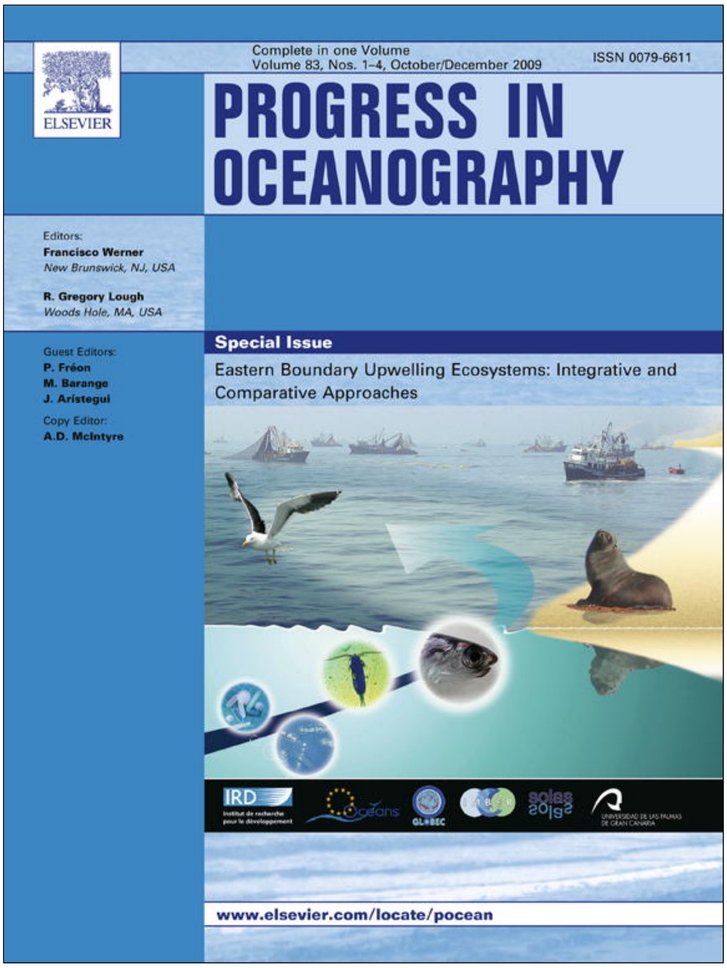
Complete in one Volume
Volume 83, Nos. 1–4, October/December 2009
ISSN 0079-6611
ELSEVIER
PROGRESS IN OCEANOGRAPHY
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Progress in Oceanography 83 (2009) 351–360

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

A surplus production model including environmental effects: Application to the Senegalese white shrimp stocks

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ARTICLE INFO

Article history:
Received 19 July 2008
Received in revised form 24 April 2009
Accepted 16 July 2009
Available online 26 July 2009

ABSTRACT

In Senegal, two stocks of white shrimp (*Penaeus notialis*) are intensively exploited, one in the north and another in the south. We used surplus production models including environmental effects to analyse their changes in abundance over the past 10 years and to estimate their Maximum Sustainable Yield (MSY) and the related fishing effort (E_{MSY}). First, yearly abundance indices were estimated from commercial statistics using GLM techniques. Then, two environmental indices were alternatively tested in the model: the coastal upwelling intensity from wind speeds provided by the SeaWifs database and the primary production derived from satellite infrared images of chlorophyll a. Models were fitted, with or without the environmental effect, to the 1996–2005 time series. They express stock abundance and catches as functions of the fishing effort and the environmental index (when considered).

For the northern stock, fishing effort and abundance fluctuate over the period without any clear trends. The model based on the upwelling index explains 64.9% of the year-to-year variability. It shows that the stock was slightly overexploited in 2002–2003 and is now close to full exploitation. Stock abundance strongly depends on environmental conditions; consequently, the MSY estimate varies from 300 to 900 tons according to the upwelling intensity. For the southern stock, fishing effort has strongly increased over the past 10 years, while abundance has been reduced 4-fold. The environment has a significant effect on abundance but only explains a small part of the year-to-year variability. The best fit is obtained using the primary production index ($R^2 = 0.75$), and the stock is now significantly overfished regardless of environmental conditions. MSY varies from 1200 to 1800 tons according to environmental conditions. Finally, in northern Senegal, the upwelling is highly variable from year to year and constitutes the major factor determining productivity. In the south, hydrodynamic processes seem to dominate and determine the primary production and the white shrimp stock productivity as well.

1. Introduction

In recent decades, partially due to the extreme overexploitation of many demersal fish stocks (Gascuel et al., 2004), shrimp have become one of the major marine resources for many coastal countries of West Africa. The white shrimp, *Penaeus notialis* (Peres-Farfante, 1967), constitutes the main exploited species. It lives on the muddy ocean floor from the coast to 65 m depth, but for the first three months, juveniles grow in estuaries. In Senegal, two stocks have been identified, the north one around Saint-Louis and the Roxo-Bijagos stock in the south (Fig. 1). Exploitation by specialised trawlers targeting shrimp during their marine phase has developed since the end of the 1960s (Lhomme, 1981; Caverivière and Thiam, 2004). Catch statistics are available starting from 1996 and indicate that the harvest from the southern stock has decreased over the last decade (from 1740 t in 1996 to 685 t in 2005), while catches from the northern stock have fluctuated between 300 and 900 t/year without any clear trend. Shrimp exploitation also occurs in estuarine waters, where juveniles are targeted; catches in the three main estuaries, Sine Saloum, Gambia and Casamance, are estimated at around 550 t/year (Laë et al., 2004).

Obviously, fishing efforts impact these stocks' abundance, and the first aim of this paper is to evaluate the status of the two stocks relative to the fishing effects. At the same time, however, shrimp distribution and abundance are strongly influenced by environmental conditions (Caverivière and Rabarison, 1997; Lhomme, 2001; Caverivière et al., 2008). The life cycle of shrimp is very short – the maximal longevity is equal to 20 months (Lhomme, 1981) – and recruitment is usually considered highly dependent on the upwelling intensity. As a result, shrimp stocks present rapid and unstable dynamics, and their potential for production varies widely from year to year. This natural variability may mask, at least partially, the impact of fishing, and modelling the stocks' dynamics

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doi:10.1016/j.pocean.2009.07.024

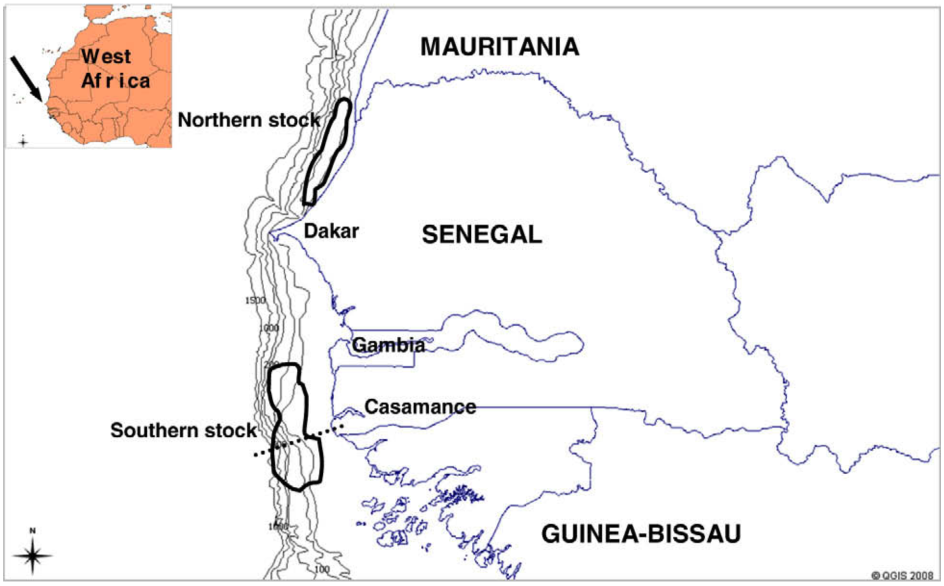

Fig. 1. Localisation of the white shrimp fishing grounds in Senegalese waters.

is challenging. In particular, the usual stock assessment models must be adapted in order to take into account both the fishing impact and the environmental effects.

In the present paper, we only considered the marine phase of the life cycle, treating the arrival of shrimp from estuaries on sea coastal bottoms as the recruitment process into the stock. We analysed changes in the abundance of the two Senegalese stocks using a surplus production model, including an additional effect of the environment (Freon, 1991). More precisely, the model is used: (i) to test the ability of two environmental parameters (the upwelling index and the primary production index) to explain changes in stock abundance; (ii) to understand and quantify the respective effects of fishing and environmental conditions on the abundance of the Senegalese shrimp stocks; and (iii) to establish a diagnosis of the stocks' status and to estimate MSYs depending on environmental conditions. The results are finally discussed from both an ecological and fisheries management perspective.

2. Materials and methods

2.1. Data collection

Data on early catches of each of the two stocks were provided by the Centre of Oceanographic Research of Dakar-Thiaroye (CRODT). Fishing effort data (in fishing days) and details of catches by month and by boat were collected from SOPASEN (Société de Pêche et d'Armements Sénégalais) for the period of January 1996–December 2005. This database covers the Senegalese industrial trawlers, which operate from January to December using a bottom trawl called the "Drezen" (headline length between 16 and 32 m) with a fishing power between 120 and 500 CV. Data include specifications of the trawlers (horsepower of the engines, length of the boat and gross tonnage) and details on fishing operations (fishing date, number of fishing days, fishing area).

Two marine environmental indices were computed:

The coastal upwelling index (CUI expressed in $m^3/s/m$) is deduced from wind speed data obtained from the website of the NOAA Environmental Research Division (ERD, Upwelling and Environmental Index Products, http://www.pfeg.noaa.gov). It is calculated according to Ekman's theory of transport of masses of surface water by wind in the north or northeast direction and rotation of the earth. The series of monthly indices contains data from January 1967 till March 2007, with two points corresponding to the shrimp stock areas (12.5 N–18 W and 15.5 N–17 W).

The primary production index (PPI) is derived from satellite infrared images of chlorophyll downloaded from the NASA website (http://daac.gsfc.nasa.gov) as monthly averages. Chlorophyll *a* concentration data come from historical data of the sensor SeaWifs. The average spatial resolution of the data was 4.5 km, and monthly images of surface chlorophyll *a* concentration were generated by simple averaging, similar to Demarcq et al. (2003). The primary production index reflects the monthly mean concentration of chlorophyll *a* (mg/m^3) between the coast and the line where concentration is 1 mg/m^3. Data are available between September 1997 and November 2005 and cover the entire western African zone (10°N–36°N).

For both indices, averages per year were calculated as input variables for the stock modelling (Fig. 2).

2.2. Abundance indices

Based on detailed data from Senegalese industrial trawlers, mean CPUEs, expressed in kg of white shrimp per fishing day, were calculated per boat, fishing area, year and month. The resulting CPUEs were used as input data to estimate abundance indices using Generalised Linear Model (GLM) statistical techniques. Based on their engine power, boats were placed in categories referred to as "engine power-classes". The CPUE is the response variable of the model, and the dependent factors are: the year, the month, the fishing area and the engine power-class of the fishing boats. White shrimp can be off-loaded in almost every tide, and occurrence of this species in the catches is therefore close to 1. Hence, a Gaussian model is used to estimate the annual abundance indices. The model is expressed as follows:

$$\ln \mathrm{CPUE}_{y,m,z,i} = \ln A_{y,z} + \ln d_m + \ln P_f + \ln \varepsilon_{y,m,z,f}$$

where $\mathrm{CPUE}_{y,m,z,i}$ is the catch per unit of effort of the year *y*, the month *m*, the area *z* and boat *i* (belonging to the engine power-class

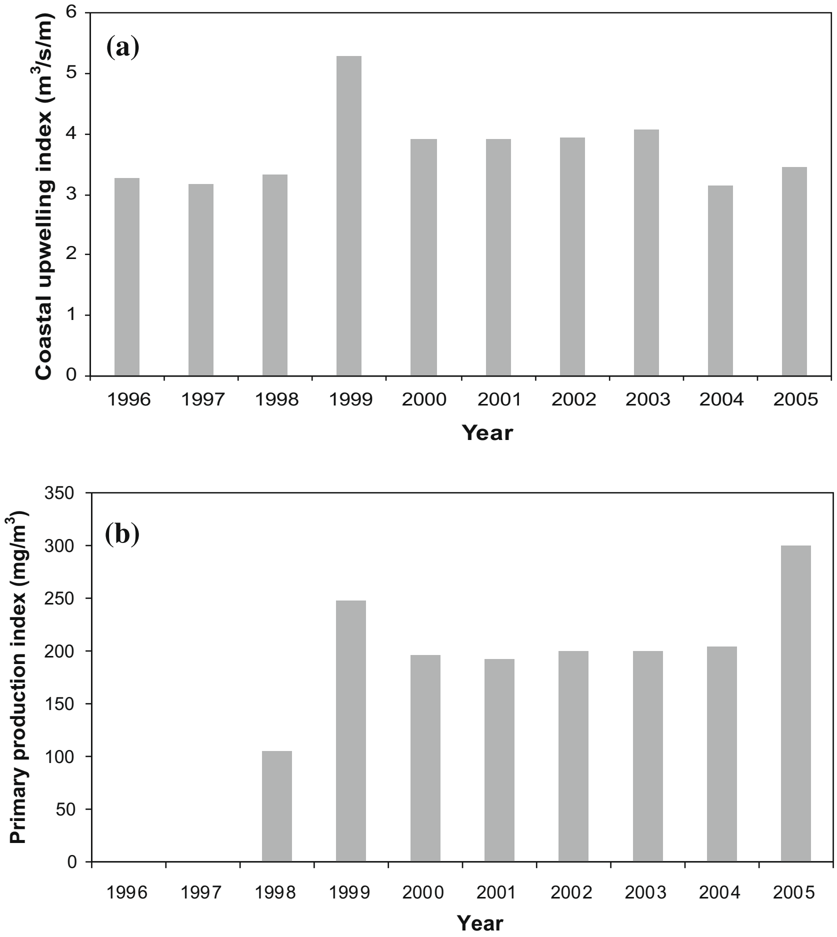

Fig. 2. Environmental indices used in the models: (a) coastal upwelling (northern stock) and (b) primary production (southern stock).

f), $A_{y,z}$ is the combined statistical effect of year and area, d_m is the month effect, P_f is the engine power-class effect, and $\varepsilon_{y,m,z,f}$ is the normally distributed residual. $A_{y,z}$ can be interpreted as an annual abundance index by fishing area under the assumption of a constant year-to-year seasonality of CPUEs and a constant fishing efficiency per engine power-class. Conversely, such an index is not biased by changes in spatial fishing patterns or by an increase in the engines' power.

The GLM models were fitted by using a negative log-likelihood loss function. The Akaike Information Criterion (AIC; Akaike, 1974) was calculated to measure the goodness of fit, with low values representing the best compromise between the model and the observed data. Statistical analyses were carried out using R software (version 2.5.0). To fit the distribution of residuals, a Gaussian error model was the most appropriate according to goodness of fit values for various statistical models. In GLM modelling, it was assumed that the response variable (CPUE) follows a Gaussian distribution, which is normally appropriate for describing spatial heterogeneity and abundance data (Swartzman et al., 1992; Maravelias, 1997; Bellido et al., 2001).

2.3. Surplus production model including an environmental variable

Surplus production models are simple and common models often used for stock assessment purposes. The surplus production is the biomass that can be harvested each year from a population without changing the population abundance. Surplus production models assume that a population's capacity to increase is a function of population density and that population density will not change if members are removed at the same rate as the population's capacity to increase (Jensen, 2005). In such models, the abundance of the stock is expressed as a function of the fishing effort. The model including the effect of environment, proposed by Freon (1991), is derived from a typical surplus production model but expresses the abundance of the stock as a function of two variables: the fishing effort and an environmental index.

In the present study, we used the abundance index (AI) derived from the CPUE of the Senegalese industrial trawlers as a measure of the relative abundance of the stock. We alternatively tested the effects of two environmental indices, CUI and PPI. The fishing effort (mE) was expressed as a multiplier of the theoretical fishing efforts of the most recent year, 2005; it was calculated from the total marine catch (Y) as follows:

$$mE_y = \frac{Y_y}{AI_y} \cdot \frac{AI_{2005}}{Y_{2005}},$$

where y refers to year.

In a preliminary step and for comparison purposes, a simple Fox (1970) model with no environment effect was created. It is expressed as:

$$AI_y = b \times e^{a \times mE_y} \qquad \text{(Model1)}$$

where a and b are parameters.

Then, environmental effects were analysed using two types of models derived from the Fox model (Freon, 1991; Freon et al., 1992). The first corresponds to a linear effect of the environmental index, V.

$$AI = (a + V^b) \times e^{c \times mE_y} \quad \text{(Model2)}$$

where a, b and c are parameters.

The second corresponds to a non-linear effect.

$$AI = (a \times V^b) \times e^{c \times mE_y} \quad \text{(Model3)}$$

Models were fitted to the 1996–2005 time series using alternatively CUI and PPI as the environmental index (*V*). Fitting was conducted in Excel based on the maximum likelihood method and assuming a lognormal distribution of residuals (in practise, this is performed by minimising the sum of squares of the log-residuals). Equilibrium curves of abundance and catches as functions of the fishing effort can be drawn for the Freon model using a given value of the environmental index, *V*. We plotted three curves for the mean value, the upper limit and the lower limit of *V*, respectively. The upper and lower limits were defined as the 95% confidence boundaries of the observed range of *V*.

3. Results

3.1. Trends in catches and stock abundance

The total number of trawlers in Senegal decreased considerably from 1996 to 2005; it has decreased almost 3-fold over the past 10 years (Table 1). Annual shrimp landings ranged from 2476 t (metric tons) (in 1996) to 1204 t (in 2005), significantly decreasing over the 1996–2005 period ($R^2 = 0.69$, $p < 0.05$) and especially during the most recent two years (Fig. 3). The decrease mostly affected the southern stock, where landings were reduced to nearly one-third of their 1998 value in 2005 ($R^2 = 0.64$, $p < 0.05$). Conversely, catches from the northern stock exhibited high year-to-year variability but no clear trend ($R^2 = 0.001$, $p > 0.05$).

Regarding the indices of stock abundance, the GLM model explains 52.9% of the deviance observed in the CPUE data set (Table 2). In the model, there is a cross effect between the year and the fishing area; therefore, the two shrimp stocks do not evolve in an identical way in the course of time. The yearly effect explains the largest part of the total deviance (17.0%). The monthly effect is also important and explains 10.1% of the total deviance. This indicates that the shrimp stocks' abundance varies widely between years and seasonally within years.

For the northern stock, the abundance index significantly fluctuates but without any clear trend (Fig. 4). The maximum abundance was observed in 1999–2001 and the minimum in 1997. Annual abundance varied by a factor of four between the years 1997 and 1999. For the southern stock, yearly indices also indicated a high variability in stock abundance but with a very clear decrease over the period. Thus, the abundance has been reduced 4-fold over the past 10 years (Fig. 4).

3.2. Surplus production models

The two Freon models (model 2 and model 3) give similar results. However, in terms of variance explained, the best statistical results are obtained with model 3. Therefore, only the first and third models (including two versions with CUI and PPI, respectively) are presented here for the northern and southern shrimp stocks.

3.2.1. Northern stock

The Fox model only explains 17.7% of the variance observed for the northern stock abundance, while the Freon model based on the upwelling index explains 64.9% of this variance (Table 3). This indicates that the fishing effort alone is not a sufficient parameter to explain changes in the stock abundance over the study period. Including the environmental parameter CUI as an additional dependent parameter significantly improves the model. Additionally, the upwelling index appears to be a better predictor of abundance than the primary production index. Indeed, taking PPI into account with the Freon model allows us to explain only 43.5% of the observed variability in abundance.

Compared to the simple Fox model, the model including the environmental effect of upwelling led to a notably better estimate of abundance in 1999 (Fig. 5a). This year was characterised by a very strong upwelling (see Fig. 2), which may explain the particularly high value of the observed biomass. Equilibrium curves of the predicted abundance (Fig. 5b) highlight the combined effects of fishing effort and the environment. Thus, compared to the virgin state ($mE = 0$), the current level of fishing pressure ($mE = 1$) induces a 2-fold decrease in the predicted stock abundance, whatever the environment. At the same time, the upwelling intensity induces strong changes in the predicted abundance. Thus, for a given fishing effort, abundance indices are multiplied by a factor of three between the lower and upper limits of the upwelling index.

As a consequence, the equilibrium curve of total catch is strongly affected by the upwelling intensity (Fig. 5c). MSY varies from 300 to 900 tons, respectively, for the lower and upper limits of the observed interval of yearly upwelling indices. Nevertheless, for all curves, the stock seems to be close to full exploitation in 2005 and slightly overexploited in 2002–2003. The effect of the environment does not change this diagnosis, and the stock should globally be considered close to full exploitation. The fishing effort resulting in the MSY is estimated at approximately 7000 fishing days (Table 4).

Finally, the predictions of the Freon model using a mean upwelling index (CUI = 3.74) appear very close to those of the simple Fox model. Adding an environmental parameter into the model allows us to explain, at least partially, the variability observed around the mean model. The low catches observed in 1997–1998 may, for instance, be interpreted as the result of a low upwelling index, while the high catches in 1999 relate to the strong upwelling observed that year.

Table 1
Number of trawl vessels and their characteristics from 1996 to 2005 in the Senegal fisheries.

Gross registered tonnage (GRT) class	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
1–24.9	3	3	3	4	3					
25–49.9	21	21	27	21	18					
50–99.9	14	15	24	20	21					
100–149.9	61	60	73	70	76					
150–249.9	90	92	95	81	78					
250–499.9	55	44	68	51	56					
500–999.9	31	29	29	26	29					
1000–1999.9	15	10	12	13	10					
2000–3999.9	3	4	7	4	1					
4000–9999.9	5	5	3	2						
Indeterminate	8	1	9	9		235	241	163	125	119
Total	306	284	350	301	292	235	241	163	125	119

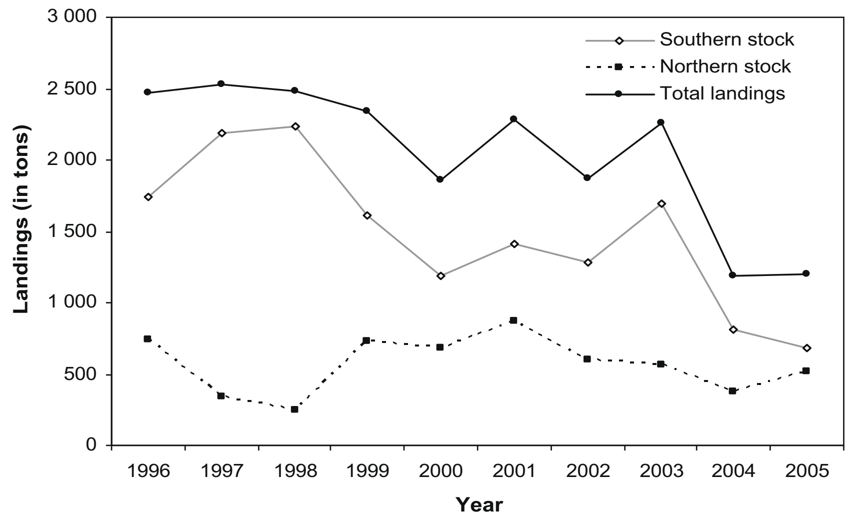

Fig. 3. Catch trends for Senegalese shrimp (*Penaeus notialis*) for the period 1996–2005.

Table 2
Goodness-of-fit statistics for the GLM fitted to *P. notialis* CPUE (variance function: Gaussian; link function: log) deviance; *F* and *P*(*F*) are the values for the last variable included in each model; residual deviance, percentage of deviance explained and AIC (Akaike's information criterion) are the values for the model.

Model	d.f.	Deviance	Deviance residual	Percentage of deviance explained	AIC	*F*	*P*(*F*)
Null	1049		1671.7				
Year	1039	284.43	1387.30	17.01	3296.26	21.30	<0.0001
Year + month	1028	169.4	1217.9	27.15	3181.52	13.00	<0.0001
Year + month + area	1021	152.44	1065.4	36.27	3055.10	20.87	<0.0001
Year + month + area + power-class	1012	133.34	932.1	44.24	2932.72	16.09	<0.0001
Year: area + month + power-class	968	506.77	786.64	52.94	2842.56	10.22	<0.0001

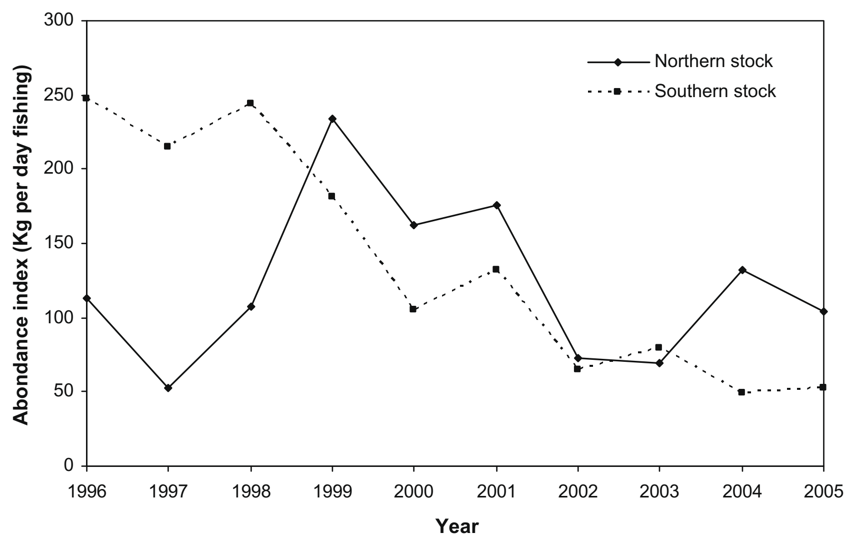

Fig. 4. Abundance indices of *Penaeus notialis* estimated from industrial data for both stocks from 1996 to 2005.

Table 3
Variance explained by the various models: corrected R^2 between observed index of abundance and predictions based on the Fox and Freon models (taking into account either the coastal upwelling index (CUI) or the primary production index (PPI)).

	Northern stock			Southern stock		
	Fox	Freon (CUI)	Freon (PPI)	Fox	Freon (CUI)	Freon (PPI)
Corrected R^2	0.177	0.649	0.435	0.707	0.656	0.752

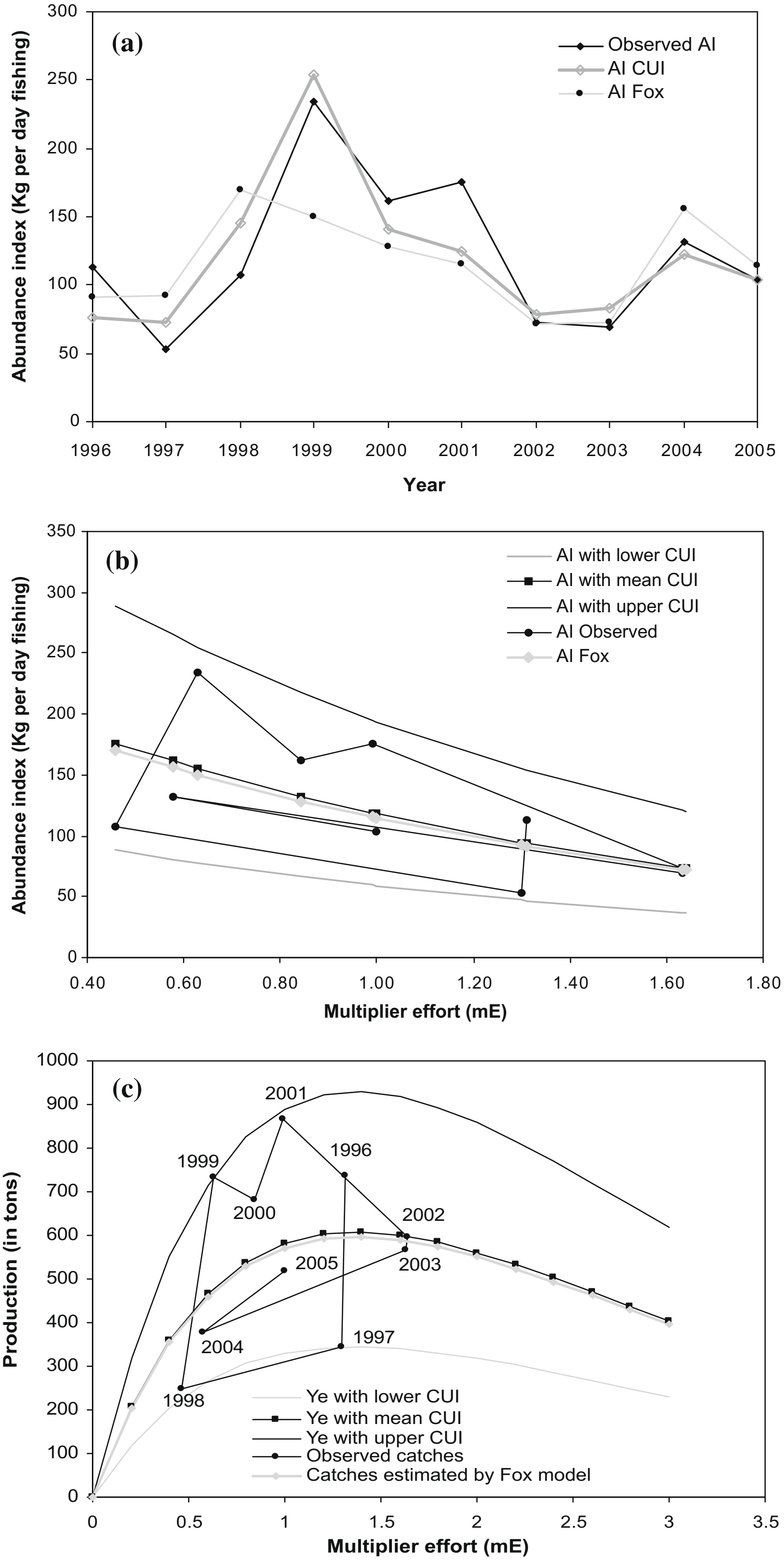

Fig. 5. Northern shrimp stock of Senegal: (a) index of abundance observed and predicted based on Fox model (AI Fox; without environmental effect) or based on the Freon model (AI CUI; taking into account the coastal upwelling index), (b) fitting of the two models to the observed abundance index, (c) Observed catches and catch equilibrium curves predicted by the two models (NB: for (b) and (c), the Freon model is plotted for three values of the upwelling index CUI; see text).

Table 4
Parameter estimates and estimated quantities for the Fox and Freon surplus production models applied to the northern shrimp stock of Senegal.

Parameters	Fox model	Freon model (CUI = 3.74 m^3/s/m)
a	−0.000147	34.59
b	238	1.43
c		−0.73
MSY (in tons)	597	608
mE_{MSY}	1.4	1.4
E_{MSY}	6980	6980
Y_{2005}/MSY	0.87	0.85

3.2.2. Southern stock

For the southern stock, the best fit is observed using the Freon model including the primary production index (PPI; Table 3). Compared with a simple Fox model (without environmental effect), considering the environment slightly improves the prediction; the variance in abundance explained by the model increases from 70.7% to 75.2%. Nevertheless, the environmental effect appears significantly smaller than for the northern stock and is only observed when considering the primary production index and not the upwelling index.

Accordingly, both the Fox and Freon models are able to mimic the decrease in biomass observed during the last 10 years (Fig. 6a). The increase in fishing pressure appears to be the main cause of this decreasing biomass (Fig. 6b), and the current abundance can be estimated at between 10% and 20% of the virgin abundance (from parameters of Table 5 for the Fox and the Freon models, respectively). In other words, exploitation induces a 5- to 10-fold reduction in the southern shrimp stock abundance, whatever the environment. Reciprocally, for a given fishing pressure, changes in the primary production index induce changes in the biomass of only about 20%.

Even if the environment seems to have only a small effect in terms of abundance, it affects the shape of the abundance/fishing effort relationship (Fig. 6b) and therefore the equilibrium catch curve and the related stock status diagnosis (Fig. 6c). Indeed, for the two models with and without the environmental effect, the southern shrimp stock currently appears to be significantly overfished. However, the "degree" of overfishing could be overestimated when the environment is not taken into account. Thus, compared to E_{MSY}, the current surplus in fishing effort (in 2005) is estimated at around 60% based on the simple Fox model and around 40% for the Freon model. Finally, based on the Freon model, the fishing effort E_{MSY} is estimated at around 7800 days, whatever the environment. The MSY varies from 1600 to 1900 tons for the lower and upper values of the observed interval of yearly upwelling indices, respectively.

4. Discussion and conclusions

The shrimp fishery off the coast of Senegal shows marked interannual variability in catches, a phenomenon common to most fisheries of short-lived species and reflecting changes in local abundance (Caverivière et al., 2002). Our analyses represent a first attempt to identify relationships between variability in shrimp landings in both stocks and factors influencing these landings. The results show that the northern stock is still underexploited or fully exploited and that the driving force of abundance, and, consequently, a sustainable catch, seems to be the upwelling intensity. Conversely, the southern stock is strongly overexploited and less affected by environmental variability. In northern Senegal, the seasonal upwelling is highly variable from year to year and constitutes the major factor determining this productivity. In the south, hydrodynamic processes seem to dominate and determine the primary production. As a result, there is a family of curves relating equilibrium yield and biomass. Both the fishing effort and environmental variables were found in previous studies (Lhomme and Garcia, 1984) to impact shrimp catch rates in the west coast trawl fishery of Senegal. The present study has permitted precise description of this phenomenon for both stocks: (1) showing more evidence for it and quantifying its range for the northern stock and (2) suggesting that there is less evidence for such a dynamic for the southern stock.

We can assume that as the environment changes, it affects both the carrying capacity and the rate of stock production (Jensen, 2005). Penaeid recruitment and population dynamics are strongly influenced by a wide range of physical mechanisms that affect the migration of planktonic stages (larvae and postlarvae) from spawning grounds in the open ocean to coastal nursery areas (Garcia and Le Reste, 1986). Several studies have analysed the association between environmental variables and the recruitment of penaeid shrimp. For example, penaeid shrimp are subtropical species whose range extends into warm temperate waters, but temperatures below 18–20 °C are suboptimal for growth (Witzell and Allen, 1982) and may have a measurable effect on production if temperature drops below 20 °C for a large part of the year (Staples et al., 1985). Ramírez-Rodríguez et al. (2003) show that between 1969 and 1994 in the south of the Gulf of Mexico (Campeche Sound), the migration of the shrimp *Farfantepenaeus duorarum* toward the nursery areas was correlated with the rainy season, primary productivity, and oceanic circulation patterns, whereas periods with peak juvenile recruitment in the fishing areas were affected by rain, river runoff, and winds from the north.

In general, penaeid shrimp have a short life cycle, rapid growth, and high rates of natural mortality associated with the early stages of life (Garcia and Le Reste, 1986; Hendrickx, 1995). Survival during the first stages of development is highly associated with abiotic variables (Díaz-Ochoa and Quiñones, 2008) such as salinity or rainfall (Le Reste, 1992, for *Penaeus notialis* in Casamance estuary). In addition, sea surface temperature may regulate both juvenile shrimp growth and adult shrimp yields (e.g., *Penaeus duorarum* off Carolina (USA) during the two coldest weeks in the year: Hettler, 1992). Another important abiotic variable for determining penaeid shrimp abundance is freshwater input (Lhomme, 2001). Rainfall was negatively correlated with *P. notialis* juvenile abundance in the Casamance estuary southeast of Senegal (Le Reste, 1992; Lhomme and Garcia, 1984). In addition, recruitment success has been associated with physical transport mechanisms, such as tides (e.g., Criales et al., 2005 for *Farfantepenaeus duorarum* in Florida Bay, USA) and meander rings (e.g., Criales and Lee, 1995; Criales et al., 2003 also for *F. duorarum* off Florida).

In the present study, we also tested the effect of the river flow (results not shown). For both the northern and the southern stock, we observed no significant correlation between shrimp abundance (using the abundance index, AI, derived from commercial CPUE) and annual variations of the water level in the Saint-Louis River mouth and Casamance River, respectively. The relationship between the river flow and the estuarine abundance of juveniles may be significant, but we did not have the data to test this effect. Conversely, our results demonstrate that marine environmental indices have a significant effect on shrimp stocks at sea.

In northern Senegal, the upwelling intensity appears linked to white shrimp production. A similar relationship was also proposed for the Colombian shrimp fishery, lagged 4–6 months, (Forsbergh, 1969) and in Panama, but the landing statistics are lagged 3 months (Díaz-Ochoa and Quiñones, 2008). The pattern of the environment-penaeid shrimp relationship that emerged from the few studies cited above seems to be consistent with the behaviour found for *P. notialis* in Senegal. White shrimp development seems to be favoured by high contributions of upwelling, precisely in the earlier life stages.

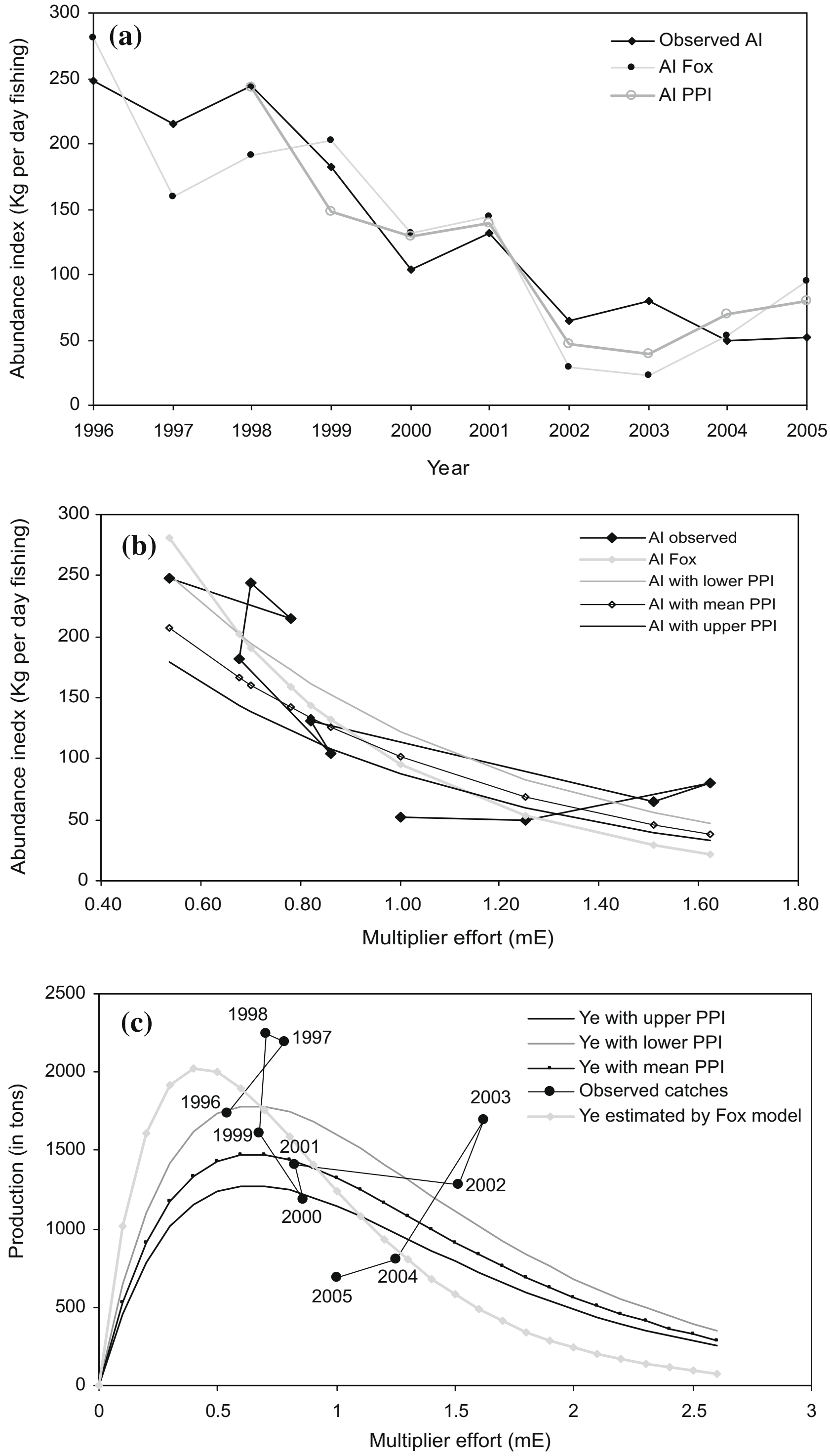

Fig. 6. Southern shrimp stock of Senegal: (a) index of abundance observed and predicted based on Fox model (AI Fox; without environmental effect) or based on the Freon model (AI PPI; taking into account the primary production index), (b) fitting of the two models to the observed abundance index, (c) observed catches and catch equilibrium curves predicted by the two models (NB: for (b) and (c), the Freon model is plotted for three values of the primary production index PPI; see text).

Our results show that the oceanographic conditions for regional circulation around the West African coast associated with global and regional climate regimes can influence the population dynamics of white shrimp. This is especially true for recruitment, which seems to be enhanced during high upwelling intensity periods (in winter). In combination with the effects of fishing exploitation, which results in a decreasing trend in yield of species, this environmental influence could be the basis of interannual fluctuations observed in landings of these and other important resources in the area (e.g., *Sardinella* sp. and *Octopus vulgaris*), most with similar periodicity (Freon et al., 1992; Olivier, 1993; Carbonell et al., 1999; Laurans et al., 2002).

Relationships between the sea level, tides or meander rings and the shrimp abundance for the two stocks were not tested because the environmental data were not available for the study period. Future research on the influence of these factors in the studied areas

Table 5
Parameter estimates and estimated quantities for the Fox and Freon surplus production models applied to the southern shrimp stock of Senegal.

Parameters	Fox model	Freon model (PPI = 205.63 mg/m^3)
a	−2.34	12,570
b	985.9	−0.615
c	–	−1.545
MSY (in tons)	2020	1470
mE_{MSY}	0.4	0.6
E_{MSY}	5225	7840
Y_{2005}/MSY	0.34	0.46

of Senegal is expected to allow description of the associations between recruitment and environmental factors such as nutrient contributions, turbidity and transport (Grimes and Kingsford, 1996). An especially interesting factor to consider for future studies is the transport of surface currents associated with Trade Wind dynamics as well as the role of the tidal currents, which, in other areas, have been shown to play a crucial role in postlarval transport toward the nursery areas (Criales et al., 2005).

The area off the Senegalese coast was described by Roy (1989) as environmentally affected by oceanographic processes such as upwelling during the period from November to May. This upwelling is closely related to atmospheric dynamics determined by the seasonal changes in the direction of Trade Winds associated with the latitudinal migrations of the Inter-Tropical Convergence Zone (ITCZ). In this context, the significant difference, as revealed through our modelling approach, in the observed dynamics of functioning (abundance and production) of the northern and southern stocks is certainly linked to the fact that the Senegalese ecosystem does not constitute a homogeneous system on the two sides of the Cap-Vert peninsula (Roy, 1989).

Another important point is the intensity of resource exploitation in Senegal. The total fishing effort applied to demersal resources, already important in Senegal at the beginning of the 1980s, was increased 2.5-fold (Gascuel et al., 2004), thus causing in the course of the last three decades environmental changes in the composition of the marine populations. In fact, many fish stocks collapsed to the advantage of other species with shorter lifespans, such as octopi and shrimp. For example, it was shown that the fishery had reduced the biomass of emblematic species (Thiof, Pageot) by about a factor of 10 (Gascuel et al., 2004, 2007) and that the trophic structure of the ecosystem has been modified (Laurans et al., 2004). This is one of the essential results drawn from studies conducted by the Fisheries Information and Analysis System project (FIAS) in 2005. Here, we showed that the southern shrimp stock, the larger one, is extremely overexploited. This can be interpreted as a new step in the process of marine resource overexploitation in Senegal.

Acknowledgements

We appreciated the invaluable collaboration of personnel from the CRODT, especially Djiga Thiaw and Modou Thiam, who provided the catch data used in the present study. We thank M. Marec, director of SOPASEN (Société de Pêche et d'Armements Sénégalais), for giving us access to complementary information and data related to this shrimp fishery (SOPASEN fishery statistics between 1996 and 2005). Thanks are also due to Dr Demarcq, IRD (Institut de Recherche pour le Développement) Montpellier (France), who provided us the environmental data.

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