conforter le schéma de la "fenêtre environnementale optimale" (Cury et Roy, 1989) schéma proposé pour relier la variabilité du recrutement avec l'intensité des upwelling. Les thèmes 3 et 4 ont mis l'accent sur l'étude des processus spatiaux qui interviennent dans le déterminisme des stratégies de reproduction et au niveau de la variabilité du recrutement. La modélisation des processus hydrodynamiques a démarré et les premiers résultats obtenus montrent l'intérêt de telles approches. La prochaine étape sera le couplage de ce modèle hydrodynamique avec un modèle individu-centré pour simuler le devenir des larves en fonction de l'advection et quantifier l'impact des processus spatiaux sur le recrutement.

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PNDR

Rapport de synthèse
Octobre 1998

Thème général :
La dynamique du recrutement dans les zones côtières d'upwelling.

ANNEXES

Projets réalisés à l'ORSTOM avec le soutien de l'action
incitative PNDR-GLOBEC.

Rapport rédigé par C. Roy
avec la collaboration de P. Cury et H. Demarcq

PRINCIPALES PUBLICATIONS:

Roy C., 1998. Upwelling-induced retention area: a mechanism to link upwelling and retention processes. *In:* Benguela Dynamics. Pillar, S. C., Moloney, C., Payne, A. I. L. and F. A. Shillington (Eds). South African Journal of Marine Science 19. HZ 88C33

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

*C. ROY**

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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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).

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 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.

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).

Upwelling is fully developed from January through May. Offshore Ekman transport reaches its maximum (1.2 $m^3 \cdot s^{-1} \cdot m^{-1}$) 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, 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 cir-

> culation, 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 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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FIGURE LEGENDS

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

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)

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

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

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

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

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

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ENVIRONMENTAL CONSTRAINTS AND PELAGIC FISHERIES IN UPWELLING AREAS: THE PERUVIAN PUZZLE

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Pelagic fish catch statistics are used as surrogates to evaluate the potential fish productivity in upwelling ecosystems. A comparison between 10 upwelling areas of the world shows that the Peruvian ecosystem is three- to ten-fold more productive than the others. The size of the ecosystem, estimated by the surface of the continental shelf, does not by itself explain the observed disparity. Upwelling systems are characterized by different combinations of two different environmental variables: the upwelling intensity and the mixing generated by the wind. Using generalized additive models, an exploratory analysis is performed in order to identify the environmental conditions that maximize the total pelagic fish catch productivity (mainly sardine, sardinella and anchovy). The analyses consider fish catch as the dependent variable and the two environmental factors as the independent variables. Optimal environmental conditions appear to be a combination of: a high upwelling index (~ 1.2 $m^3 \cdot s^{-1} \cdot m^{-1}$) and moderate wind-mixing (~250 $m^3 s^{-3}$). The Peruvian ecosystem is the only upwelling system that has these characteristics, making it unique and singularly productive. These empirical results stress the importance of considering a combination of environmental factors when explaining pelagic fish productivity in upwelling systems.

Approximately 100 million tons of fish and shellfish have been extracted annually from the sea and inland waters since 1989 (F A.O. 1997). The total marine fish catch represents 75% of that amount and approximately one-third is pelagic fish. The most important pelagic fisheries are located in the upwelling areas of eastern boundary currents, i.e. the Canary, the Benguela, the California and the Humboldt Current systems. Two fisheries contribute most to the world pelagic fish catch: the Peruvian and the Chilean fisheries. Annually, the landings off Peru and Chile reach millions of tons, whereas such countries as Morocco, California, South Africa and Ivory Coast-Ghana can contribute several hundred thousand tons. The size of an ecosystem is an important factor when considering productivity, but this may not be the only factor affecting pelagic fish productivity. It may be believed that large upwelling systems are able to sustain large fisheries. However, will a medium-size upwelling system produce as much as a large one? Pelagic fish stocks are well known for their instability, and numerous authors have examined the causes of recruitment and catch fluctuations (Sharp and Csirke 1983, Pauly and Tsukayama 1987, Pauly *et al.* 1989, Cury and Roy 1991, Kawasaki 1992, Lluch-Belda *et al.* 1992, Cury *et al.* 1995, Bakun 1996). Environmental factors such as wind-mixing, offshore transport and upwelling intensity play an important role in recruitment success or failure. Do environmental factors involved in fish population fluctuations also cause the observed difference in pelagic fish productivity among upwelling systems?

The comparative approach is a powerful tool in ecological science, because it makes it possible to establish the generality of phenomena (Bakun 1985, 1996) and, as mentioned by Maynard Smith and Holliday (1979 p. 7) "we must learn to treat comparative data with the same respect as we would treat experimental results". However, whereas the comparative approach is a method currently adopted in evolutionary biology (Harvey and Pagel 1991), the method is seldom used in ecology. A comparative method can lead to an empirical understanding of the disparity in fish productivity among upwelling systems by identifying the responsible environmental factor(s) that contribute to low or high productivity. In this paper, pelagic fish productivity in 10 upwelling systems is compared and the relationships with the environment are examined using variables such as the size of the continental shelf, the upwelling intensity and wind-mixing.

IS BIGGER BETTER FOR ECOSYSTEM SIZE?

Biological productivity of an ecosystem can be estimated in many ways, through planktonic production,

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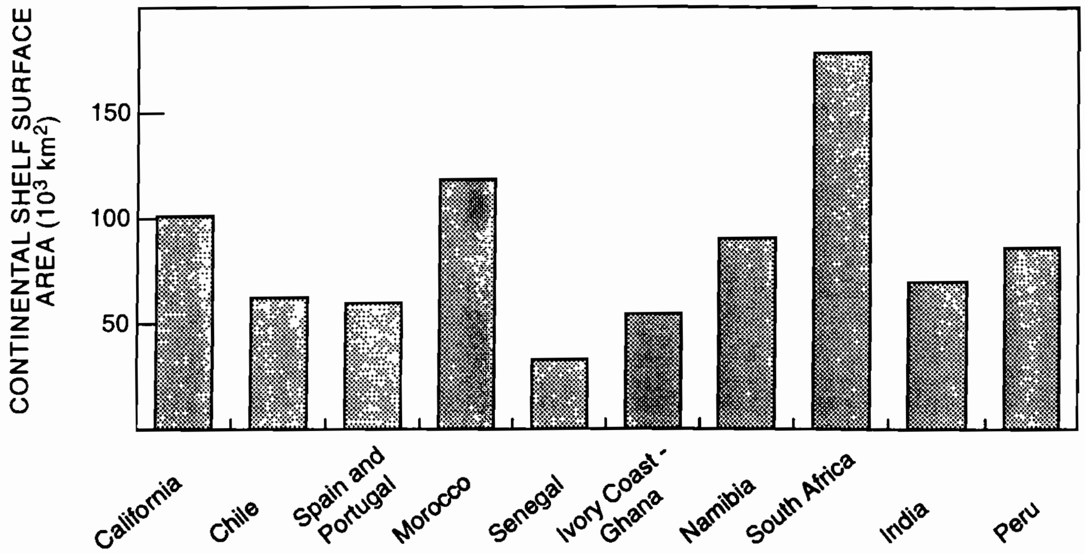

Fig. 1: Size of the continental shelf for each of the 10 upwelling areas

living matter turnover, energy transfer, fish biomass, etc. However, long time-series of such indices are not available in most upwelling systems and extended comparisons are difficult to perform. Fish catch statistics are the only data that have been collected in most upwelling systems over long periods (most of them from the beginning of the fisheries). These data are biased for a multiple of reasons: changes in the availability of fish, in the fishing effort, in the target species, in the markets, etc. However, when used as a surrogate, fishery data can provide a rough estimate of biological productivity. Therefore, these values can be considered adequate, because they give an order of magnitude estimate of "what it is possible to fish" in an ecosystem, ranging from several thousand tons to millions of tons.

A maximum pelagic fish catch "productivity index" is used here, by considering the maximum catch value observed during the whole time period of a fishery. This value is used to track the carrying capacity of pelagic fish in the ecosystem. This productivity index is calculated for the main pelagic species (i.e. sardine, sardinella and anchovy). Important catch-level differences are observed between pelagic fisheries (Table I). The Peruvian ecosystem clearly distinguishes itself, with a maximum catch of

Table I: Maximum pelagic fish catch, surface area of the shelf and maximum pelagic fish catch per unit of surface area for 10 upwelling areas and for three main pelagic species (sardine, sardinella and anchovy).

Upwelling areas	Latitude	Longitude	Period considered	Maximum pelagic fish catch (10^3 tons)	Surface area of the shelf (10^3 km^2)	Maximum productivity per unit of surface area (tons·km^2)
California	22–38°N	–	1924–1991	609	101	6.0
Chile	18°N–43°S	–	1966–1993	3 708	62	59.3
Spain and Portugal	32–44°N	5–9°E	1937–1989	368	59	6.2
Morocco	21–36°N	2–0°E	1950–1991	362	118	3.1
Senegal	12–16°N	–	1964–1991	194	32	5.9
Ivory Coast-Ghana	2–8°N	0–8°W	1966–1993	270	54	5.0
Namibia	16–28°S	–	1966–1992	1 561	90	17.3
South Africa	28–36°S	18–26°E	1950–1992	623	178	3.5
India	8–15°N	–	1948–1988	448	70	6.4
Peru	5–18°N	–	1958–1993	12 286	86	142.0

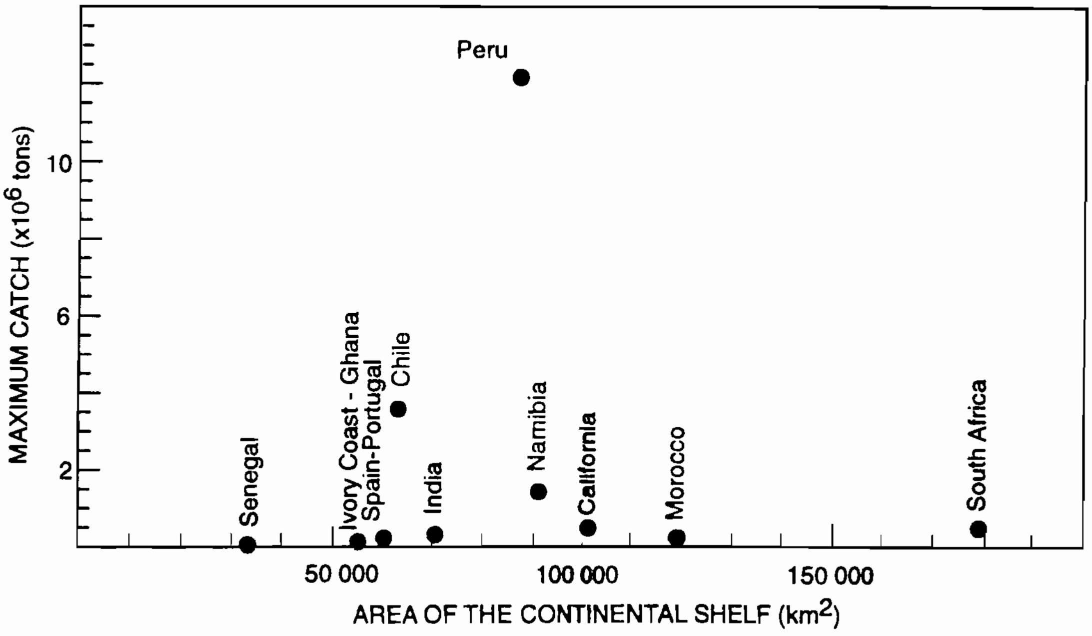

Fig. 2: Maximum pelagic fish catch productivity indices (tons) v. the area of the continental shelf (km^2) for the 10 upwelling areas

12 millions tons, and only two other fisheries have been able to catch more than one million tons within a year: Chile and Namibia. The other areas have never fished more than 623 thousand tons.

In order to quantify the size of the ecosystems, the surface area of the continental shelf was estimated (Fig. 1, Table I). The sizes of the continental shelves vary from 32 887 km^2 for Senegal to 178 315 km^2 for South Africa. South Africa, Morocco and California have large continental shelves (>100 000 km^2) whereas Spain-Portugal, Senegal and Ivory Coast-Ghana have medium-sized to small ones (<60 000 km^2).

The Peruvian and Chilean productivity indices are the largest among the 10 estimated, whereas the continental shelf surface areas of these countries are medium in size (Figs 1, 2). Conversely, the South African and the Moroccan ecosystems have a wide continental shelf and a poor fish productivity per unit shelf area compared with the others (Figs 1, 2). Even when the productivity index is divided by the size of the shelf, there is no clear relationship between the productivity per unit area of the ecosystems and their size (Fig. 3). Therefore, ecosystems with a large continental shelf are not necessarily among the most productive. Other environmental variables undoubtedly play a role in the intrinsic pelagic fish production of the upwelling ecosystems.

ENVIRONMENTAL CONSTRAINTS AND FISH PRODUCTIVITY

Environmental factors cause fish population fluctuations, because they are recognized to play a major role in recruitment success (Parrish and MacCall 1978, Bakun and Parrish 1982, Cury and Roy 1989, Lluch-Belda *et al.* 1989, Cushing 1990, 1995, Lluch-Belda *et al.* 1992). Two environmental variables were selected for the analysis: a Coastal Upwelling Index (*CUI*, $m^3 \cdot s^{-1} \cdot m^{-1}$), which is the offshore component of the wind-induced Ekman transport (Bakun 1973), and a wind-mixing index (V^3, $m^3 \cdot s^{-3}$) calculated as the cube of the wind speed. A CD-Rom-based version of the COADS data (Comprehensive Ocean Atmosphere Data Set), collected by merchant ships all around the world oceans (Woodruff *et al.* 1987) was used to build monthly time-series of wind data (Mendelssohn and Roy 1996) and to calculate the *CUI* and V^3 indices. Mean values of the two indices from 1946 to 1990 were then calculated for these indices for the different upwelling areas (Table II).

Upwelling indices vary from 0.31 $m^3 \cdot s^{-1} \cdot m^{-1}$ for South Africa to 1.28 $m^3 \cdot s^{-1} \cdot m^{-1}$ for Namibia. Three areas exhibit strong upwelling indices: Namibia, Peru and Ivory Coast-Ghana. The wind-mixing index varies

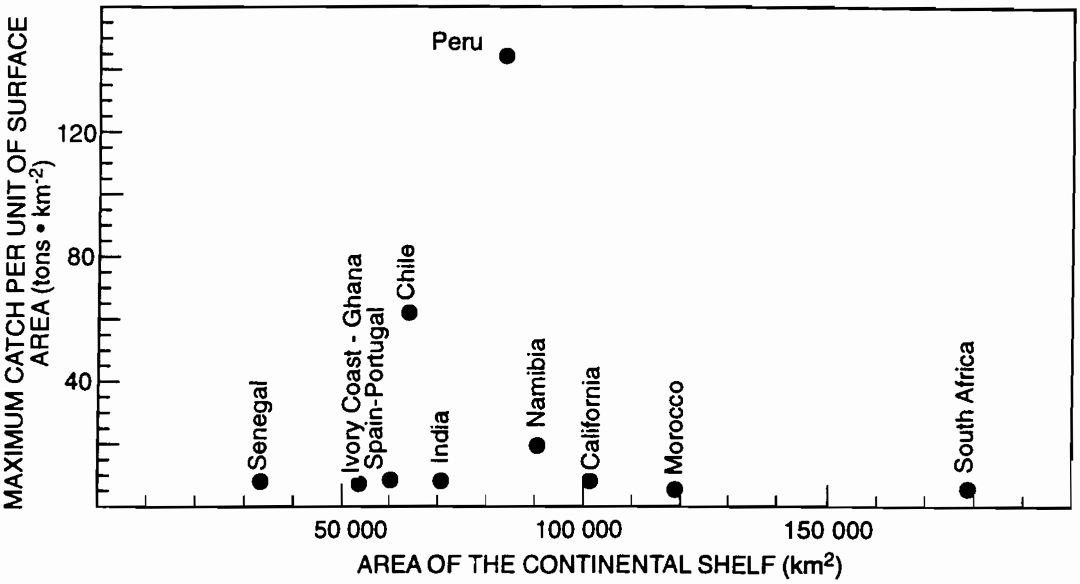

Fig. 3: Maximum pelagic fish catch per unit area (tons·km^2) for the 10 upwelling areas

from 103 m^3·s^{-3} for Ivory Coast-Ghana to 770 m^3·s^{-3} for South Africa. Classically, a high upwelling intensity is associated with a high wind-mixing intensity (in Namibia and Chile), but in low-latitude ecosystems, moderate wind-forcing can generate rather intense upwelling because of the latitude-dependency of the *CUI*. This is the case off Peru and Ivory Coast-Ghana, which are characterized by a moderate wind-mixing intensity but a fairly strong upwelling index. In the same way, moderate upwelling indices can be associated with strong wind-mixing in mid-latitude ecosystems such as California, Spain-Portugal and South Africa.

Table II: Environmental characteristics (coastal upwelling and wind-mixing indices) calculated from COADS (mean from the period 1946–1990) of the 10 upwelling areas (latitude and longitude as in Table I)

Upwelling areas	Coastal upwelling index (m^3·s^{-1}·m^{-1})	Wind-mixing index (m^3·s^{-3})
California	0.36	654
Chile	0.93	345
Spain and Portugal	0.36	627
Morocco	0.66	305
Senegal	0.59	150
Ivory Coast-Ghana	1.04	103
Namibia	1.28	517
South Africa	0.31	770
India	0.44	239
Peru	1.20	224

The relationship between the productivity indices and the two environmental factors is explored using non-parametric regression models. Iterative algorithms that extend linear multiple regression analysis to generalized additive models provide a method to explore the relationship between the response and the predictor variables when the form of these relationships is unknown. The non-linearity of the relationships as well as the multiplicity of factors can be considered. The Alternating Conditional Expectation (ACE) and the Generalized Additive Interactive Modeling (GAIM) statistical methods estimate optimal transformations for multiple regressions (Hastie and Tibshirani 1990). The usual linear multiple regression model for predicting a response variable Y from p predictor variables X_i, $i = 1, \ldots, p$ and for n observations, $j = 1, \ldots, n$, is given by:

$$Y(j) = \Sigma\, b_i\, X_i(j) + e(j) \quad , \tag{1}$$

where b_is are coefficients estimated by the model and $e(j)$s are error terms and are independent.

In the non-parametric model, the response variable Y and the predictor variables $X_1 \ldots\ldots X_p$ are replaced by functions $T_1(Y)$ and $T_2(X_1) \ldots\ldots T_{p\text{-}1}(X_p)$:

$$T_1(Y(j)) = \Sigma\, b_i\, T_{i+1}(X_i(j)) + w(j) \quad , \tag{2}$$

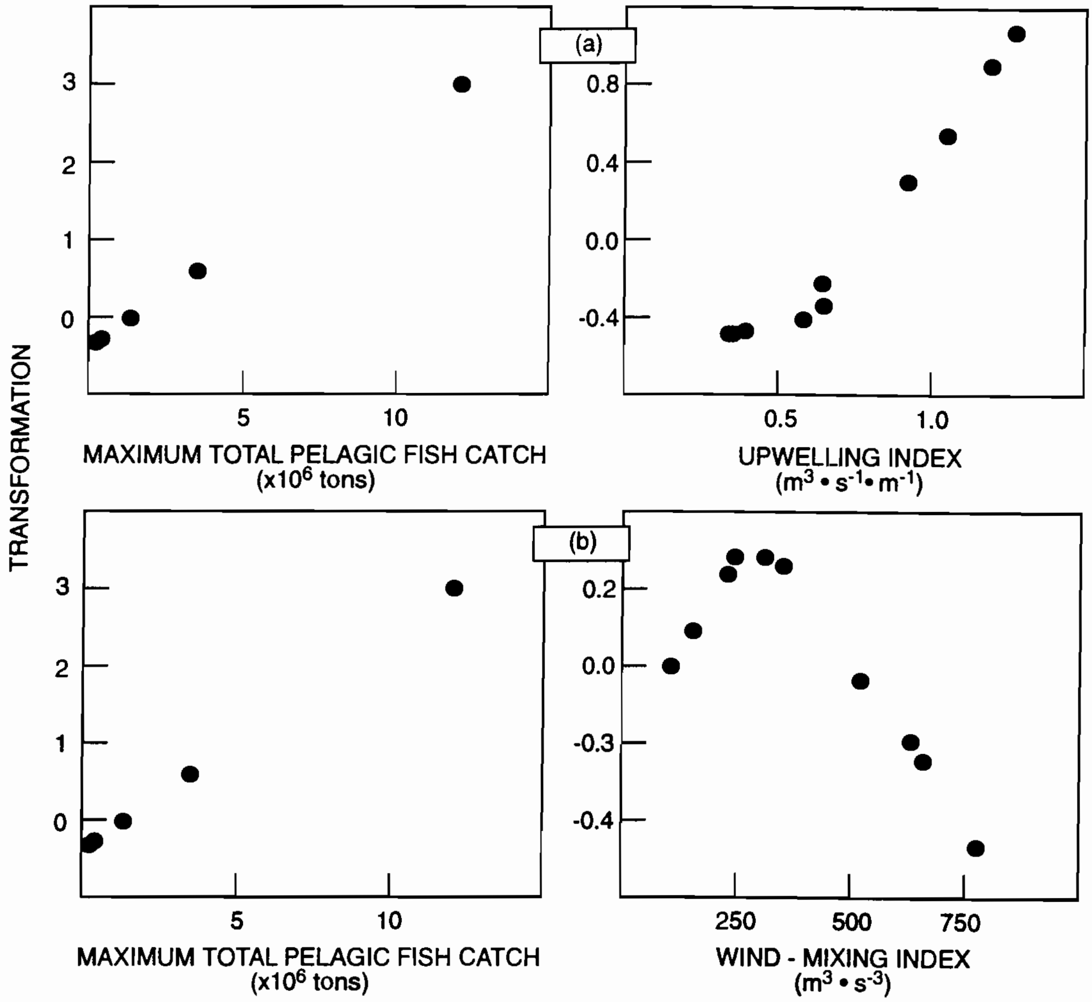

Fig. 4: Optimal empirical transformations from the ACE algorithm using (a) the maximum total pelagic fish catch (productivity index) as the dependent variable and the upwelling index as the independent variable ($r^2 = 0.35$), (b) the maximum pelagic fish catch productivity index as the dependent variable and the wind-mixing index as the independent variable ($r^2 = 0.12$)

where $w(j)$ is an error term and $T_1(Y)$ and $T_i(X)$ are unknown and estimated by minimizing:

$$E((T_1(Y) - \Sigma\, b_i\, T_{i+1}\, (X_i))^2) \,/\, \mathrm{var}\, (T_1(Y)) \quad . \quad (3)$$

Several approaches exist to estimate Equation 3. ACE includes the b_i in the function $T_i()$, whereas GAIM estimates b_i in order to perform analysis of deviance tests on the parameters. GAIM produces an analysis of deviance as well as coordinates for plotting the function estimates and their standard errors. The algorithms converge to optimal solutions for a given criterion because they have their own smoothers and convergence criteria (see Cury *et al.* 1995 for a detailed application to fishery data).

A regression analysis is done using the productivity index as the response variable and the environmental factors as the predictor variables. The shape of the transformation is found by plotting the transformed values of a variable versus the original values. Results given by the ACE algorithm are presented below.

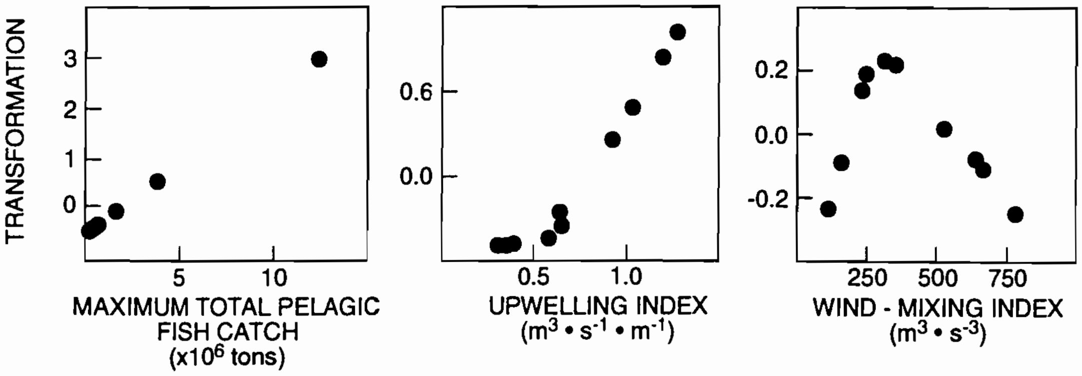

Fig. 5: Optimal empirical transformations from the ACE algorithm using the maximum total pelagic fish catch (productivity index) as the dependent variable and the upwelling index and the wind-mixing index as the independent variable ($r^2 = 0.43$). Data are used from all 10 ecosystems

The relationships between the productivity index and each individual environmental variable are first explored. Optimal transformations (*T*1, *T*2) for the multiple regression are calculated:

$$T1\ (\text{Productivity index}) = T2\ (CUI) \qquad r^2 = 0.35 \quad (4)$$

$$T1\ (\text{Productivity index}) = T2\ (V^3) \qquad r^2 = 0.12\ . \quad (5)$$

Although the methodologies produce non-linear transformations for both dependent and independent variables, in order to produce a readily-interpretable result, the transformation was forced for the productivity index (*T*1) to be linear. The transformation produced for the upwelling index is linear and positive (Fig. 4a). The wind-mixing index is transformed to a nearly dome-shaped curve with a breaking point around 250 $m^3 \cdot s^{-3}$ (Fig. 4b).

Multivariate analyses are carried out by considering simultaneously the two environmental variables in the model. The optimal transformations (*T*1, *T*2, *T*3) for the multiple regression are calculated using the productivity index as the response variable and wind-mixing and the upwelling index as the predictors in Model 6 (Fig. 5).

$$T1(\text{Productivity index}) = T2\ (CUI) + T3\ (V^3) \qquad r^2 = 0.43\ . \quad (6)$$

The transformation of the response variable is again forced to be linear (Fig. 5). The transformations for wind-mixing and the upwelling index are similar to those given by the univariate analysis: the upwelling transformation is linear and positive and the transformation for wind-mixing is dome-shaped with a breaking point around 250 $m^3 \cdot s^{-3}$ (Fig. 5). The scale of the transformed value gives an indication of the relative contributions of the environmental variables to the variance. It indicates a greater contribution by upwelling intensity than by wind-mixing. Both univariate and multivariate analyses suggest similar patterns that relate fish catch productivity to environmental variables.

This comparative and exploratory analysis of the relationship between estimates of fish productivity and environmental characteristics in upwelling systems reveals that a combination of several factors is necessary to promote a high fish productivity (Faure and Cury 1998). These "optimal environmental conditions" that appear to maximize the pelagic fish catches in upwelling areas are:

(i) a high upwelling intensity (the maximum observed is 1.28 $m^3 \cdot s^{-1} \cdot s^{-1}$);
(ii) a moderate wind-mixing (around 250 $m^3 \cdot m^{-3}$).

DISCUSSION

The Peruvian puzzle

The results of the statistical analysis must be considered with caution, because important limitations arise from using a comparative approach based on only 10 data points. Consequently, the statistical validity of the results is questionable as a result of few degrees of freedom, particularly for the multivariate analyses. This is unavoidable because:

(i) the number of ecosystems with documented pelagic fisheries and for which environmental

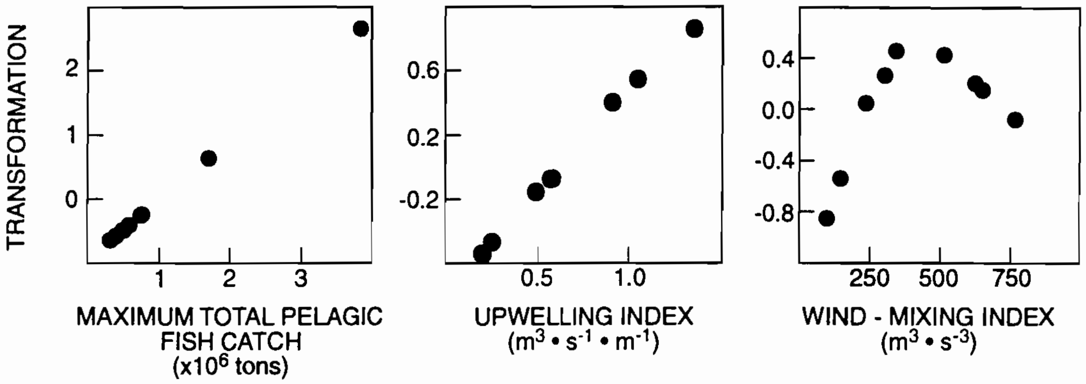

Fig. 6: Optimal empirical transformations from the ACE algorithm using the maximum pelagic fish catch (productivity index) as the dependent variable and the upwelling index and the wind-mixing index as the independent variable ($r^2 = 0.53$). Data from the Peruvian ecosystem are excluded

data exist is limited;

(ii) the number of environmental factors that are hypothesized to play a role in productivity is large compared with the number of ecosystems considered.

Nevertheless, the relationships between the fish productivity and the environmental variables appear to be in agreement with independent ecological knowledge on ecosystem functioning. High upwelling intensity as a source of food availability (Wroblewski and Richman 1987, Cushing 1990) and small-scale turbulence that increases the encounter rate between food particles and larvae (Rothschild and Osborn 1988, Mackenzie and Leggett 1991) are thought to be beneficial to larval survival. The positive relationship between the upwelling intensity and the pelagic fish catch could be related to these combined effects. In contrast, intense wind-driven turbulent mixing that disperses patches of larval food appears to be detrimental (Lasker 1975, Peterman and Bradford 1987, Cury and Roy 1989). Bakun (1996) identified a "fundamental triad" of three major processes that combine to yield favourable environmental conditions for successful fish reproduction: an enrichment process (e.g. upwelling, mixing), a concentration process (e.g. water column stability, convergence) and processes favouring retention within the appropriate habitat. To some degree, the environmental factors that have been selected here could be considered as proxy variables that account for some of the processes involved in the "triad". For example, the upwelling intensity determines the global enrichment of the ecosystem and wind-mixing is involved in the processes that concentrate food for larvae.

From this analysis, it appears that the size of the ecosystem does not strongly influence the productivity index. In upwelling areas, the maximum pelagic fish productivity depends on a combination of environmental factors with values within specific ranges. The values should be maximum for the upwelling index (1.28 $m^3 \cdot s^{-1} \cdot m^{-1}$) and moderate for the wind-mixing index (250 $m^3 \cdot s^{-3}$). These optimal values are very close to those observed off Peru (1.2 $m^3 \cdot s^{-1} \cdot m^{-1}$ and 224 $m^3 \cdot s^{-3}$ respectively), which is the most productive upwelling ecosystem and the only one that combines these optimal environmental conditions. Can it be that these "optimal conditions" are responsible for the very high productivity of the Peruvian ecosystem?

The Peruvian data were included in the analysis described above. As a consequence, it could be tautological to explain the high productivity in that area using data from it. In other words, it must be questioned whether the results are essentially derived from the Peruvian values or not. To avoid circularity in the study, a similar analysis was performed without the Peruvian data, giving almost identical results (Fig. 6); the transformation of the upwelling index is linear and positive and the transformation of the wind-mixing index is dome-shaped, but with a breaking point around 400 $m^3 \cdot s^{-3}$ ($r^2 = 0.53$). Removing the Peruvian data point had little effect on the shape of the transformation, but a difference is observed when considering the absolute value of the breaking point of the wind-mixing transformation. This result supports the previous consideration: the high productivity of the Peruvian upwelling ecosystem results from a unique combination of intense upwelling and moderate wind-mixing. In Chile and Namibia, the upwelling index is favourable, but is associated with a negative effect of too strong wind-mixing. The same high upwelling index is found off Ivory Coast-Ghana, but it is associated with a low mixing index. Off South Africa, Spain and California, the wind-mixing index is high and associated with a low upwelling intensity, so limiting productivity. In each upwelling area, except Peru, at least one environmental condition differs from that of the "optimal conditions" and consequently tends to limit productivity. The Peruvian ecosystem appears to be the only one that combines the optimal environmental conditions.

CONCLUSION

Optimal environmental conditions that maximize the pelagic fish catch in upwelling ecosystems have been identified using a comparative approach with fishery and environmental data from 10 upwelling areas in the Atlantic, Indian and Pacific oceans. This comparative analysis provides a framework for considering the relative impact of several environmental factors on fish productivity. It emphasized the relative importance of limiting factors such as wind-mixing, upwelling intensity or the size of the ecosystem, but many others can play a major role in the recruitment process (see Hutchings *et al.* 1998 for a review). The present results should promote new insights of how to relate environmental variables to fish productivity in a multivariate context. Palaeoecological studies reveal that pelagic fish populations have experienced large natural fluctuations that were clearly unrelated to fishing pressure, and that past abundance was sometimes much higher than that during the last century in California or in Peru (Soutar and Isaacs 1974, De Vries and Pearcy 1982, Baumgartner *et al.* 1992). For California, factors are identified that limit fish productivity (low coastal upwelling intensity and high wind-mixing), but this was impossible for Peru. This stresses the limit of the approach presented here, because it is clear that the Peruvian ecosystem might be able to produce even more under other, but still unknown, environmental conditions. Upwelling regions of the world have short foodwebs, with only one or two steps between phytoplankton, and are a major source of food for man, whereas there are up to six substantial trophic levels in ecosystems such as coral reefs (Birkeland 1997). Productivity is not limiting in upwelling systems, but the efficiency with which the foodweb is coupled is important. Many upwelling systems appear to have large, organic-rich deposits, which is suggestive of inefficient use of primary productivity. A fundamental factor to consider appears to be how to enhance the efficiency of the foodwebs.

To predict the effect of climate change on living marine resources is a challenge for the scientific community. At present, there is no reliable computer-generated, climate-impact scenario for the next several decades, but generalizations derived from case-by-case assessments of past and present experiences can be used (Glantz 1992). Such assessments can provide first approximations of how fisheries might respond to environmental changes. The comparative analysis constitutes a good base of information to begin an assessment of the possible impacts of environmental changes on fish productivity (Faure and Cury 1998). Some scenarios for fish productivity under climatic changes derived from previous study can therefore be used to forecast by analogy (Glantz 1992). How and how much will the productivity evolve if one or several environmental variables change in upwelling areas? The present comparative analysis provides a framework for considering the relative impact of several environmental factors on fish productivity. Assume, for example, two simple scenarios. First, a marked increase in the upwelling intensity, providing more available nutrients, would probably improve fish productivity in many ecosystems. The consequences could certainly be stronger in areas where low upwelling intensity is the main limiting factor, i. e. Morocco or Senegal. Second, with a decrease in the wind-mixing intensity, a greater fish productivity would be expected in areas where high mixing appears to be an important limiting factor, i.e. California, Chile, Spain-Portugal, Morocco, Namibia and South Africa. The reality is more complex because environmental factors change simultaneously. A scenario involving one environmental variable is a very simplified view of what might occur under climatic changes. However, a qualitative approach allows one to predict the increase or decrease of fish productivity and can give some preliminary answers.

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colloques et séminaires

Global versus Local Changes in Upwelling Systems

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* *prepared by F. Torres Jr. (ICLARM)*

Preface and Acknowledgments

THE EDITORS

This volume is comprised of 33 contributions, most originally presented at an international conference held on 6-8 September 1994 in Monterey, California, USA under the auspices of the Climate and Eastern Ocean Systems Project (CEOS).

The CEOS was a collaborative project linking a variety of research institutions, notably ORSTOM, NMFS and ICLARM and devoted to a study of the potential effects of global change on the resources of upwelling systems through identification of global and local effects impacting on these systems.

This volume is one of the two major products of CEOS, the other being a set of CD-Roms that will empower more researchers, especially in developing countries, to study oceanographic processes (see Roy and Mendelssohn, this vol.).

We apologize for the delay in publishing this volume, due mainly to the inherent difficulty of coordinating a vast cast of authors in different parts of the world, and most with first languages other than the English we have chosen to present the result of CEOS.

We thank our respective institutions, ORSTOM, NMFS and ICLARM for their support of the effort that led to this volume. Also we take this opportunity to thank Ms Marie-Christine Pascal for the typing and layouting of this book and also Ms Nathalie Richard, Ms Barbara Chollet, Ms Sandra Gayosa, Mr Emmanuel Suisse de Sainte-Claire and Mr Francisco Torres Jr. for their assistance in the production of this volume.

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Spatial and Temporal Dynamics of the Upwelling off Senegal and Mauritania: Local Change and Trend

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ABSTRACT

A specific processing chain applied to the infrared data of the Météosat series satellites has been elaborated. The high repetitiveness of the observations allows to obtain 5 days synthesis SST maps over West Africa at a 6 km resolution. The resulting data set precisely describes the spatio-temporal dynamic of the coastal upwelling, from Mauritania to Guinea (21°N-9°N), since 1984. The study area is dominated by the seasonal coastal upwelling which displays important interannual variations. The study of the superficial thermal field structure enables to link the mean position of the upwelled water to the topography of the continental shelf. Continuous monitoring of SST along the shelf allows the spatial estimation of an upwelling index and to characterize the seasonal dynamic of the upwelling via parameters such as the intensity and the duration of the seasonal transition phase and its seasonal lags. The example of an anomalous migration of *Sardina pilchardus* in Senegal leads to the hypothesis that neither the mean seasonal intensity nor the precocity of the upwelling is sufficient to initiate an abnormal southward migration and that the seasonal transition leads may be a key parameter in this process.

RÉSUMÉ

L'élaboration d'une chaîne de traitement spécifique aux données infrarouge thermique des satellites de la série METEOSAT a été réalisée. L'abondance des données satellitales liées à la répétitivité des observations permet d'accéder à une résolution de 5 jours et 6 km, soit très en deçà des méthodes d'investigation utilisables en routine en océanographie côtière. La description spatio-temporelle précise et régulière de l'upwelling côtier de la Mauritanie à la Guinée est ainsi accessible depuis 1984. La zone étudiée est soumise à la très forte saisonnalité de l'upwelling côtier, lequel présente aussi de fortes anomalies interannuelles. La connaissance de la structure des champs thermiques superficiels permet de relier la position moyenne des zones de remontée à la topographie du plateau continental. La détermination de la TSM sur une bande continue centrée sur le maximum de résurgence permet le calcul d'indices d'upwelling spatialisés et de caractériser la dynamique saisonnière de l'upwelling à travers des paramètres tels que : intensité et durée mais aussi décalages saisonniers et progressivité des transitions saisonnières. A partir de l'exemple de ***Sardina pilchardus*** au Sénégal, on émet l'hypothèse que ni l'intensité saisonnière moyenne, ni la précocité de l'upwelling ne permettent d'expliquer à eux seuls certaines migrations exceptionnelles de cette espèce, mais que la dynamique des transitions saisonnières semble également déterminante.

INTRODUCTION

Remote sensing of sea surface provides synoptic and repetitive overviews, especially for large scale monitoring of climatic parameters. At a lower space and time scale, satellite infrared imagery allows satisfactory observation of coastal areas. Due to their low cloud coverage, coastal upwelling areas may be particularly well monitored via sea surface temperature (SST) mapping, at a time and a space scale adapted to their particularly high dynamic. A specific data processing chain has been developed from METEOSAT infrared data and ships of opportunity data (Citeau and Demarcq, 1990; Demarcq and Citeau, 1995) and tested in West African upwellings.

The upwelling zone studied extends from North Mauritania to Guinea and corresponds to the seasonal zonal displacement of the trade winds along the western African coast. Directly depending on this dynamic, the seasonal variability of the SST reaches 14°C (Rébert, 1983), and is one of the largest in the world. The high pressure regime of the northern anticyclone which governs NE trades leads to weaker cloudiness (and permits better remote sensed observations of SST) during the cold season (October to June, depending on the latitude).

The enrichment of these coastal areas depends on both intensity and variability of the corresponding upwellings. Important fluctuations of pelagic fishes population abundance and particularly of *Sardinella* species, a major resource for Senegal, have been recorded, in spite of the ability of these species to tolerate some environmental fluctuations (Fréon, 1988; Cury and Fontana, 1988). The irregular presence of species depending of geographically neighboring stocks (as for *Sardina pilchardus*) is noticeable and may also be related to environmental fluctuations.

1. THE SPECIFIC DATA PROCESSING FOR SST RETRIEVAL FROM METEOSAT INFRARED IMAGERY

In terms of radiometric and spatial resolution, the accuracy permitted by geostationary satellites (0.5°C and 5 x 5 km subsatellite in the case of METEOSAT infra-red channel) is lower than the accuracy currently obtained from polar orbital satellites (0.12°C and 1 km for NOAA/AVHRR). Nevertheless, this lowest resolution is not really a constraint, even in coastal areas, if compared with the size of the oceanic structures observed at sea level, on the one hand, and with the strong thermal gradients encountered, on the other hand. On the contrary, the regularity of the earth scan provided by METEOSAT allows a simpler processing for geometric corrections, while its repetitiveness (every 30 minutes) allows improvements in discriminating the sea from clouds.

1.1. Pre-processing

Data pre-processing takes advantage of the half-hourly availability of earth scans by METEOSAT. Each satellite view of the earth is classically calibrated (transformation of the energy emitted by the earth to temperature by inversion of Planck's Law). An extraction of the working area is then performed and the image is geometrically corrected to a linear latitude and longitude projection.

In tropical areas, the infra-red radiance measured by the satellite sensor is systematically lower than the infra-red rariance emitted by the sea surface (except in the presence of suspended dusts), due to cold atmospheric water vapor. Consequently, by assuming that the SST is constant over 24 hours, the 48 images of the day are combined into a new image synthesis, retaining for each pixel the 'warmest' one of the time series.

Cloud cover in west Africa may strongly vary during one day, especially when the trade winds are weak. The efficiency of the 'maximum temperature method' is shown for 27 days, from 5 to 31 May 1991 (Fig. 1) by comparing the instantaneous cloud cover at 12h00 GMT (generally low cloud cover) and the daily synthesis index. The advantage of the repetitiveness of observations by a geostationary orbit appears clearly.

This important benefit in term of usable pixels for SST retrieval will also determine the performance of the sea-cloud discrimination, the major step of the processing in SST restitution.

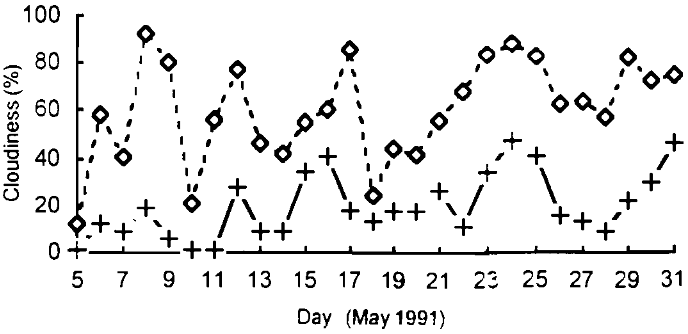

Fig. 1: Reduction of the cloud cover (%) on the daily thermal synthesis (solid line; crosses) compared to the instantaneous cloud cover (dotted line; open dots) at 12h00 GMT.

1.2. Sea-cloud discrimination

In remote sensing processing, sea-cloud discriminations are very often based on visible/infra-red comparisons. Nevertheless, this technique has some constraints. The major one for acquisition and processing is the large amount of data required, five times more in the case of METEOSAT. Furthermore, some low level clouds are strongly absorbent in the IR channel and remains transparent in the VIS one. The visible/infrared algorithm is then unusable.

The method we developed for sea-cloud discrimination is based on a comparison of a daily synthesis with the 'most probable' real SST field. This field is provided either from a climatology of SST or, more often, from a previously processed SST field. For adequate masking, this reference situation is chosen as close as possible to the daily synthesis, in terms of upwelling spatial extent.

A comparison of the radiative temperature synthesis (Fig. 2a) with this reference is then performed and the values with temperature deviation greater than a definite threshold (around 3°C according to the similarities of both fields) are considered to refer to clouds, and are masked (in black on Fig. 2b).

1.3. Atmospheric correction and SST restitution

The above resulting temperature field remains affected by atmospheric absorption, mainly due to the atmospherical water vapor. In tropical area, the apparent thermal absorption generally lies between 2°C (trade wind region) and 5°C or more (equatorial region).

According to the previous pre-processing steps (maximum temperature synthesis), and considering the difficulty to obtain direct information on atmosphere structure compatible with space and time resolution of the SST fields (6 km and 5 days in our case) the most adequate way to correct this temperature field from the atmospheric absorption is to use an exogenous source of SST data. The ships of opportunity data disseminated by the Global Transmission System (GTS) in the 'SHIP' meteorological messages (including SST, wind, air temperature, etc.) and synthesized in

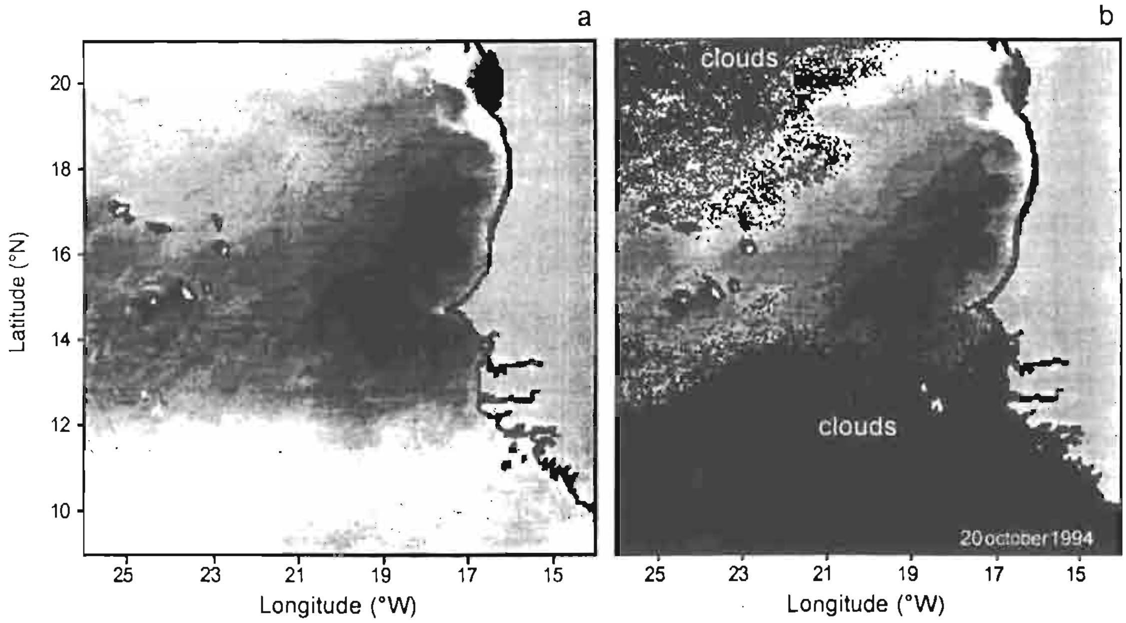

Fig. 2: Raw daily infrared synthesis on October 20, 1994 (a) and after cloud masking (b) in the beginning of the cold season. The SST decrease from dark grey to white while the cloudy area is displayed in black.

the COADS database (Roy and Mendelssohn,1994, this vol.) are rather convenient for this, by providing an adequate density of SST measurements, especially in Mauritanian and Senegalese areas (Fig. 3). Note that Figure 3a corresponds to the satellite situation displayed in Figure 2 and that SHIP data would not allow to detect the presence of the coastal upwelling in South Mauritania and North Senegal.

Because of their generally irregular spatial distribution, their poor sampling of the coastal area, (especially damaging during the beginning and the end of the upwelling season) and their relatively high instrumental noise, the usefulness of the SHIP *in-situ* data for precisely describing the SST field in coastal upwelling areas is generally very low.

The suspect SHIP data are first eliminated from the original data set, initially by comparison with a global SST climatology i.e., the Reynolds monthly SST climatology (Reynolds, 1982) or with our own climatology, preliminary computed from 1984 to 1989 (Demarcq and Citeau, 1995). Only values whose departure from the climatology is greater than 5°C are removed given the strong SST anomalies that are encountered in this upwelling area.

Despite the above limitations, the SHIP data provide a very satisfying estimation of the residual atmospheric absorption field. The latter is obtained by coupling ship data with the uncorrected satellite data (Fig. 2b) in order to give corrected SST field: the field of 'atmospheric correction' is then computed as the statistical departures of the satellite synthesis from the *in-situ* SHIP SSTs. An example of atmospheric field and the resulting corrected satellite SST field is displayed on Figure 4.

Standard SST processing was applied on a temporal basis of 5 days from 1984 to 1995. During the upwelling season off Senegal and Mauritania (from October to June), approximately 90% of the daily METEOSAT infrared synthesis can be used. This percentage is in fact seasonally variable, and depends on the mean coastal nebulosity, which is inversely proportional to trade wind intensity.

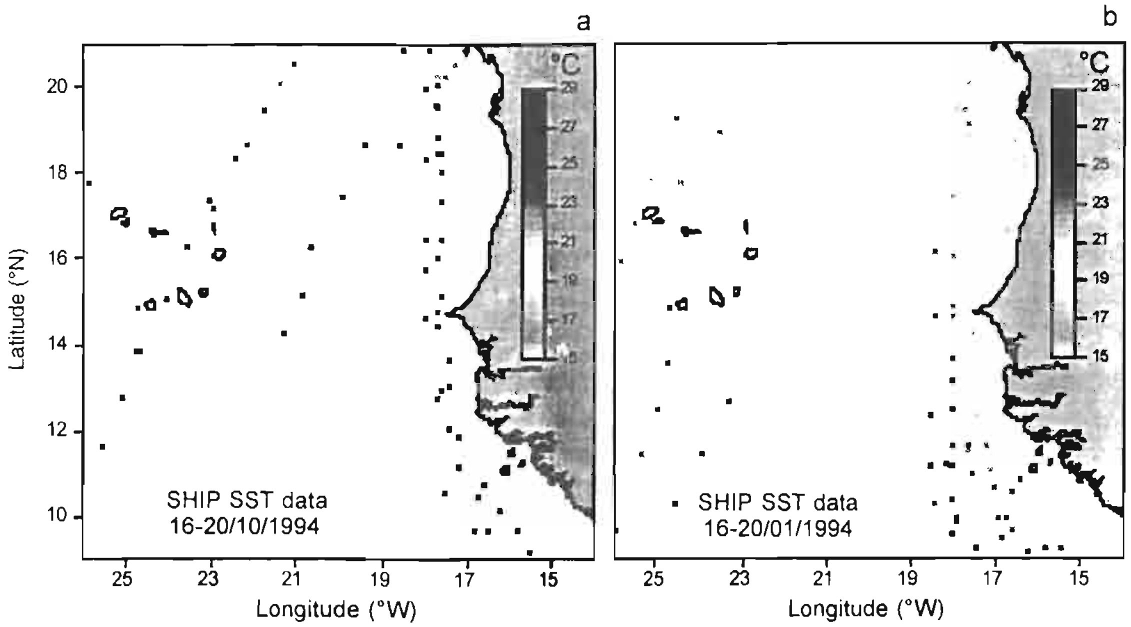

Fig. 3: Typical examples of "SHIP" data distribution offshore Mauritania and Senegal during 5-days periods at the beginning (a) and in the middle (b) of the upwelling season.

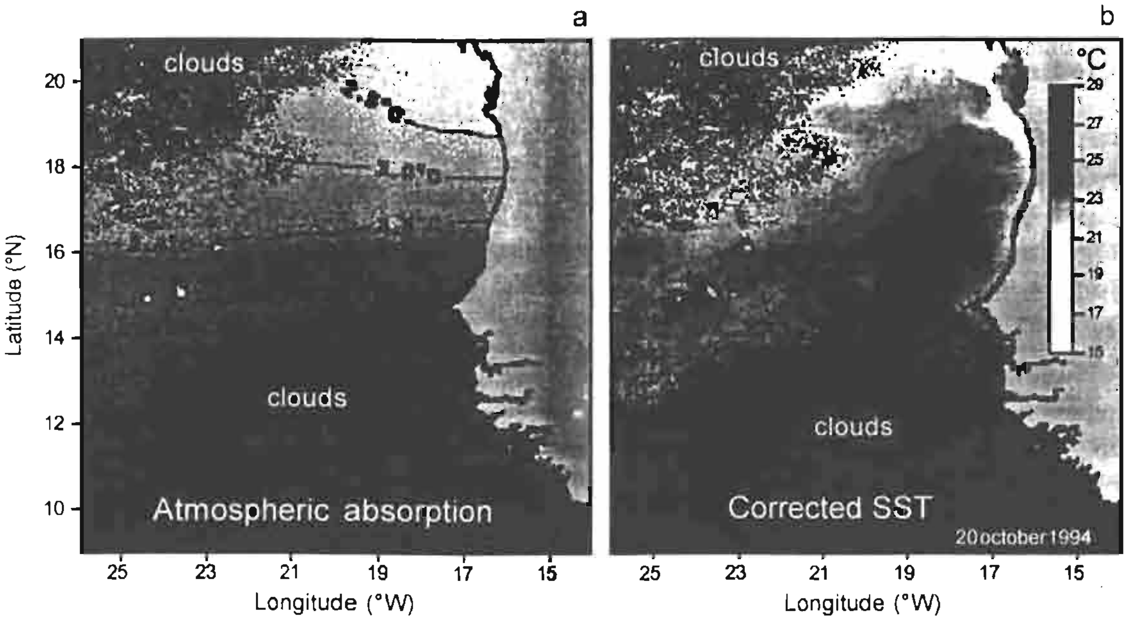

Fig. 4: Example of atmospheric absorption field (a) on 20 October 1994 (beginning of the upwelling season) and the resulting corrected satellite SST field (b).

For each daily synthesis, the cloudy area is masked and a radiative temperature field is calculated by a 5 day period. This field is then atmospherically corrected by adjusting the raw temperature values with the corrected SHIP SST measurements as described above.

2. COMPUTATION OF COASTAL UPWELLING INDEXES FROM SST FIELDS OFF MAURITANIA AND SENEGAL

The upwelling structures observed off Mauritania and Senegal from October to June are representative of a complex spatial dynamic, characterized by several local SST minima, mainly depending on wind direction and local bathymetry. The SST contrast with offshore waters depends mainly on the history of the upwelling in the preceding few weeks and tends to decrease during weak upwelling episodes. Superficial upwelling filaments moving offshore are frequently observed and reveal the concentrating effect of the shelf topography.

Figure 5 displays some commonly observed features. The main differences in SST field are linked to the large scale wind field variation, in both intensity and direction. According to Ekman's theory (Ekman, 1905), upwelling is maximum along coast lines parallel to the wind. The localization of this maximum varies according to wind direction and is particularly visible during the beginning of an upwelling event (see for example Figure 5a, b). During more intense phase of the trade winds, the cooling extent is continuous along the coast line, from 21°N to 10°N approximately (Fig. 5c). The southern most extent occurs around March, according to the most southern latitudinal position of the ITCZ/trades system which occurs in February and March (Citeau ***et al.***, 1989).

The localization of the maximum flow of upwelled waters at the sea surface can be defined by a continuous area of minimum SST. This area is relatively fixed and closely linked to the local bathymetry (Fig. 6). SST at these locations is related to the instantaneous response of the upwelling system to wind forcing. This local spatio-temporal signal does not reflect the dilution effects due to past upwelling events that would be reflected in the mean SST calculated on a larger space scale.

An SST based upwelling index is calculated by differencing the local SST ('SSTsat') located at the minimum SST line (see Fig. 6) and a reference offshore temperature at the same latitude, to avoid taking into account large scale SST anomalies due to planetary climatic anomalies, not reflected in coastal areas. This reference temperature is chosen as the climatic SST temperature (and not the current offshore SST), calculated from 1984 to 1994 in the tropical Atlantic from a routinely elaborated product calculated from METEOSAT and SHIP data (Demarcq and Citeau, 1995; Demarcq and Suisse de Sainte-Claire, 1995).

According to Jacques and Tréguer (1986), the upwelled water off Mauritania and Senegal is essentially composed of SACW (South Atlantic Central Water). Regular coastal measurements in several oceanographic stations in Senegal (Roy *et al.*, 1985) show that the extreme coldest events correspond to very stable values of SST between 14.0°C and 14.5 °C. In this case, the salinity of the upwelled water (between 35.4‰ and 35.5‰) confirms its SACW origin.

According to the Ekman's theory and oceanographic coastal measurements off Senegal, the departure of the SST (measured as close as possible to its arrival location at the sea surface) from its minimum value (pure SACW) is

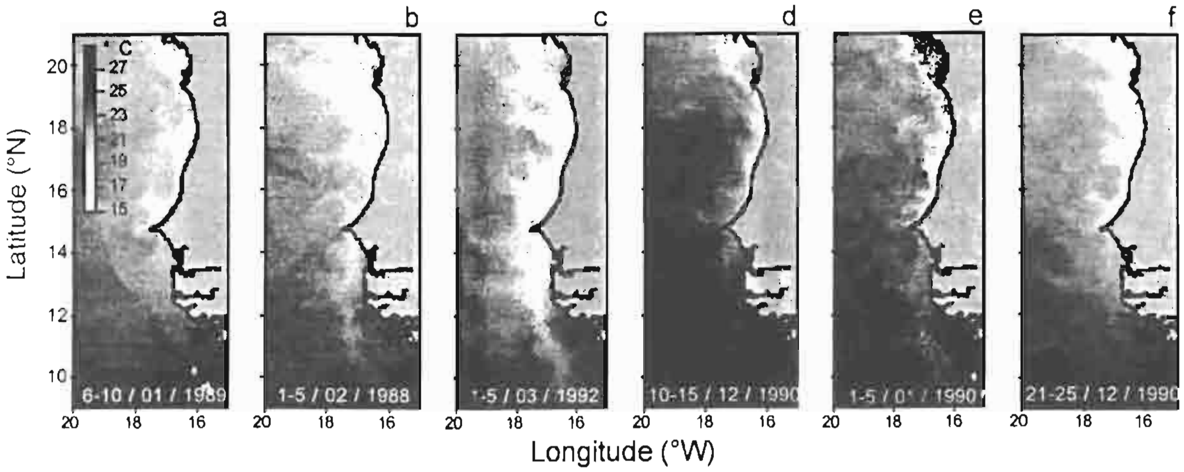

Fig. 5: Commonly observed superficial SST fields during the upwelling season off Mauritania and Senegal. The SST decrease from black (27°C) to white (17°C) for all images. Numerous filaments of upwelled waters moving offshore are clearly visible.

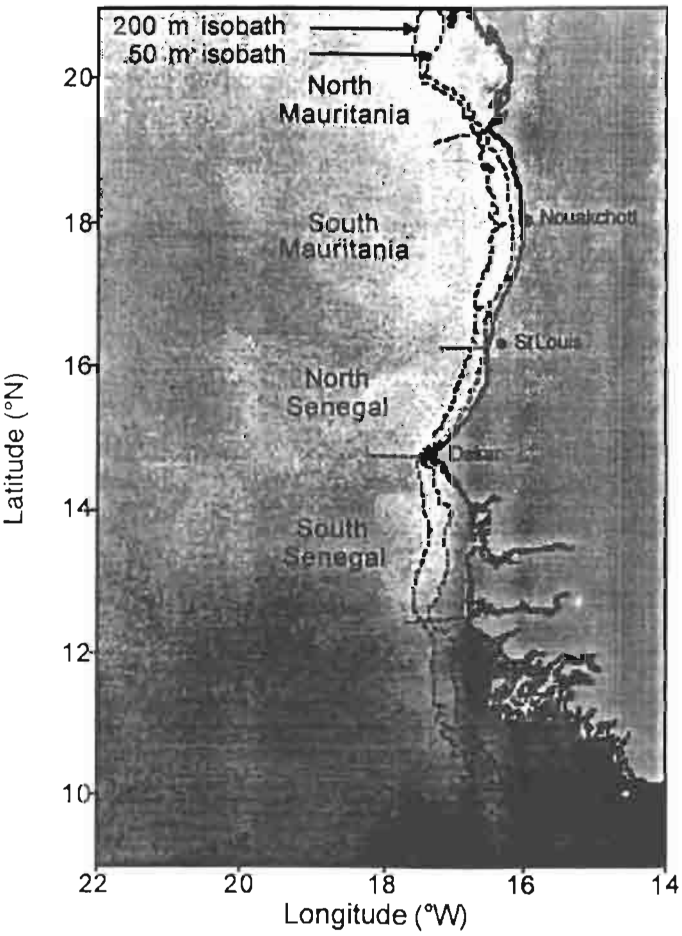

Fig. 6: Localization of the maximum flow of upwelled waters at the surface in relation to the local bathymetry and localization of coastal areas for upwelling index computation.

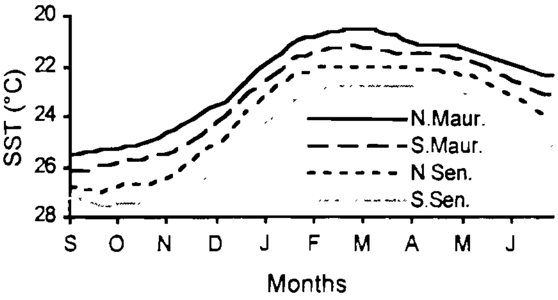

Fig. 7: Offshore SST (SSTmax [lat,month]) at 23°W off Mauritania and Senegal, calculated for the upwelling season of the years 1984-94 from satellite climatology.

directly linked to the upwelling flow. On the other hand, the maximum SST recorded from oceanographic coastal measurements in upwelling season during very weak upwelling phases varies seasonally, and converges towards the offshore SST at the same latitude, where the upwelling influence is negligible (because of the dilution of the upwelled water due to wind-generated turbulence).

The minimum value of SST expected at the upwelling centers, noted SSTmin, is the temperature of SACW as it reaches the surface. The maximum temperature, noted SSTmax, is chosen as the offshore climatic SST recorded at 23°W. Figure 7 displays this mean seasonal signal, calculated from the satellite climatology elaborated for the 1984-1994 period, from North Mauritania to South Senegal. This offshore signal is representative of the mean offshore upwelling influence. For a given year, it reflects the mean 'seasonal past' of the upwelling in the coastal area, but not its current intensity.

As reported in the time series of coastal oceanographic measurements of wind and SST, the seasonal variation of the observed value of SSTsat reflects the fact that, for a definite level of wind forcing, SST cooling is greater at the beginning or at the end of the upwelling season in a relatively warm environment than during the middle of the season in colder surrounding waters (Teisson, 1982). This makes it possible to compare the upwelling intensity during the whole season. The main difference with the Ekman index is the spatio-temporal integrating effect intrinsically linked to an SST based index and clearly displayed in Figure 8.

Important discrepancies remain between these two parameters (Fig. 8) partly due to the spotty sampling of the ship data close to the coast (especially in the south Mauritania region), because of the ship route locations (see Fig. 3). This fact is clearly shown across the differences in mean SST separately calculated from SHIP data (by objective analysis) and from satellite data over the same coastal area (Fig. 9). This difference leads to a severe under-estimation of upwelling extent and intensity calculated from the SHIP data. This under-estimation is high at the beginning of the upwelling season (when the offshore extent of the upwelling is generally weak, see for example Fig. 4 and 5d). In addition this under-estimation is different from one year to another, depending on the variability in the distribution of SHIP data.

From these observations, a relative SST-based upwelling index, ('SSTI') was calculated from the deviations of the locally observed SST from their extreme theoretical values, respectively fixed and seasonally varying.

To take into account the effect of the spatial dilution of the upwelled waters at the surface mixed layer, the SSTI may

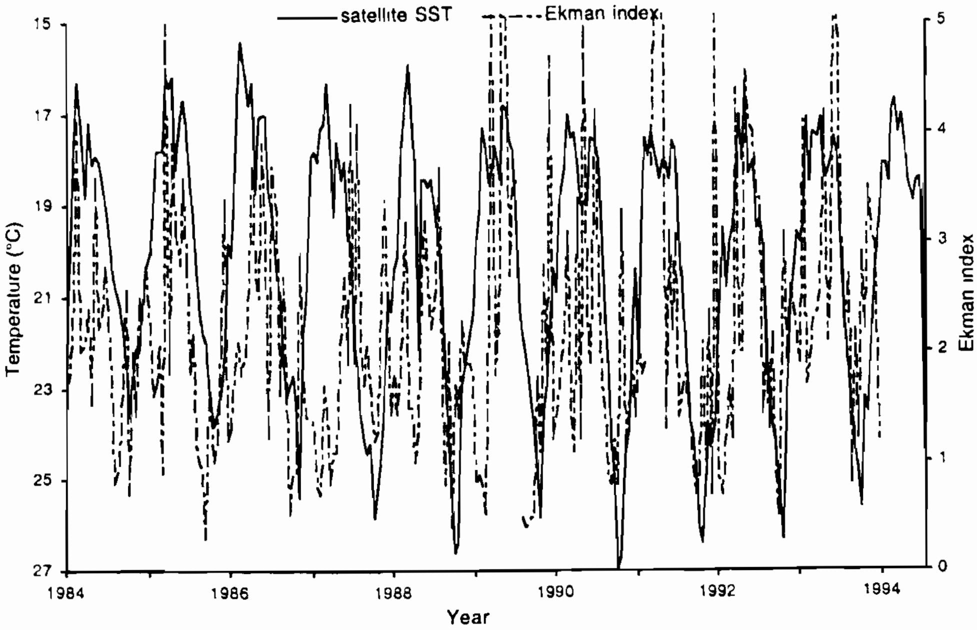

Fig. 8: Direct comparison of Ekman index and satellite SST (°C).

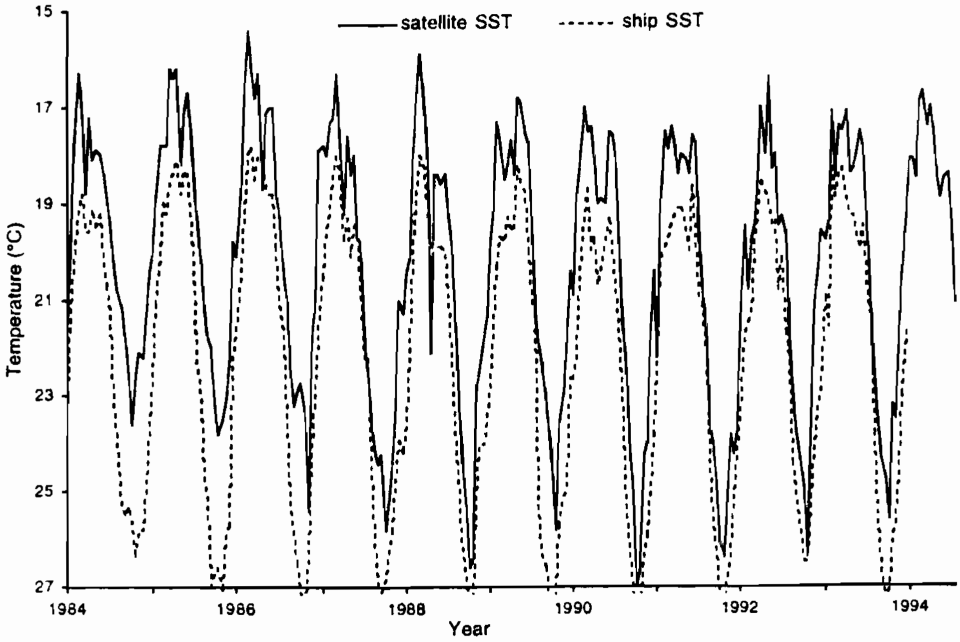

Fig. 9: Simple SST-based index calculated from SHIP data only (dotted line) and from the satellite product (solid line) in the south Mauritania region.

be expressed by the relation:

$$SSTI = (SST_{sat}-SST_{max}[lat,month]) /(SST_{min}-SST_{max}[lat,month])$$

Figure 10 shows the upwelling dynamic calculated using this index for 4 areas (see also Fig. 6) from North Mauritania to South Senegal for the 1984-1993 period. The 5-days time scale reproduces the short term dynamic of the upwelling intensity. Major bias (other than a systematic one) seem improbable, considering the large amount of input data and the processing homogeneity of the time series.

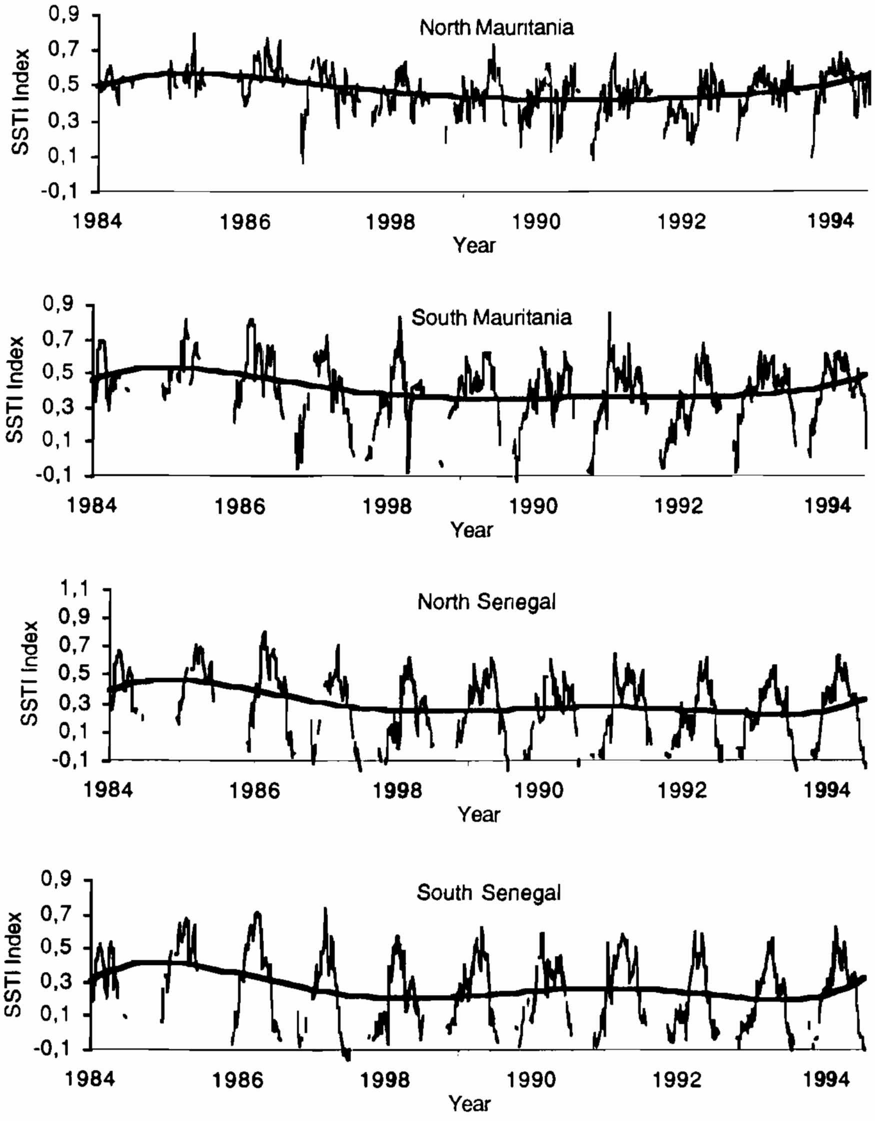

Fig. 10: SSTI index calculated from North Mauritania to South Senegal from 1984 to 1993.

3. TRENDS AND RELEVANT PARAMETERS IN UPWELLING DYNAMIC

The very high seasonal upwelling dynamic off West Africa is clearly shown through the SST-based upwelling index from 1984 to 1993 (Fig. 10) and is indirectly confirmed by the short scale spatial dynamics seen across the series of daily satellite images which suggest a daily response to the wind forcing, according to previous coastal measurements of SST.

Relative bias seems avoided in such SST satellite product, and no linear trend is obvious in term of upwelling intensity change considering a period of 11 years. Nevertheless, groups of 'cold' and 'warm' years are exhibited when a polynomial adjustment of 5th degree is used (Fig. 10, heavy lines). The years 1984 and 1985 are the coldest of the time series and 1988, 1989 and 1992 the warmest. It is interesting to note that 1985 was a warm year in the tropical Atlantic, due to the impact of the 1982-83 El Niño, and that the intensification of the coastal upwelling off Mauritania may be a local effect of this warming.

The general similarity of the short term trends of SSTI is obvious for the four areas (Fig. 11). An interesting observation is the case of the 89/90 and 90/91 cold seasons, for which an inversion of the trends is observed, from warm years in North Mauritania to cold years in South Senegal. The very regular North-South gradient of this phenomenon allows to reject the hypothesis of a processing artifact and to think that a temporary change in the zonal trade wind fields for this years did occur. This observation expresses a decline of the normal decreasing zonal gradient of the upwelling-favorable component of the trade winds, from Mauritania to Senegal. The temporal evolution of the SSTI (Fig. 11) shows that a strengthening in the trade winds in this region is sometimes in phase (in the case of the 85-90 period) and sometimes in opposing phase (in the case of the 90-94 period). It has been shown in this region that the intensity of the zonal gradient between the north of Mauritania and the Senegal enhances the migratory response of several migratory species (Cury and Roy, 1988; Binet, 1988; Binet this vol.).

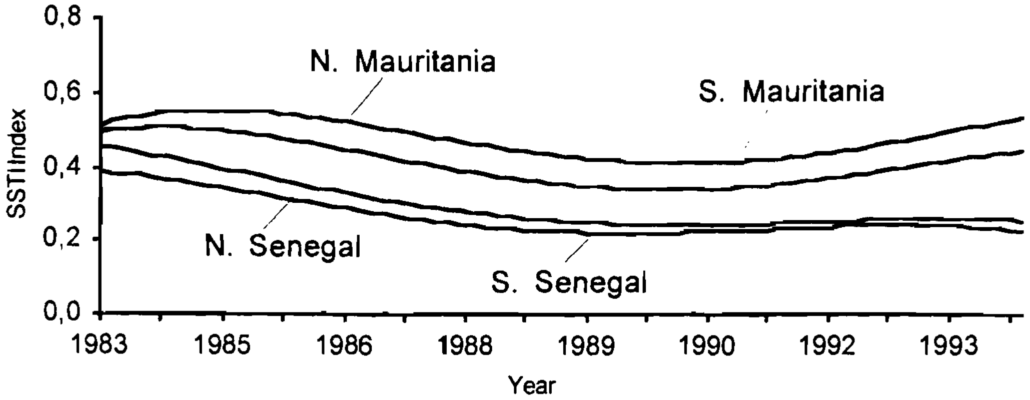

Fig. 11: Zonal structure of SSTI trends from North Mauritania to South Senegal (1984-93).

Long term changes in upwelling intensity have been examined from 1964 to 1993 from SHIP data. Both Ekman CUI (Fig. 12) and SST (Fig. 13) show a weak increase of upwelling intensity. This increase seems coherent with the other long-term observations in trade wind intensity (Bakun, 1990, 1992). Nevertheless, reducing potential impact on coastal fish populations to the unique long term trend due to the global warming would be restrictive, as it can be shown that the amplitude of the medium-term interannual variations are several times greater (or inverse) than the global warming amplitude. Also, the upwelling intensity off Senegal measured from remote sensed data presents a weak decrease in the trade winds for the 84-93 period (see Fig. 10).

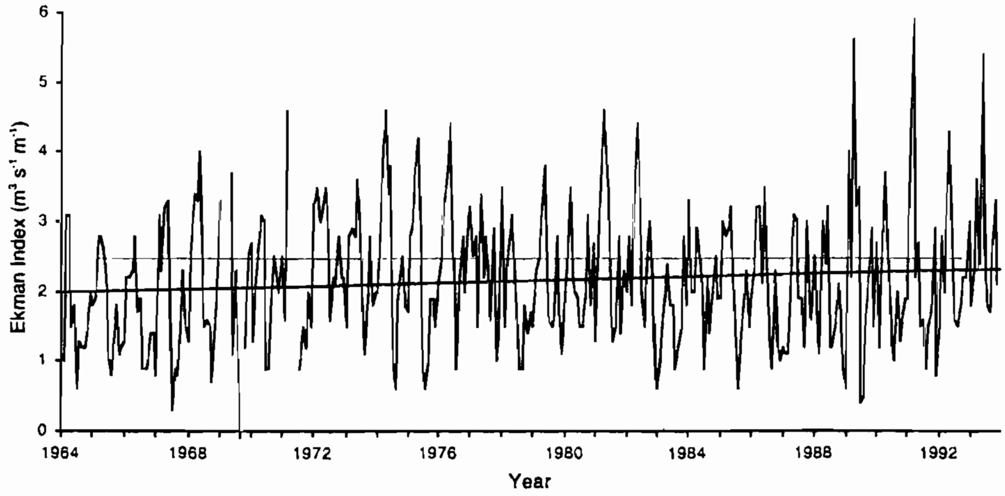

Fig. 12: Ekman CUI calculated from SHIP data in the Mauritania region, from 1964 to 1992.

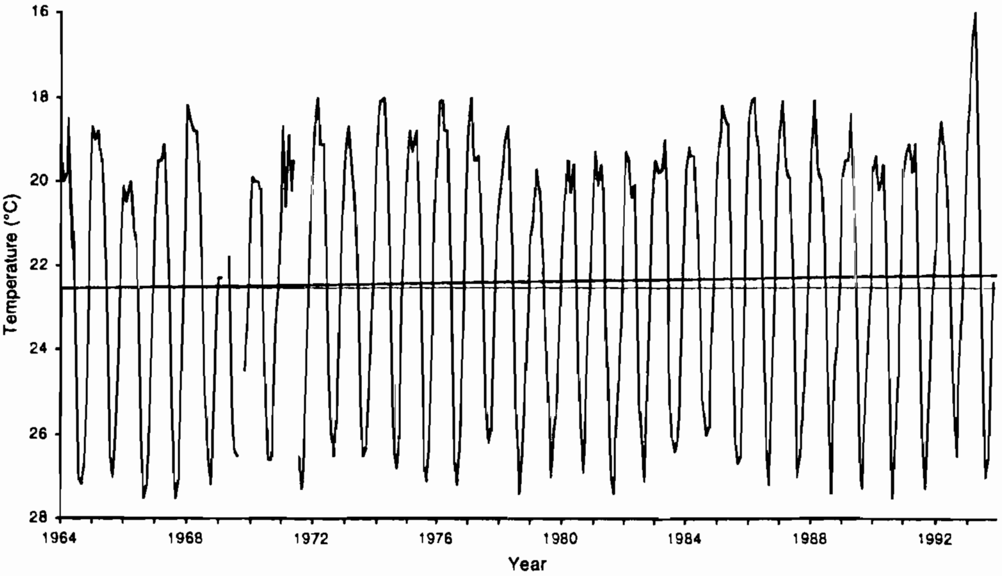

Fig. 13: SST from SHIP data in Mauritania region from 1964 to 1993.

Also, reducing upwelling dynamic to its mean intensity term would be restrictive, as it is obvious that many parameters are required to describe the upwelling dynamic at the different space and time scales involved. Among these, the duration of the upwelling season seems to be a very complementary parameter since no relation can be shown among upwelling intensity, season duration and seasonal timing, whether one uses satellite data or coastal oceanographic measurements (Portolano, 1986).

Similarly, the importance of timing of the hydrological transition on the local fisheries has been shown in Mauritania (Chavance *et al.*, 1991). In other upwelling regions, e.g., in Côte-d'Ivoire, the trend in upwelling season duration appears to have played a major role in the recovery of the *Sardinella aurita* fishery during the last years (Pezennec and Bard, 1992).

4. AN APPLICATION TO THE UNDERSTANDING OF THE SARDINE MIGRATION OFF SENEGAL

A very exceptional seasonal migration of *Sardina pilchardus* (Walb.) occured in Senegal at the end of 1993 (Binet, this vol.; I. Sow, pers. comm.), and represents the main event of the 93-94 fishing cold season for the local small-scale fishery. It seems interesting to examine some possible environmental causes for this anomaly, based on the dynamic of the upwelling seasonality observed from satellite data.

Sardina pilchardus is a pelagic species whose southern occurence (and the associated fishery) in West Africa was extended gradually from north Morocco in the 1920s, to South Morocco and North Mauritania around the 1950s (Belvèze, 1984). The southern extent of the fishery was estimated at 18°N in 1973 (Domanovsky and Barkova, 1981), while specimens where occasionally fished in Senegal in 1974 (Conand, 1975) and 1976 (Fréon, 1988). This species supports important fisheries in Morocco since the 1950s, the main period of southern extension of the species. The microphageous/phytoplanctonic regime of this species enables its development in strong upwelling ecosystems, as off Morocco and Mauritania, where the food web is short and dominated by phytoplanctonic production (Binet, 1991).

The long-term trade winds' increase from 1964 was related to the sardine fishery changes from 26°N to 14°N by Binet (this vol.). The dynamic of the upwelling as depicted from satellite observation from 1984 to 1994 is synthesized in a latitude/time diagram (Fig. 15), Binet's hypothesis.

Satellite observations show that the 1985-86 upwelling season was one of the coldest in term of both mean upwelling intensity and duration. These mean characteristics are confirmed by the SHIP observations, especially for the duration parameter (Fig. 14), while the satellite data shows that the cooling was particularly sudden and uniform from 20°N to 15°N (Cape Vert).

On the contrary, the 1992-93 cold season was characterized by a weak upwelling, associated with a remarkable regularity in the seasonal southward cooling.

We hypothesize that this progressive dynamic – induced by the same regularly zonal propagation of the trade winds – may have an 'attractive' effect on the seasonal migration amplitude of *Sardina pilchardus*, by reducing the natural barrier caused by the spatio-temporal discontinuities of SST it usually encounters. The 19-20°N upwelling discontinuity due to the local upwelling unfavorable coast line orientation (Fig. 5 and Fig. 6) may constitute a thermal barrier to the southward

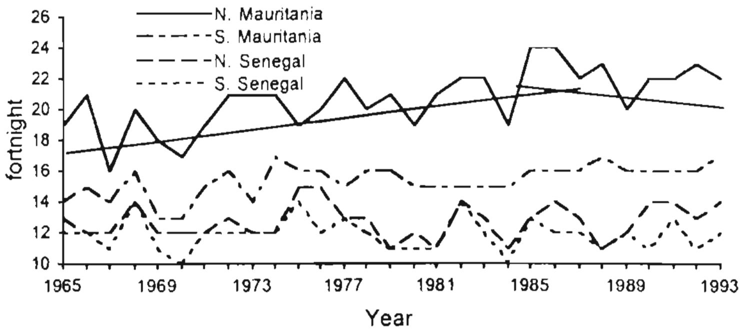

Fig. 14: Cold season duration from North Mauritania to South Senegal calculated from SHIP data for the 1965-1993 period.

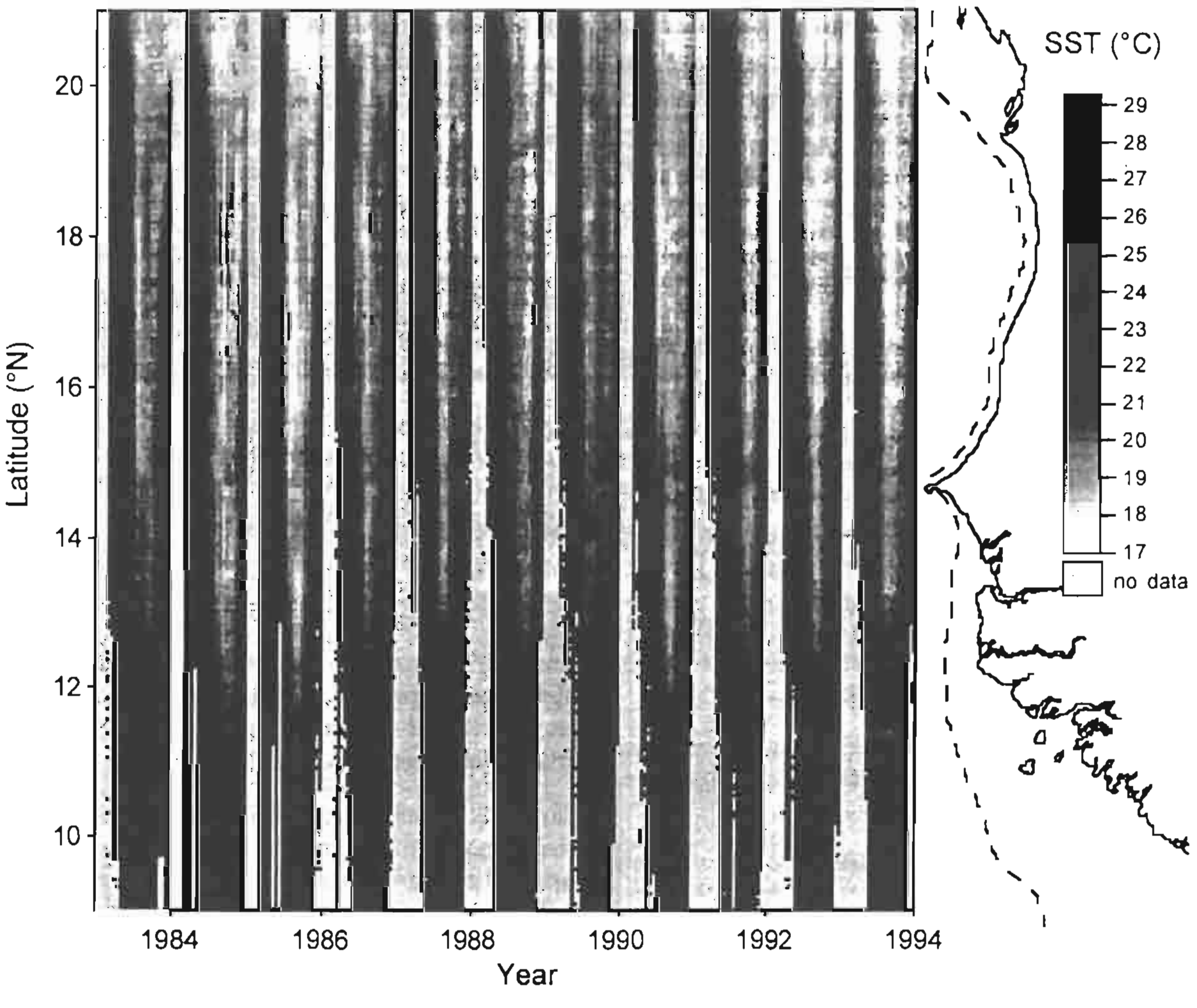

Fig. 15: Spatio-temporal dynamic of SST off West Africa, computed from satellite data for the 1984-1994 period.

migration of *S. pilchardus*. This discontinuity, very well evidenced by satellite observations (Demarcq and Citeau, 1995), reinforces the annual mean thermal gradient around 20°N and may be related to the estimated southern limit of *S. pilchardus*, which fluctuates around 18°N to 21°N since the 1970s.

Thus, the dynamic of the seasonal southward cooling seems to be one of the key parameters that affects the large amplitude seasonal migration of *S. pilchardus*. Thus, Binet's hypothesis appear validated.

CONCLUSION

Calculation of an SST based coastal upwelling index from satellite data made it possible to describe the short-term dynamic of the coastal upwellings off West Africa. Parameters such as mean upwelling intensity, long-term, trends, short-term, variability, SST zonal gradient, duration of the upwelling season, trends in seasonal variations and spatio-temporal modalities of seasonal transitions must be taken into account to understand the key processes that govern the biological cycles of fish species of economical importance in coastal upwelling areas. This is particularly true regarding the seasonal migrations of small pelagic species in upwelling areas,which are affected by long-term environmental variations and exceptional seasonal conditions. These changes may be considered responsible for the major species substitutions and alternation generally observed in upwelling regions, independently of the effects of fishing effort.

The processed data set shows that the informative potential of precise spatial and temporal remote sensed information would be of great interest for wider areas (such as the whole West African coast). Comparative studies should be conducted to analyze the impact of local environmental anomalies on biological processes in similar coastal upwelling ecosystems.

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Pelagic Fisheries and Environmental Constraints in Upwelling Areas: How much is Possible?

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ABSTRACT

The relations among fish productivity and five environmental variables are analyzed for eleven upwelling areas of the world. Three 'fish catch productivity' indices, calculated from fish catch statistics, are used as surrogates for fish productivity in the ecosystems. Five environmental parameters are considered in each upwelling areas: coastal upwelling and turbulence indices, sea surface temperature, continental shelf surface and length. On its own, the size of the ecosystem does not explain the observed differences of the pelagic fish productivity indices. Using non-parametric regression methods, it is shown that a combination of several environmental factors is required for high fish productivity. These optimal conditions are a high upwelling index (around 1.3 $m^3/s/m$), a moderate turbulence (around 200-250 m^3/s^3), a medium sea surface temperature (15-16°C) and a relatively large continental shelf (around 100 000 km^2). The Peruvian ecosystem is the only system which combines all of these environmental conditions. The environmental factors which limit fish productivity are identified in each upwelling zones; they can help to predict changes under future climatic events. The limits of the analysis as well as some possibly circular aspects of the analysis are emphasized.

RÉSUMÉ

La productivité halieutique est analysée en relation avec cinq variables environnementales pour onze zones d'upwelling mondiales. Trois indices de productivité sont estimés à partir des statistiques de captures disponibles ; ils sont assimilés à la productivité en poisson d'un écosystème. Cinq variables environnementales sont considérées pour chaque zone d'upwelling : indices d'upwelling côtier et de turbulence, température de surface de la mer, surface et longueur du plateau continental. La taille d'un écosystème en elle-même n'explique pas la disparité observée entre les différentes productivités en poissons pélagiques des zones d'upwelling. Des méthodes régressives non paramétriques révèlent qu'une combinaison de plusieurs facteurs environnementaux est en effet nécessaire pour qu'une forte productivité en poisson soit réalisable. Les conditions optimales sont les suivantes : un fort indice d'upwelling (proche de 1.28 $m^3/s^1/m^1$), une turbulence modérée (proche de 200-250 m^3/s^3), une température de surface moyenne (15-16 °C) associés à un plateau continental relativement vaste (d'environ 100 000 km^2). L'écosystème péruvien s'avère être le seul qui regroupe l'ensemble des conditions environnementales optimales. Le ou les facteurs environnementaux qui sont supposés limiter la productivité en poisson sont identifiés pour chacune des zones d'upwelling ; ils peuvent aider à prédire les éventuels changements consécutifs aux futurs événements climatiques. Les limites ainsi que les aspects tautologiques de cette analyse sont soulignés.

INTRODUCTION

Approximately one hundred million tonnes of fish and shellfish are extracted every year from the sea and the inland waters since 1989 (Fig. 1). The total marine fish catch represents 75% and around one third of it is composed of pelagic fish (Fig. 1).

Pelagic fisheries are mainly located in the four main upwelling areas which are located in the eastern boundary currents, i.e., the Canary, the Benguela, the California and the Humbolt currents. Two fisheries contribute most to the world pelagic fish catch: the Peruvian and the Chilean fisheries. Annually they land millions of tonnes whereas countries like Morocco, the USA (California) or South Africa contribute hundred thousand of tonnes, while the catches in Côte-d'Ivoire or Ghana remain in the order of a few thousand tonnes. It is natural to think that large upwelling systems are able to produce more than small ones. However is it correct to say that a large upwelling system will always produce as much as a medium one? This is not obvious: the size of an ecosystem is an important factor when considering productivity, however it may not be

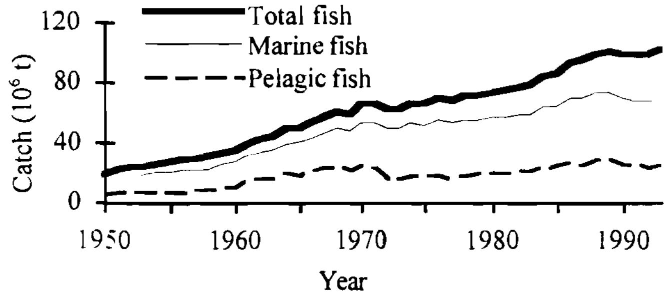

Fig. 1: Marine and pelagic fish contributions to world catches (FAO, 1995).

the only factor affecting pelagic fish productivity. Pelagic fish stocks are known for their instability and numerous authors have examined the causes of catch variations (Sharp and Csirke, 1983; Lluch-Belda *et al.*, 1991; Kawasaki, 1992; Bakun, 1994; Cury *et al.*, 1995). Environmental factors such as turbulence, upwelling intensity, offshore Ekman transport were found to be responsible for recruitment successes or failures. Do environmental factors involved in fish population fluctuations also explain the observed difference in pelagic fish productivity among upwelling systems? The comparative approach constitutes a powerful tool in ecological science as it allows to establish the generality of phenomena (Bakun, 1985). However, as stated by Maynard Smith and Holliday (1979) "we must learn to treat comparative data with the same respect as we would treat experimental results". Whereas it is a currently adopted method in evolutionary biology (Harvey and Pagel, 1991), it is not so frequently used in ecology. A comparative approach could lead to an empirical understanding of the disparity between fish productivity among upwelling systems by identifying the responsible environmental factor(s) which contribute to a low or high productivity. In this paper, the productivity of pelagic fish in eleven upwelling systems is therefore compared and its relationship with the environment examined, using variables such as the area and extent of continental shelves, upwelling intensity, turbulence, and sea surface temperature.

1. IS SYSTEM SIZE ENOUGH?

Numerous variables can be used to estimate the biological production of an ecosystem, for example planktonic production, fish biomass, turn-over of living matter, etc. However, such measurements are not available in most upwelling systems, making their comparison impossible. Fish catch statistics are the only data that have been collected in most upwelling systems during long time periods (Table 1). These data are biased for multiple reasons: changes in the availability of fish, in the fishing effort, in the target species, in the markets, etc. However used as a surrogate, fishery data can give an approximate value for biological productivity which can be considered adequate when comparing extreme range of values (from several thousand to millions of tonnes).

'Fish catch productivity' indices can be derived in several ways from catch data (Table 2):

- a 'mean fish catch productivity' index can be calculated by averaging the catch data for the period during which the fishery was sustained;
- a 'maximum fish catch productivity' index can be estimated from the observed maximum catch value; and
- a 'maximum fish catch productivity per unit of surface' index can be calculated by dividing the maximum fish catch productivity index by the surface of the continental shelf.

All of these three options were used here.

Upwelling areas	Pelagic fish species	Time period	Data sources
California	*Sardinops sagax*	1879-1990	NMFS (National Marine Fishery Service)
	Engraulis ringens	1928-1991	
	Scomber japonicus	1926-1991	
Peru	*Sardinops sagax*	1950-1993	IMARPE (Instituto del Mar del Perú)
	Engraulis ringens	1950-1993	
	Scomber japonicus	1964-1993	
Chile	*Sardinops sagax*	1964-1993	IFOP (Instituto de Fomento Pesquero)
	Engraulis ringens	1952-1993	
	Scomber japonicus	1964-1993	
Spain and Portugal	*Sardina pilchardus*	1940-1988	FAO (Food and Agriculture Organization of the United Nations) 1995
	Engraulis encrasicolus	1968-1988	
Morocco	*Sardina pilchardus*	1925-1991	FAO (1995) and ISPM (Institut Scientifique des Pêches Maritimes)
	Engraulis encrasicolus	1964-1991	
	Scomber japonicus	1964-1991	
Senegal	*Sardinella aurita*	1966-1991	CRODT (Centre de Recherches Océanographiques de Dakar-Thiaroye)
	Sardinella maderensis	1966-1991	
Côte-d'Ivoire - Ghana	*Sardinella aurita*	1966-1991	CROA (Centre de Recherches Océanologiques d'Abidjan) and FRUB (Fisheries Department Research and Utilisation Branch)
	Sardinella maderensis	1966-1991	
	Scomber japonicus	1966-1993	
Namibia	*Sardinops ocellatus*	1949-1992	Crawford *et al.* (1987) and Crawford (pers. comm.)
	Engraulis japonicus	1964-1992	
South Africa	*Sardinops ocellatus*	1950-1991	Crawford *et al.* (1987) and Crawford (pers. comm.
	Scomber japonicus	1963-1991	
Venezuela	*Sardinella aurita*	1957-1989	Guzman *et al.* (in press)
India	*Sardinella longiceps*	1896-1989	Longhurst and Wooster (1990) and FAO (1995)
	Rasterlliger kanagurta	1925-1989	
	Anchovy nei	1963-1989	

Table 1: Fishery data from eleven upwelling areas and for three main pelagic species (sardine, anchovy and mackerel) collected during different time period.

These productivity indices are calculated for two main pelagic species (sardine and anchovy), and for the pelagic species total (sardine, anchovy and mackerel) (Table 2).

Important differences are observed among pelagic fisheries (Table 2). Three fisheries catch more than one million tonnes. Peru, Chile and Namibia. The Peruvian ecosystem has a maximum total pelagic catch productivity well above that for other systems. Species productivity is also different from one geographic zone to another. For Venezuela maximum catch for sardine is around 80 000 t whereas more than 2 million t are caught in Chile. The anchovy in Morocco never reached more than 19 000 t and more than 12 million t were landed in Peru.

Large ecosystems should a priori be able to produce more fish than small ones. In order to quantify the size of the ecosystems, the length and the surface of the continental shelf were measured. The surfaces of the continental shelves vary from 17 000 km^2 for Venezuela to 178 300 km^2 for South Africa (Table 3). South Africa, Morocco and California have large continental shelves (higher than 100 000 km^2) while Spain-Portugal, Senegal, Côte-d'Ivoire-Ghana or Venezuela have medium to small ones (lower than 60 000 km^2).

The Peruvian and Chilean total pelagic catch productivity are the highest among the others whereas their continental shelf surfaces are of medium sizes (Fig. 2a). On the other hand, the South African and the Moroccan ecosystems have a wide continental shelf and a poor fish productivity compared to the others (Fig. 2b). Thus, areas with a large continental shelf

Upwelling areas	Sardine 'catch productivity' index				Anchovy 'catch productivity' index				Total pelagic 'catch productivity' index			
	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km²/year)	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km²/year)	Time period considered	Mean (t/year)	Maximum (t/year)	Maximum per unit of surface (t/km²/year)
1 California	1924-1990	130919	572661	15 6	1970-1991	141316	310811	141 9	1924-1991	200901	609979	6 0
2 Peru	1978-1993	2068449	3470422	43 4	1960-1993	4486294	12277022	21.6	1958-1993	5299183	12286264	142 0
3 Chile	1978-1993	1528795	2709926	15.5	1962-1993	571572	1350626	4.2	1966-1993	1540109	3708071	59.3
4 Spain-Portugal	1927-1988	161752	241000	5.7	1968-1988	30988	66700	3 1	1937-1989	331839	368893	6 1
5 Morocco	1950-1991	169858	338100	3.9	1965-1991	3552	19124	1.1	1950-1991	192885	362023	3 1
6 Senegal	1974-1991	101008	194693	5.9	—	—	—	—	1964-1991	77234	194693	5.9
7 Côte-d'Ivoire - Ghana	1966-1993	74809	172977	3.2	1966-1993	52007	92988	1.7	1966-1993	7188405	270570	5 0
8 Namibia	1963-1992	371720	1400100	4.0	1963-1990	161996	376000	1.1	1966-1992	507663	1561300	17 3
9 South-Africa	1960-1991	113916	410200	2.9	1969-1992	234752	596000	0 2	1950-1992	274312	623200	3 5
10 Venezuela	1957-1989	38032	80079	4 7	—	—	—	—	1957-1989	38032	80079	4 7
11 India	1956-1989	190523	274772	2 3	1963-1989	35529	79655	3 3	1948-1988	249382	448206	6 4

Table. 2: Fish catch productivity indices of eleven upwelling ecosystems.

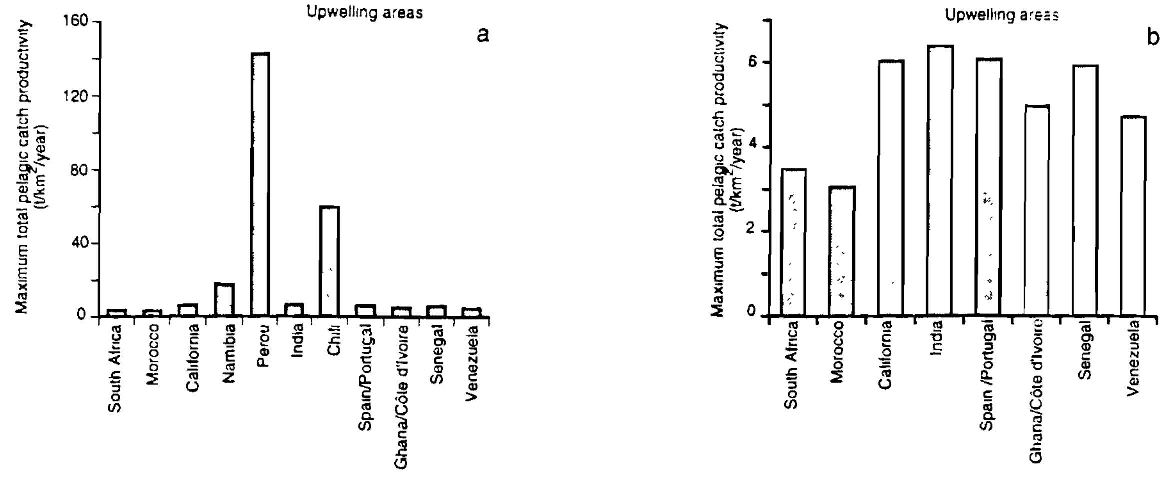

Fig. 2: a) Maximum total pelagic catch productivity per unit of surface (t/km²) for the studied upwelling areas; b) the same as Fig. 2a, but without the Chilean and Peruvian values.

are not necessarily among the most productive. Other environmental variables than surface area undoubtedly play a role in the intrinsic production of upwelling ecosystems.

2. HOW MANY ENVIRONMENTAL FACTORS?

Environmental parameters cause fish population fluctuations mainly through their role in the recruitment process (Parrish and MacCall, 1978; Bakun and Parrish, 1982; Cury and Roy, 1989; Lluch-Belda *et al.*, 1989; Cushing, 1990; Cushing, 1995). Five environmental parameters were selected for the analysis: coastal upwelling index (CUI in $m^3/s/m$) using standard assumptions[1], turbulence index (V^3 in m^3/s^3), sea surface temperature (SST in °C) and continental shelf length or surface (CSl in km and CSs in km^2). The turbulence index was calculated by averaging all the cubed wind measurements. The COADS data (Comprehensive Ocean Atmosphere Data Set) collected by merchant ships of opportunity all around the world oceans were used (Roy and Mendelssohn, this vol.). As they are obtained in a similar fashion in all areas, they are strictly comparable and they also provide a data base which is compatible in time with the fishery data. Mean environmental values were calculated for the different upwelling areas (Table 3). Upwelling index varies from 0.36 $m^3/s/m$ for Spain-Portugal to 1.28 $m^3/s/m$ for Namibia. Three areas exhibit strong upwelling indices: Namibia, Peru and Côte-d'Ivoire-Ghana. Turbulence index varies from 10^3 m^3/s^3 for Côte-d'Ivoire-Ghana to 723 m^3/s^3 for South Africa. A high

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[1] *CUI* = $rCdV^2 / 2\Omega \sin\phi$ *with* V^2 *wind component perpendicular to coast, r air density (0.0012 g.cm*^{3}*),* Ω *angular velocity of earth rotation,* ϕ *latitude, Cd roughness coefficient at interface air/sea.*

		Geographic characteristics				Environmental parameters (mean from 1946 to 1990)		
	Upwellings areas	Latitude	Longitude	Continental shelf		Upw. index	Turbulence	Sea surface
				surface (km^2)	length (km)	(m^3/s/m)	(m^3/s^3)	temperature (°C)
1	California	22°-38°N	—	101167	1778	0,54	654	15,6
2	Peru	5°-18°N	—	86523	1444	1,20	225	19,1
3	Chile	18°N-43°S	—	62516	2778	0,93	346	16,5
4	Spain and Portugal	2°-44°N	5°-9°	59864	1667	0,36	628	16,3
5	Morocco	21°-36°N	2°-0°	118539	1667	0,66	306	19,6
6	Senegal	12°-16°N	—	32887	445	0,59	150	23,7
7	Côte-d'Ivoire - Ghana	2°-8°N	0°-8°	54647	667	1,04	103	27,1
8	Namibia	16°-28°S	—	90508	1334	1,28	517	16,8
9	South-Africa	28°-36°S	—	178315	1778	0,65	723	16,9
10	Venezuela	8°-11°N	62°-65.5°	17000	389	—	332	27,1
11	India	8°-15°N	—	70135	778	0.40	240	28.1

Table 3: Environmental characteristics of the eleven upwelling areas compared in this study.

upwelling intensity is classically associated with a high turbulence intensity (in Namibia and Chile), but sometimes, it corresponds to a moderate turbulence index (in Peru and Côte d'Ivoire-Ghana). In the same way, moderate upwelling indices may be associated with strong turbulence indices (in California, Spain-Portugal, South-Africa). The mean sea surface temperature ranges between 15.6°C for California and 28.1°C for India.

The relationship between fish catch productivity and environmental factors is explored using non-parametric regressive models. Iterative algorithms that extend linear multiple regression analysis to generalized additive models provide a method to explore the relationship between the response and the predictor variables when the form of these relationships are a priori unknown. The non-linearity of the relationships as well as the multiplicity of factors can be considered. The ACE (Alternating Conditional Expectation) and the GAIM (Generalized Additive Interactive Modeling) statistical methods estimate optimal transformations for multiple regressions (Hastie and Tibshirani, 1990).

The usual linear multiple regression model for predicting a response variable Y from p predictor variables X_i, i =1,..., p and for n observations, j = 1,...,n, is given by :

$$Y(j) = \Sigma\, b_i X_i(j) + e(j) \qquad e(j) \text{ are independent}$$

The response variable Y and the predictor variables X1.....Xp in the nonparametric model are replaced by functions $T_1(Y)$ and $T_2(X_1)....T_{p-1}(X_p)$:

$$S(Y(j)) = \Sigma\, b_i T_i(X_i(j)) + w(j)$$

S(Y) and $T_i(X)$ are unknown and estimated by minimizing: $E((T_1(Y) - \Sigma\, T_{i+1}(X_i))^2) / \mathrm{var}(T_1(Y))$

Several approaches exist to estimate the last equation. ACE includes the b_i in the function $T_i()$, while GAIM estimates the b_i's in order to perform analysis of deviance tests on the parameters. GAIM produces an analysis of deviance as well as coordinates for plotting the function estimates and their standard errors. The algorithms converge to optimal solutions for a given criterion as they have their own smoothers and convergence criterion (See Cury *et al.*, 1995 for a detailed application).

A regressive analysis is done using the fish catch productivity index as the response variable and five environmental parameters as predictor variables. The transformation shape is found by plotting the transformed values of a variable versus the original values. Results using the ACE algorithm are presented.

2.1. Maximum total pelagic catch productivity as a response variable

The relationships between fish catch productivity index and every environmental variable are first explored. Optimal transformations (T1,T2) for the multiple regression were calculated using maximum total pelagic catch productivity index as the response variable and the upwelling index, the turbulence index, sea surface temperature and/or continental shelf surface as the predictor.

T1 (maximum total pelagic catch productivity) = T2 (CUI) R^2 : 0.34 (1)
T1 (maximum total pelagic catch productivity) = T2 (V3) R^2 : 0.11 (2)
T1 (maximum total pelagic catch productivity) = T2 (SST) R^2 : 0.49 (3)
T1 (maximum total pelagic catch productivity) = T2 (CSs) R^2 : 0.93 (4)

The transformations for the maximum total pelagic catch productivity are positive and linear in models (1) and (2) (Fig. 3a and 3b) and are close to a log transformation in models (3) and (4) (fig. 3c and 3d). On the whole, the upwelling transformation is linear and positive (fig. 3a). The turbulence is transformed to a nearly dome shaped curve. It first increases to a value around 200 m^3/s^3 then decreases strongly (Fig. 3b). The transformation for the sea surface temperature decreases strongly and linearly (Fig. 3c). The estimated transformation of continental shelf surface is close to logarithmic in form, with a breaking point around 100 000 km^2 (Fig. 3d). The R^2 value for model (4) is very high; however when the response variable is forced to be linear, its value decreases to 0.17.

Multivariate analyses are realized by considering several environmental variables simultaneously in the model. Results which combine three environmental predictors are presented on figures 4 and 5.

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using first maximum total pelagic catch productivity index as the response variable and turbulence, sea surface temperature and upwelling index as predictors in model (5) (Fig. 4) or the upwelling index, the turbulence and the continental shelf surface as the predictors in model (6) (Fig. 5). Thus, we have

T1(maximum total pelagic catch productivity) = T2 (V3) + T3 (SST) + T4 (CUI) R^2 : 0.59 (5)
T1(maximum total pelagic catch productivity) = T2 (CUI) + T3 (V3) + T4 (CSs) R^2 : 0.44 (6)

The response variable transformation is forced to be linear (Fig. 4a). Both transformations of turbulence and of sea surface temperature are linear and negative (Fig. 4b and 4c). On the whole, the upwelling transformation is linear and positive, particularly above a value around 0.7 $m^3/s/m$ (Fig.4d).

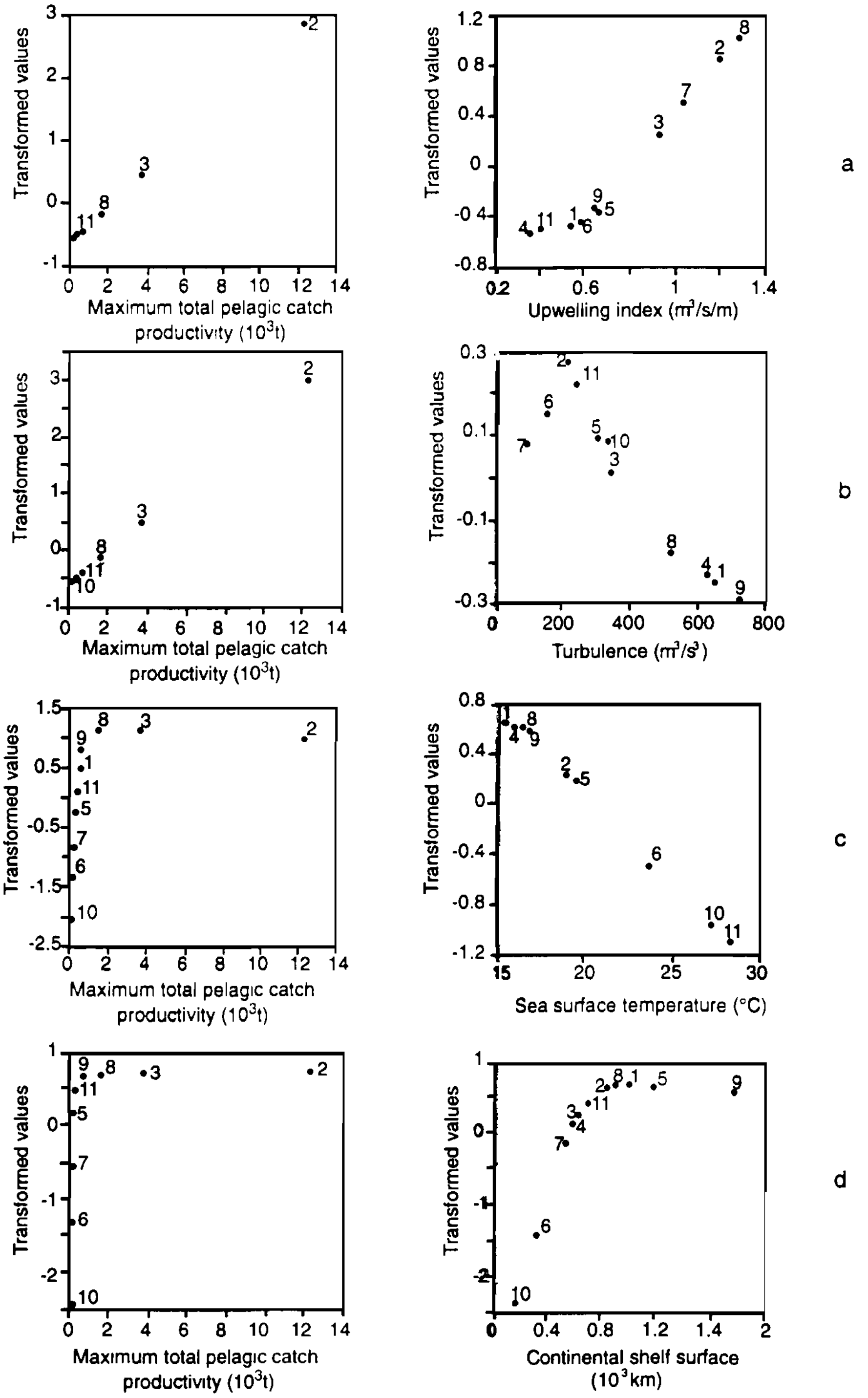


Fig. 3: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence, sea surface temperature and continental shelf surface as the predictor variables. R² values are for figure a: 0.34; b: 0.11; c: 0.49; and d: 0.93. Numbers identify ecosystems (see Tab. 2 and 3).

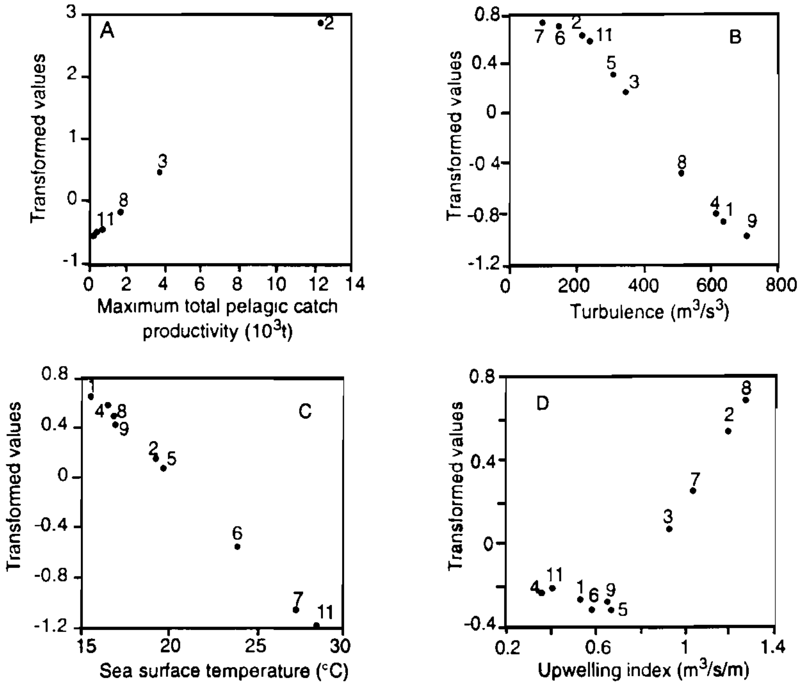


Fig. 4: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and turbulence, upwelling index and sea surface temperature as predictor variables. The transformation of the response variable is forced to be linear. $R^2 = 0.59$. Numbers identify ecosystems (see Tab. 2 and 3).

The productivity index transformation can be forced to be linear (Fig. 5a). Generally, a linear and positive relationship appears between upwelling intensity index and the productivity index (Fig. 5b), particulary above a value around 0.7 $m^3/s/m$. The transformation of the turbulence is dome-shaped with a breaking point around 250 m^3/s^3 (Fig. 5c). The transformation of the continental shelf surface is close to a log transformation Fig. 5d). It first increases, then stabilizes beyond a value around 100 000 km^2.

The transformed value scale gives indication of the relative contributions of the environmental variables to the variance. It indicates a higher contribution either of turbulence and sea surface temperature for model (5) or of upwelling intensity for model (6). The percentage of the observed variance in the total pelagic catch productivity (R^2) are: 59% and 44% for models (5) and (6), respectively.

2.2. Maximum sardine catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using the maximum sardine catch productivity versus upwelling index, turbulence index and sea surface temperature, i.e.,

$$T1\ (\text{maximum sardine catch productivity}) = T2\ (CUI) + T3\ (V3) + T4\ (SST) \quad R^2{:}\ 0.74 \qquad (7)$$

The estimated transformation of maximum sardine catch productivity as well as the transformation of the upwelling index are linear and positive (Figs. 6a and 6b). The turbulence transformation has a flat top then decreases linearly beyond 200 m^3/s^3 (Fig. 6c). The sea surface temperature transformation is strongly negative and linear (Fig. 6d). The resulting model explains 74% of the observed variance of maximum sardine catch productivity.

Fig. 5: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as predictor variables. The transformation of the response variable is forced to be linear. R²= 0.44. Numbers identify ecosystems (see Tab. 2 and 3).

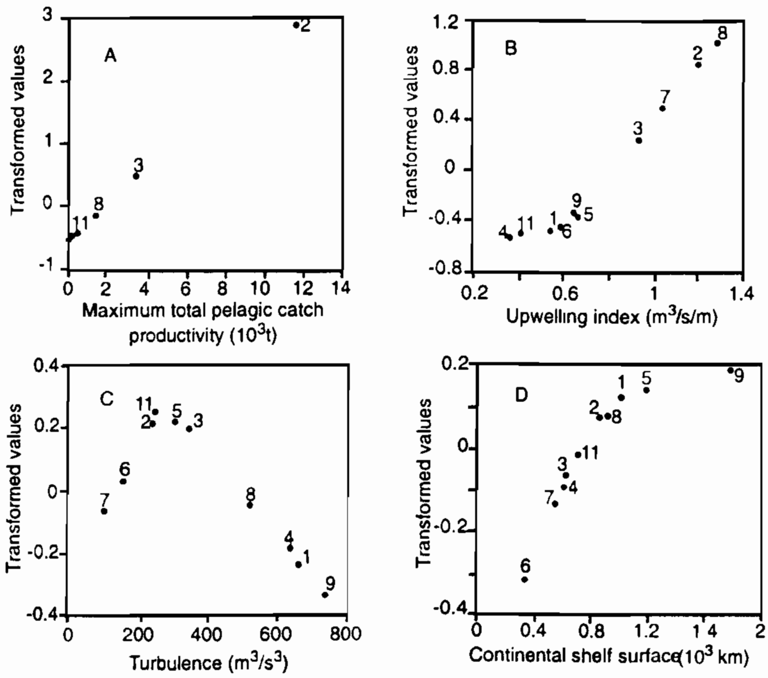
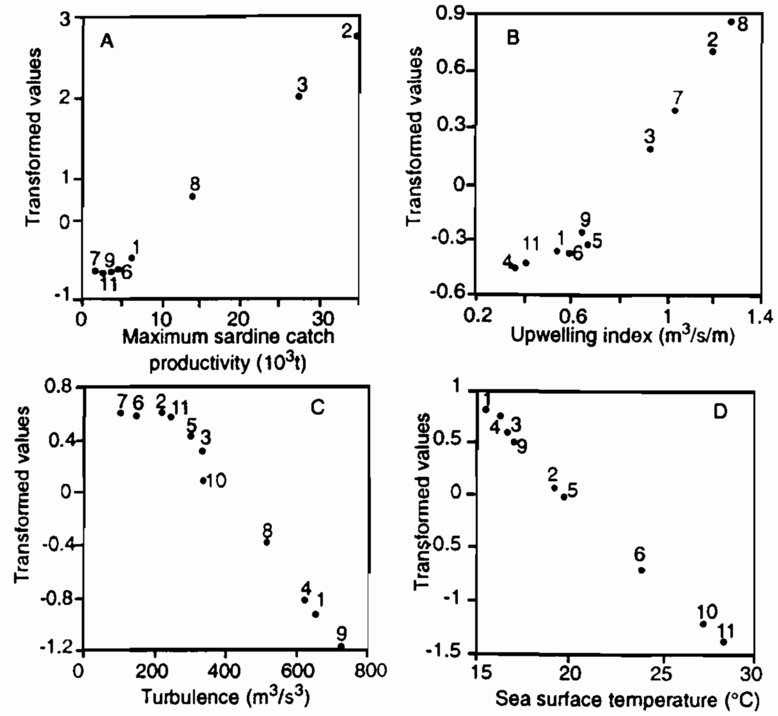


Fig. 6: Optimal empirical transformations from the ACE algorithm using maximum sardine catch productivity as dependent variable and upwelling index, turbulence and sea surface temperature as predictor variables. R²= 0.74. Numbers identify ecosystems (see Tab. 2 and 3).



2.3. Maximum anchovy catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for the multiple regressive model (8) were calculated using the maximum anchovy catch productivity index versus upwelling index, continental shelf surface and turbulence index, i.e.,

T1 (maximum anchovy catch productivity) = T2 (CUI) + T3 (CSs) + T4 (V3) R^2 : 0.40 (8)

The transformation of maximum anchovy catch productivity is forced to be linear (Fig. 7a). The upwelling index transformation is on the whole linear and positive, particularily beyond a value around 0.7 m^3/s/m (Fig. 7b). Continental shelf surface is transformed to a nearly log shaped curve with a breaking point around 100 000 km^2 (Fig. 7c). Turbulence is transformed to a linear and negative transformation (Fig. 7d). The model explains 40% of the observed variance of maximum anchovy catch productivity.

Similar results are found when using continental shelf length instead of its surface. Also, using mean fish catch productivity instead of maximum fish catch productivity indices provide similar results (not shown). Results using the GAIM algorithm instead of the ACE algorithm are similar as well (Fig. 8).

Both monovariate and multivariate analyses suggest similar patterns for the relations among fish catch productivity and environmental variables :

-the transformation of the upwelling index is mostly linear and positive;

-the transformation of the turbulence index is close to be linear and negative particulary after a value around 200-250 m^3/s^3.

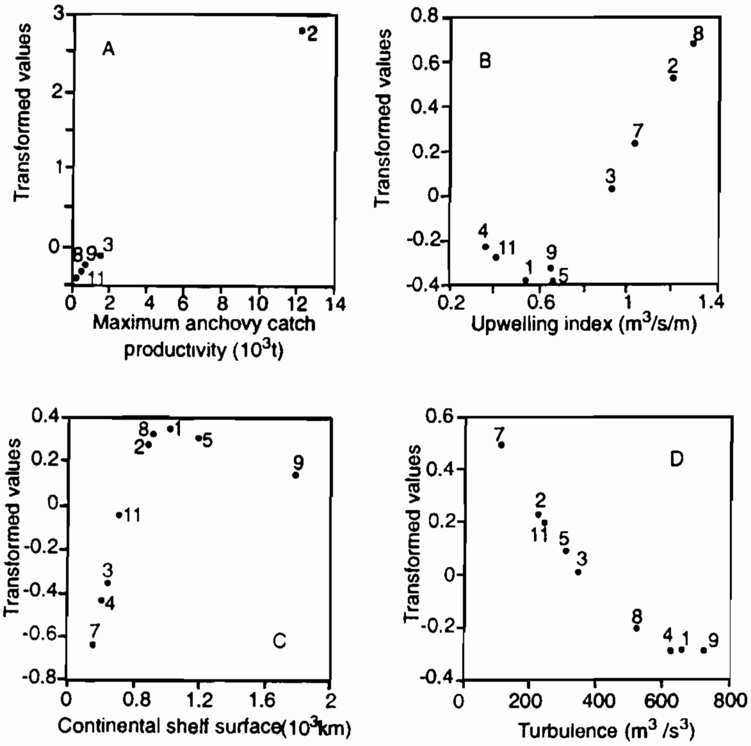


Fig. 7: Optimal empirical transformations from the ACE algorithm using maximum anchovy catch productivity as dependent variable and upwelling index, continental shelf surface and turbulence as predictor variables. The transformation of the response variable is forced to be linear. R^2 value is 0.4. Numbers identify ecosystems (see Tab. 2 and 3).

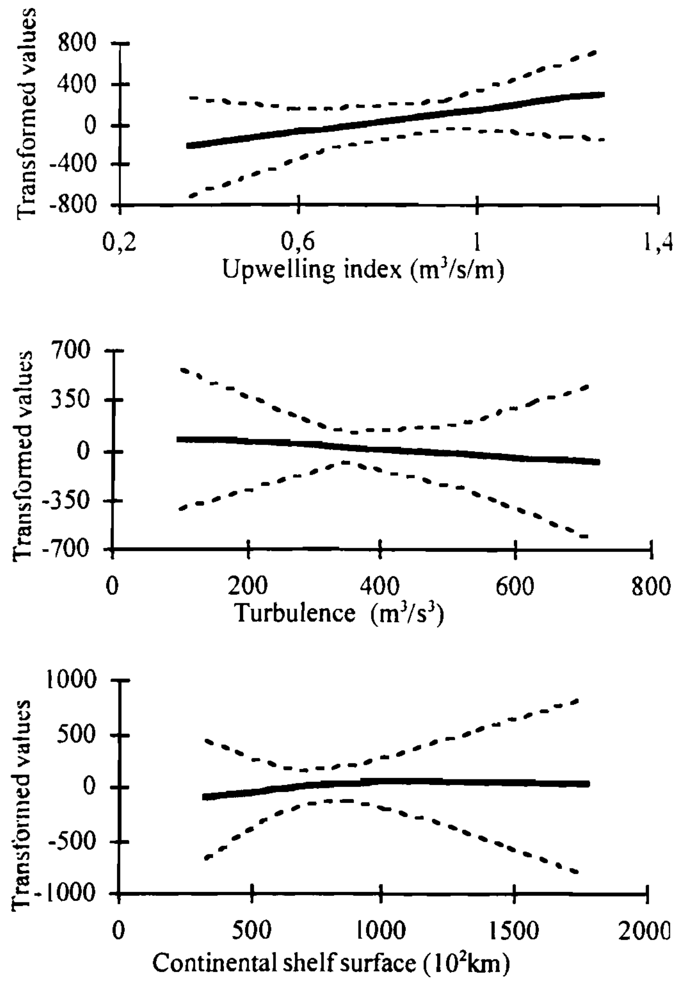


Fig. 8: Optimal empirical transformations from the GAIM algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as the predictor variables. The dashed lines indicates the lower and the upper standard error curves. R2= 0.36.

- the transformation of sea surface temperature is linear and negative; and
- the transformation of continental shelf surface is close to a log transformation with a breaking point around 100 000 km^2.

The comparative and exploratory analysis of the relationship among estimates of fish productivity and environmental features of upwelling systems reveals that a combination of several factors is necessary for high productivity:

- a high upwelling intensity (near to 1.28 $m^3/s/m$);
- a moderate turbulence (around 200-250 m^3/s^3);
- a medium sea surface temperature (15-16°C);
- a relatively large continental shelf (approximately 100 000 km^2).

The results of our statistical analysis must be considered with caution, however, as important limitations do exist:

- the comparisons are based on only eleven data points, and consequently, the statistical validity of the results is questionable due to the low number of degrees of freedom;
- one system with extreme values (Peru) plays an important role in all analyses.

This represents important limitation in our comparative analysis. However, it is also true that:

- the number of ecosystems with a documented pelagic fisheries and for which environmental data exist are limited; and
- the number of environmental factors which have been hypothesized impact on productivity is large compared to the number of ecosystems that can be compared.

Nevertheless, the present analysis gives some valuable information and cues. First, it appears that the size of the ecosystem is not the only parameter that influences its fish catches. Upwelling strength, turbulence, and sea surface temperature also play an important role. Only a combination of several environmental factors ensure a high fish productivity. The relationships between fish catch productivity and environmental variables appears to be in agreement with independent ecological knowledge on ecosystem functioning. High upwelling intensities as source of food availability (Wroblewski and Richman, 1987; Cushing, 1990) and small-scale turbulences that increase the encounter rate between food particles and larvae (Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991) are thought to be beneficial to larval survival. The positive relationship between upwelling intensity and fish catch productivity could be related to these combined effects. In contrast, intense wind-driven turbulent mixing that mixes up patches of larval food appears to be detrimental (Lasker, 1975; Peterman and Bradford, 1987; Cury and Roy, 1989). Bakun (this vol.) identified a 'fundamental triad' of three major processes that combine to yield favorable environmental conditions for fishes: an enrichment process (upwelling, mixing...), a concentration process (water column stability, convergence...) and processes favoring retention within appropriate habitat. In some degree, the environmental parameters we selected may be considered as proxy variables that account for some of the processes involved in such triad. For example, the size of the ecosystem combined with upwelling intensity determines global enrichment of the ecosystem while turbulence is involved in processes that concentrate and retain food and larvae.

A comparison of the environmental values of the upwelling areas with the 'optimal environmental values' is presented on Figure 9 and the limiting factor(s) to productivity are identified (Table 4).

First, it is apparent that the Peruvian ecosystem is the only one which combines all the optimal environmental conditions (Fig. 9). In Chile and Namibia, the upwelling index is favorable; however, it is associated with an excessively high turbulence index. The same high upwelling index is found off Côte d'Ivoire-Ghana, but is associated with low turbulence. In South Africa, Spain and California, the turbulence index is high and associated with a low upwelling intensity, therefore limiting productivity.

In every upwelling areas, except Peru, at least one environmental condition differs from the 'optimal conditions' and consequently tends to limit productivity. But what will happen under changes of one or several environmental factors?

The effect of a gradual or a rapid climatic change on living marine resources is a challenge as numerous parameters are involved. There is no reliable computer-generated climate impact scenario about the next several decade, but generalizations derived from case-to-case assessments of past and present experiences can be used (Glantz, 1992). Such assessments can indeed provide first approximations on how fisheries might respond to environmental changes. Comparative analysis constitutes a good base of information to begin such assessment of possible impacts of environmental changes on fish productivity. Some scenarios for fish productivity under climatic changes derived from previous studies (Fig. 9) can thus be considered for forecast by analogy (Glantz, 1992). How and how much will productivity evolve if one or several environmental parameters change? Let's assume for example two simple scenarios. First, a drastic increase of upwelling intensity that provides more nutrients would probably improve the fish productivity in major ecosystems. The consequences may be stronger in areas where low upwelling intensity is the main limiting factor: Morocco, Senegal and Venezuela (Table 4). Secondly, under a decrease of the intensity of turbulence, a higher fish productivity may be expected in areas where high turbulence is limiting factor: California, Chile, Spain-Portugal, Morocco, Namibia, South-Africa and Venezuela (Table 4).

The reality is obviously more complex as environmental factors change simultaneously. A scenario involving one environmental parameter is thus only a very simplified view of what might occur under climatic changes. However, a qualitative approach allows to predict the increase or the decrease of the fish productivity and can give some preliminary answers.

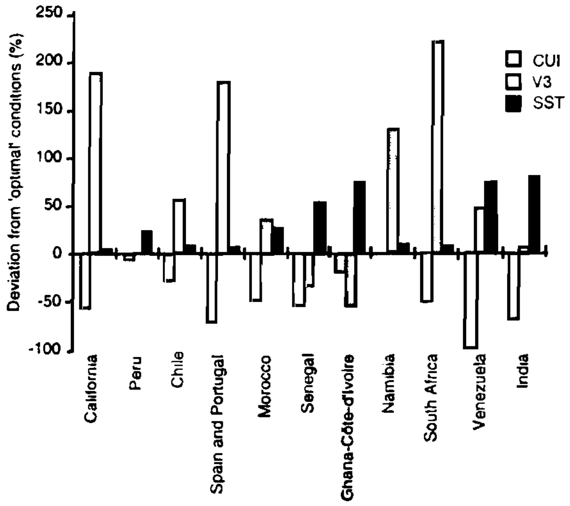


Fig. 9: Relative deviation of the environmental values (%) from the 'optimal environmental values' as defined in the comparative analysis.

Tab. 4: The limiting factor(s) to productivity in upwelling areas. The signs (+ and -) indicate negative or positive deviation from the 'optimal environmental values'. The limiting factors are noted in decreasing order of deviation.

	Upwelling areas	Limiting factors		
1	California	V3 +	CUI -	SST -
2	Peru	SST +	-	-
3	Chile	V3 +	CUI -	-
4	Spain-Portugal	V3 +	CUI -	
5	Morocco	CUI -	V3 +	SST +
6	Senegal	CUI -	SST +	V3 -
7	Côte d'Ivoire - Ghana	SST +	V3 -	CUI -
8	Namibia	V3 +	CUI +	-
9	South Africa	V3 +	CUI -	SST +
10	Venezuela	CUI -	SST +	V3 +
11	India	SST +	CUI -	V3 +

3. OPTIMAL ENVIRONMENTAL CONDITIONS IN THE PERUVIAN ECOSYSTEM: REALITY OR TAUTOLOGY?

It is possible to compare environmental variables in a given upwelling area to what appears to be the optimal environmental conditions. These, however, were largely derived from the Peruvian ecosystem's values. Peters (1991) defines a tautology as "purely logical constructs that describe the implication of given premises and never reveal more than those premises contain". As Peru is known to be the most productive upwelling area, it is clear that using our approach it will define the optimal environmental combination of factors. Thus, our results may be regarded as a tautology of poor scientific value. However, our comparative analysis did provide a framework for considering the relative impact of several environmental factors on fish productivity. It emphasized the importance of limiting factors such as turbulence, upwelling intensity or size of the ecosystem. This should promote new insights of how to relate environmental variables to fish productivity in a multivariate context. Paleoecological studies reveal that pelagic fish populations experienced large natural fluctuations which were clearly unrelated to fishing pressure and that past abundances in California or in Peru were sometimes much higher than during the last century (Soutar and Isaacs, 1974; De Vries and Pearcy, 1982; Baumgartner *et al.*, 1992). For California, we identified factors that limit fish productivity but whithout any reference point; this was not possible for Peru. This stresses the limit of our approach as it may be that the Peruvian ecosystem is able to produce even more under other, but still undefined, environmental conditions.

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Clupeoids Reproductive Strategies in Upwelling Areas: a Tentative Generalization

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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 $0.2\text{-}0.3\ m^3/s/m$). 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

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	A̲	M̲	J̲							Ahlstrom (1960), Rosa and Laevastu (1960), Ahlstrom (1967), Parrish *et al* (1981, 1983).
Baja California (26-30°N)								A̲	S̲				Ahlstrom (1967).
CANARY CURRENT ***Sardina pilchardus***													
Spain, Bay of Biscay			M̲	A̲	M̲								Wyatt and Pérez-Gandaras (1989), Sola (1987), Lago de Lanzos *et al.* (1988), Sola *et al.* (1992).
Portugal (37-41°N)	J̲	F̲	M̲								N	D̲	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)	J̲	F										D̲	Fumestin and Fumestin (1959), Parrish *et al.* (1983), Domanevsky and Barkova (1976), FAO (1985).
Western Sahara (22-26°N)			M	A	M					O̲	N̲	D̲	
HUMBOLDT CURRENT ***Sardinops sagax***													
Peru (6-14°S)	J	F					J̲	A̲	S̲	O			Sharp (1980), Parrish *et al* (1983), Muck *et al.* (1987).
Chile, Arica (18-24°S)							J̲	A̲	S̲	O			Parrish *et al* (1983).
BENGUELA CURRENT ***Sardinops ocellatus***													
Walvis Bay (20-24°S)	J̲	F̲	M̲						S	O	N		Matthews (1960), Parrish *et al.* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°S)	J̲	F̲							S̲	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)							J̲	A̲	S̲				Conand (1977), Boëly *et al.* (1982), Fréon (1988).
Southern Senegal (12-15°N)					M̲	J̲				O	N		Conand (1977), Boëly *et al.* (1982), Fréon (1988).
INDIA ***Sardinella longiceps***													
Malabar Coast (8-16°N)						J	J̲	A̲	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)		F̲	M̲	A̲									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	M̲	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)						J̲	J̲	A̲					Fumestin and Fumestin (1959).
HUMBOLDT CURRENT ***Engraulis ringens***													
Peru (6-14°S)		F	M					A̲	S̲	O̲			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	A̲	S	O			Parrish *et al* (1983).
BENGUELA CURRENT ***Engraulis capensis***													
Walvis Bay (20-24°S)	J̲	F̲	M̲									D̲	Parrish *et al* (1983), Le Clus (1990), Hutchings (1992).
Western Agulhas Bank (34-36°S, 18-20°E)	J̲	F							S	O̲	N̲	D̲	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).

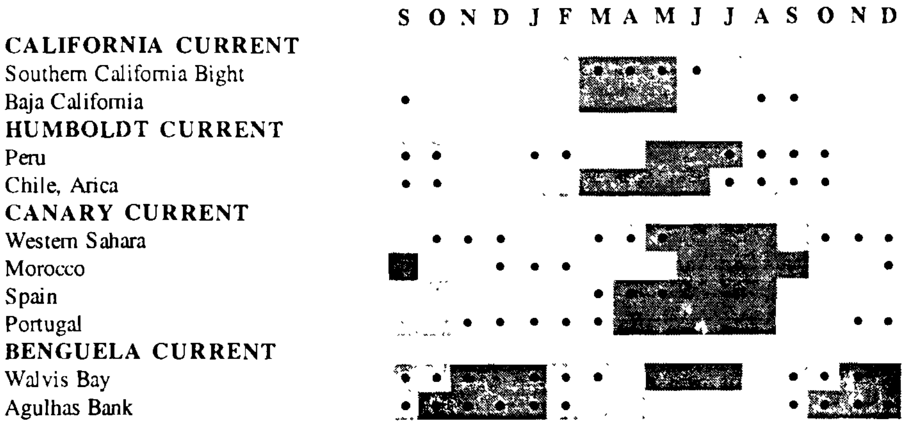

Fig. 1: Temporal relationships between sardines reproduction seasons and upwelling seasons. Spawning periods are represented by black points, upwelling seasons are in light grey, and upwelling peaks in dark grey (references for upwelling seasons : Cushing, 1971; Chesney and Alonso-Noval, 1989).

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).

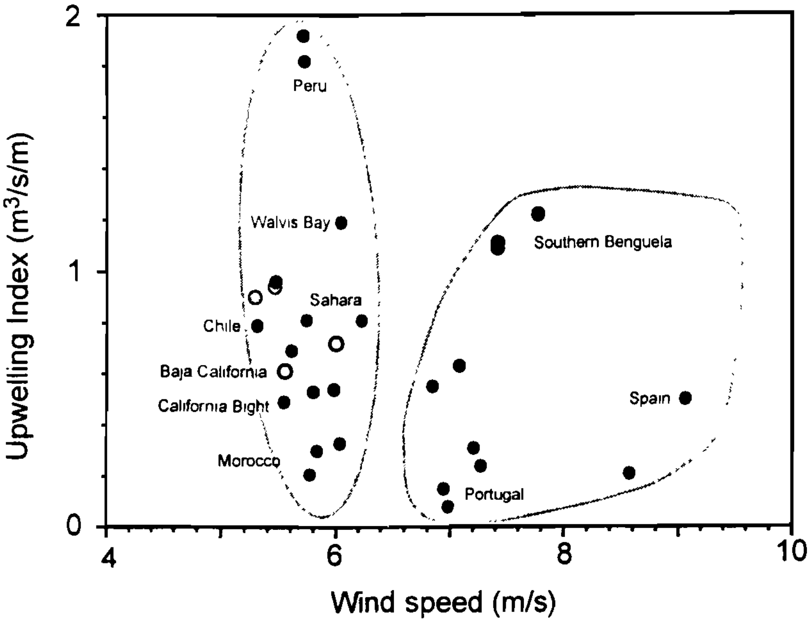

Fig. 2: Plots of spawning peaks of sardines against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

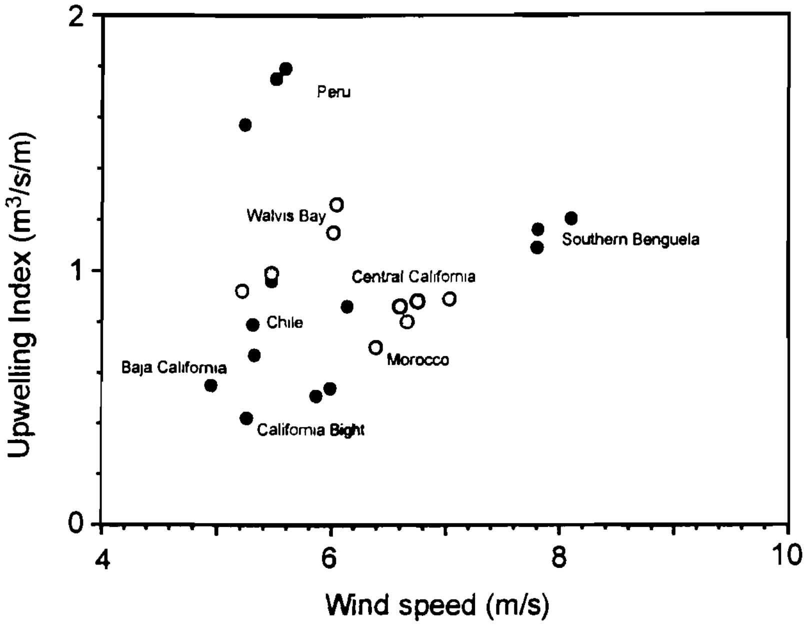

Fig. 3: Plots of spawning peaks of anchovies against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

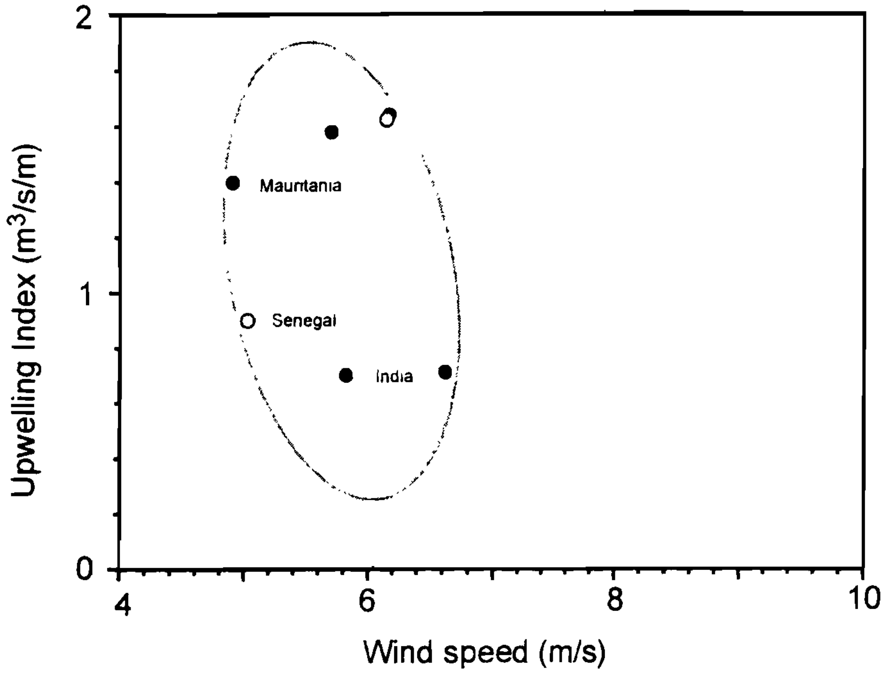

Fig. 4: Plot of spawning peaks of sardinella against monthly means of wind speed and of coastal upwelling index (CUI), by ecosystem.

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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