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Analysing environmental and fishing effects on a short-lived species stock: the dynamics of the octopus *Octopus vulgaris* population in Senegalese waters

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Short-lived species are extremely dependent on the seasonal and interannual variability of environmental conditions, and determining their stock status is often difficult. This study investigates the effects of environmental variability and fishing pressure on the stock of octopus *Octopus vulgaris* in Senegalese waters over a 10-year period from 1996 to 2005. Monthly catches-at-age were estimated based on catch-at-weight data and a polymodal decomposition constrained by a given growth curve. Octopus recruitments and fishing mortalities were then estimated using a catch-at-age analysis performed on a monthly basis. Yield and biomass per recruit were simulated using a Thompson and Bell model and used to generate a diagnostic of the fishery's impacts. Results indicate that the high interannual and seasonal variability of the octopus stock biomass is linked to the spring recruitment event, the annual intensity of which was significantly correlated with the coastal upwelling index and sea surface temperature. Yield per recruit varied seasonally but remained almost unchanged from one year to the next. Even when catches vary strongly according to recruitment, the octopus stock appears to be consistently fully exploited, or slightly overexploited in some years. In this context of environmental variability, usual indicators such as the maximum yield per recruit, and the related fishing mortality and spawning potential ratio, remain useful for fisheries management purposes.

Keywords: environment, fishery, indicators, population dynamics, Senegal, stock assessment, West Africa

Introduction

The cephalopod *Octopus vulgaris* (Cuvier 1797) is one of the main demersal fishery resources in the Eastern Central Atlantic. The resource shows marked interannual and seasonal variability in catches (Caverivière et al. 2002), a phenomenon commonly exhibited by most fisheries involving short-lived species, and which reflects changes in local abundance (Wang et al. 2003). In Senegal, the octopus stock has been caught primarily in the south of Dakar, near the fishing port of Mbour (Figure 1). High levels of abundance were first observed during the summer of 1986. Exploitation started that year, and in subsequent years, catches varied considerably, from <5 000 tonnes (t) to 15 000 t, and reaching a peak of nearly 45 000 t during the summer of 1999 (Caverivière et al. 2002, Diallo et al. 2002).

Octopus recruitment is usually highly variable from year to year, and changes in abundance and recruitment between years may be attributed to fluctuations in environmental conditions that affect the early phases of cephalopod populations (Rodhouse et al. 1992, Caverivière et al. 2002, Thiaw 2010). Previous studies have demonstrated the effects of sea surface temperature (SST) and retention processes on recruitment fluctuations in the following cephalopods: *Loligo gahi* in the South Atlantic (Agnew et al. 2000), *Loligo forbesi* in the English Channel (Robin and Denis 1999, Royer et al. 2002, 2006) and *O. vulgaris* along the Galician coast (Otero et al. 2008), on the Saharan Bank (Demarcq and Faure 2000, Faure et al. 2000, Balguerías et al. 2002) and in Senegal (Caverivière and Demarcq 2002, Laurans et al. 2002). In addition, the effect of environmental variability (SST variability) on the abundance of *O. vulgaris* on a seasonal scale was also observed off the Canary Islands (Caballero-Alfonso et al. 2010). As a result, the global octopus stock exhibits rapid and unstable dynamics, and the stock's potential production varies widely from year to year. This natural variability may at least partially mask the impact of fishing. Thus, modelling the impact of the environment and fishing pressures on the dynamics of the octopus stock is challenging.

Based on both catch and environmental data from a 10-year period (1996–2005), the present paper examined the population structure and the influence of environmental changes and fishing pressure on the dynamics of the Senegalese stock of octopus over this period. For this purpose, this study undertook the following investigations:

1. Recruitment, stock size in numbers and fishing mortality of the octopus stock were estimated using a virtual population analysis model (VPA) computed on a monthly resolution step and covered a range of more than 100 monthly cohorts (from January 1996 to December 2005).
2. The VPA estimates (on recruitments and abundances) were used in addition to complementary catch data to explore correlations between the main stock characteristics and selected environmental variables (i.e. variables that potentially influence its dynamics). Statistical analyses were performed to test the ability of the coastal upwelling index (CUI) and SST to explain changes in recruitment or a significant part of the variability observed in population abundance and catches.
3. Estimates of recruitments and fishing mortalities were also used as input data in a Thompson and Bell (1934) simulation model. Monthly age-structured production models were aggregated for each year over the entire data time period, providing a diagnosis of the current status of the octopus stock in Senegal as well as a global assessment of the impact of the fishery on this short-lived resource.

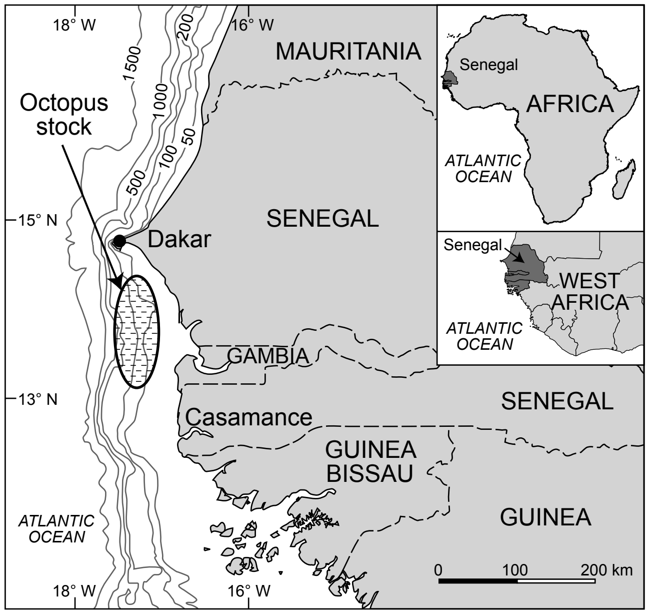

Figure 1: Map showing the location of the main octopus fishing ground in Senegalese waters

Table 1: Weight limits (eviscerated fresh weight) defining Mitsubishi classification for octopus fisheries (Jouffre et al. 2002)

Commercial category	Individual weight (g)
T10	≤200
T9	200–300
T8	300–500
T7	500–800
T6	800–1 200
T5	1 200–1 500
T4	1 500–2 000
T3	2 000–3 000
T2	3 000–4 500
T1	>4 500

Material and methods

Data

Monthly catch-at-weight

The total catch in weight of octopus fished monthly in Senegal were provided by the Oceanographic Research Centre of Dakar-Thiaroye (CRODT, Centre de Recherches Océanographiques de Dakar-Thiaroye) from January 1996 to December 2005, in addition to the catches from artisanal and industrial fisheries for that time period.

Monthly catches-at-weight were deduced from total catch using two datasets. The 'factories sample' was provided by two of the main factories that process fish products in Senegal for both the artisanal and industrial fisheries. This dataset includes the monthly factory production by commercial category according to the Mitsubishi classification (Table 1). This sample represents more than 50% of the total Senegalese catch for octopus, and covers a large area (all octopus landings sites are included) and long periods of time, and is thus considered to be highly representative. It allowed for the estimation of the Senegalese octopus production by month and by commercial category for both the artisanal and the industrial fisheries.

In addition, data from a 'quality control' study performed by representatives of the purchasers were also provided by factories. During this study, catches of octopus sorted into commercial categories were randomly undersampled, and the individual weights of each octopus were determined. These data allowed for the estimation of average weight distributions within each commercial category.

The number of octopus caught in Senegal each month per weight class (per 50 g) was deduced from these samples, adding the catch-at-weight value of the 10 commercial categories.

Biological parameters

Growth parameters, which were required for the conversion of catches-at-weight into catches-at-age (see below), were estimated by Domain et al. (2000), from *in situ* mark-recapture experiments. The following equation was used:

$$W_t = e^{a(t+b)}$$

Table 2: Annual environmental data used in the statistical correlations analysis

Year	CUI ($m^3\ s^{-1}\ m^{-1}$)			SST (°C)		
	Yearly mean	February–April	Mean CUI > 3.5	Yearly mean	March–May	March–April
1996	2.42	4.12	4.14	24.90	22.09	21.21
1997	2.52	4.53	4.53	25.15	21.75	20.98
1998	2.88	5.31	5.45	25.26	22.58	22.42
1999	3.18	7.32	6.33	24.32	21.26	19.89
2000	2.90	5.36	5.30	25.50	23.21	23.08
2001	2.81	5.32	5.10	25.59	23.15	22.22
2002	3.12	6.34	6.24	25.03	20.86	20.55
2003	2.96	6.16	5.79	24.98	22.14	21.29
2004	2.29	3.81	4.51	25.11	22.29	22.14
2005	1.90	3.77	4.52	25.94	23.50	22.70

CUI = coastal upwelling index

where a = 0.0135, b = 290.75, W is the weight (in g) and t is the age in number of days.

The natural mortality (M) was estimated by Jouffre et al. (2002; also described in Jouffre and Caverivière 2005), using the method proposed by Caddy (1996) and assumed a lifespan of close to one year (Domain et al. 2000, Jouffre et al. 2000) and an average fecundity level ranging from 300 000 to 500 000 eggs per laying (see Mangold 1983). Thus, we considered mortality to be 0.25 month^{-1} for the entire exploited phase, from the fifth month to death.

Environmental data

To investigate the effects of environmental conditions on octopus recruitment, two environmental factors were computed. These factors have an important influence on spring and summer primary production and may potentially affect the survival of early life stages (Faure et al. 2000, Caverivière et al. 2002, Gröger et al. 2007, Bartolino et al. 2008) (Table 2):

1. The CUI (expressed in $m^3\ s^{-1}\ m^{-1}$) was deduced from wind speed data obtained from the NOAA Environmental Research Division website (ERD, Upwelling and Environmental Index Products, http://www.pfeg.noaa.gov). The index was calculated according to Ekman's theory of the transportation of masses of surface water by wind in the north or north-east direction, coupled with the rotation of the earth. Monthly mean coastal upwelling indices were calculated for the octopus stock area for the time period January 1967–March 2007.
2. Monthly mean values from remote sensing data on SST for a 20-year period were obtained from the advanced very high resolution radiometer (AVHRR) satellite data at a spatial resolution of 5 km. Data covered the period between January 1985 and December 2005 and included the entire western African zone (10°–36° N).

These two environmental factors were considered to be exploratory variables and were used to determine the environmental index that most effectively measures the coastal upwelling intensity of North-West Africa. Environmental conditions occurring in yearly and seasonal (winter and spring) scales were taken into account because of possible direct and indirect effects on the survival rates of octopus recruits, considering that both larvae and young recruits are abundant in spring (Jouffre et al. 2002). For both environmental indices, annual and monthly averages were calculated as input variables for a correlation analysis between recruitment and upwelling intensity. Averages for two months (March–April), three months (February–April or March–May) and mean CUI higher than 3.5 $m^3\ s^{-1}\ m^{-1}$ were also computed.

Age-based population modelling

Dynamics of the octopus population was modelled using an age-structured approach. Because the octopus is a fast-growing and short-lived species with an exploitation phase of less than one year, the model was structured on a monthly time-scale using ages and catch rates expressed in months (Jouffre et al. 2002, Jouffre and Caverivière 2005). Thus, calculations include 120 monthly cohorts from age 5 months (recruitment) to 14 months during the period 1996–2005. The approach was divided into three main steps.

Catches-at-age estimate

Monthly catches-at-age were deduced from catches-at-weight using a method of polymodal decomposition that included shrinkage (Gascuel 1994a, Chassot et al. 2008). For this approach, we assumed that catches-at-weight for each age group exhibited a normal distribution centred on the mean weight of the age group, constrained using octopus growth curves from Domain et al. (2000). Age groups 5–14+ months were used, where the 14+ age group encompassed catches of the 14-month-old and older animals. The method was applied for each month and resulted in the catches-at-age matrix (see Appendix), used as input for the VPA. Note that, compared to the 'slicing method' previously used by Jouffre et al. (2002), the polymodal decomposition is a clear improvement on the age-based approach for the dynamics of the octopus population. This method takes into account the impact of cohort abundance on the weight-to-age conversion (Gascuel 1994a).

Virtual population analysis (VPA)

A VPA was used to model past stock dynamics and to estimate the input data required by the next stages (simulations and diagnosis), namely monthly recruitment vectors and fishing mortality matrices. Calculations were computed using Excel, and alternatively used three basic equations:

Catch equation

$$C_{t,i} = \frac{F_{t,i}}{F_{t,i}+M} \times N_{t,i} \times (1-e^{-(F_{t,i}+M)})$$

Survival equation

$$N_{t+1,\,i+1} = N_{t,i} \times e^{-(F_{t,i}+M)}$$

Pope approximation of the survival equation (Pope 1972)

$$N_{t,i} = N_{t+1,i+1} \times e^{-M_{t,i}} + C_{t,i} \times e^{-\frac{M_{t,i}}{2}}$$

where i denotes the month, t the age group, C the total catch (in number), F the fishing mortality, M the natural mortality, and N the number of individuals.

For each cohort, calculations were initialised by a terminal fishing mortality referring to the oldest age group (see below). This mortality was used in the catch equation to generate the abundance of the terminal age group, which, in turn, was used in the Pope's equation to estimate the abundance of the preceding age class of the same cohort. Pope's equation was used to generate the abundances of all age classes. Fishing mortalities in each age group were calculated from abundance estimates using the reverse form of the survival equation.

Terminal fishing mortalities for the last age group ($F_{T,i}$) and the last month ($F_{t,I}$) were estimated iteratively (repeating the calculation until stabilisation), initialising the calculations with arbitrary values and then assuming that:

- $F_{T,i}$ is equal to the average fishing mortality of the five oldest age groups (from $F_{9,i}$ to $F_{13,i}$).
- $F_{t,I}$ is equal to the average fishing mortality in December for the three previous fishing seasons, in order to take account the seasonality of the landings (December 2002, December 2003 and December 2004).

Results from the VPA (i.e. estimates of the monthly population numbers at age $N_{t,i}$, including the recruitment $N_{5,i}$), and the weight-at-age estimated by Jouffre et al. (2002), were used to derive values of biomass at age and monthly total stock biomass.

Simulation model and diagnosis

Yield and biomass per recruit models (Thompson and Bell 1934 in Sparre and Venema 1998 and Gascuel 2008) were used to analyse the fishing impact on the octopus stock. Input data included the matrix of fishing mortalities-at-ages $F_{t,i}$ and the vector of monthly recruitments R_i estimated over the period 1996–2005 from the VPA, the vector of stock numbers at age N_t estimated from the VPA for the first month of simulation (January 1996), the mean individual weights at age W_t estimated by Jouffre et al. (2002), and the natural mortality M.

For each monthly cohort, diagnoses were created taking into account constant exploitation (no changes in relative fishing mortalities at age) using multipliers of monthly fishing mortalities ranging from 0 (no fishing) to 2 (multiplier mF = 1, corresponding to the current fishing effort). The yield per recruit (Y/R) and biomass per recruit (B/R) were estimated using the following equations:

$$\mathrm{Y/R} = \sum_{t=5}^{T-1} \left(\overline{W_t} \cdot \frac{\mathrm{mF}\cdot F_t}{\mathrm{mF}\cdot F_t + M} \cdot \left(1 - e^{-(\mathrm{mF}\cdot F_t + M)}\right) \cdot e^{-\sum_{i=5}^{t-1}(\mathrm{mF}\cdot F_i + M)} \right) + \overline{W_T} \cdot \frac{\mathrm{mF}\cdot F_T}{\mathrm{mF}\cdot F_T + M} \cdot e^{-\sum_{i=5}^{T-1}(\mathrm{mF}\cdot F_t + M)}$$

$$\mathrm{B/R} = \sum_{t=5}^{T} \overline{W_t} \cdot e^{-\sum_{i=5}^{t-1} \mathrm{mF}\cdot F_t + M} \cdot \frac{1 - e^{-(\mathrm{mF}\cdot F_t + M)}}{mF \cdot F_t + M}$$

Animals older than 13 months were assumed to be mature. Thus, the equation for spawning stock biomass per recruit (SSB/R) is:

$$\mathrm{SSB/R} = \sum_{t=13}^{T} \overline{W_t} \cdot e^{-\sum_{i=5}^{t-1} \mathrm{mF}\cdot F_i + M} \cdot \frac{1 - e^{-(\mathrm{mF}\cdot F_t + M)}}{\mathrm{mF}\cdot F_t + M}$$

The spawning potential ratio (SPR) is the SSB/R at a given fishing mortality divided by the SSB/R without fishing mF = 0 (Beverton and Holt 1957 in Gascuel 2008):

$$\mathrm{SPR} = \frac{\mathrm{SSB/R}}{(\mathrm{SSB/R})_{\mathrm{mF=0}}}$$

Yield per recruit, biomass per recruit and the spawning potential ratio calculated for the 12 monthly cohorts of the same year (i.e. whose recruitment at age 5 month occurs during the same year) were summed to obtain a diagnosis of the exploitation of each yearly cohort between 1996 and 2005. Finally, the following reference points were used to characterise the status of the stock: $F_{25\%}$, the mean fishing mortality rate F from age 9 to 13 months that corresponds to the point where SPR is equals to 25% of the virgin $(\mathrm{SSB/R})_{\mathrm{mF=0}}$; F_{max}, the mean fishing mortality (from 9 to 13 months) that produced the maximum yield per recruit; and Y/R_{max} and the spawning potential ratio, SPR_{max}. These reference points are generally accepted indicators and are therefore useful for fisheries management purposes.

Results

Stock dynamics

The commercial catch of common octopus varied between years and seasons (Figure 2). The monthly average number of octopus caught over the period was 1.4 million, with a high coefficient of variation of 207% (minimum = 0.01 million in November 2001 and maximum = 21.3 million in August 1999). There was no clear trend in the catches, but a clear seasonal pattern emerged with higher catches observed during summer. In summer, 10 monthly age classes were being exploited simultaneously. This structure illustrates the species' short life cycle, resulting in an exploitation phase of less than one year. The octopus life cycle is characterised

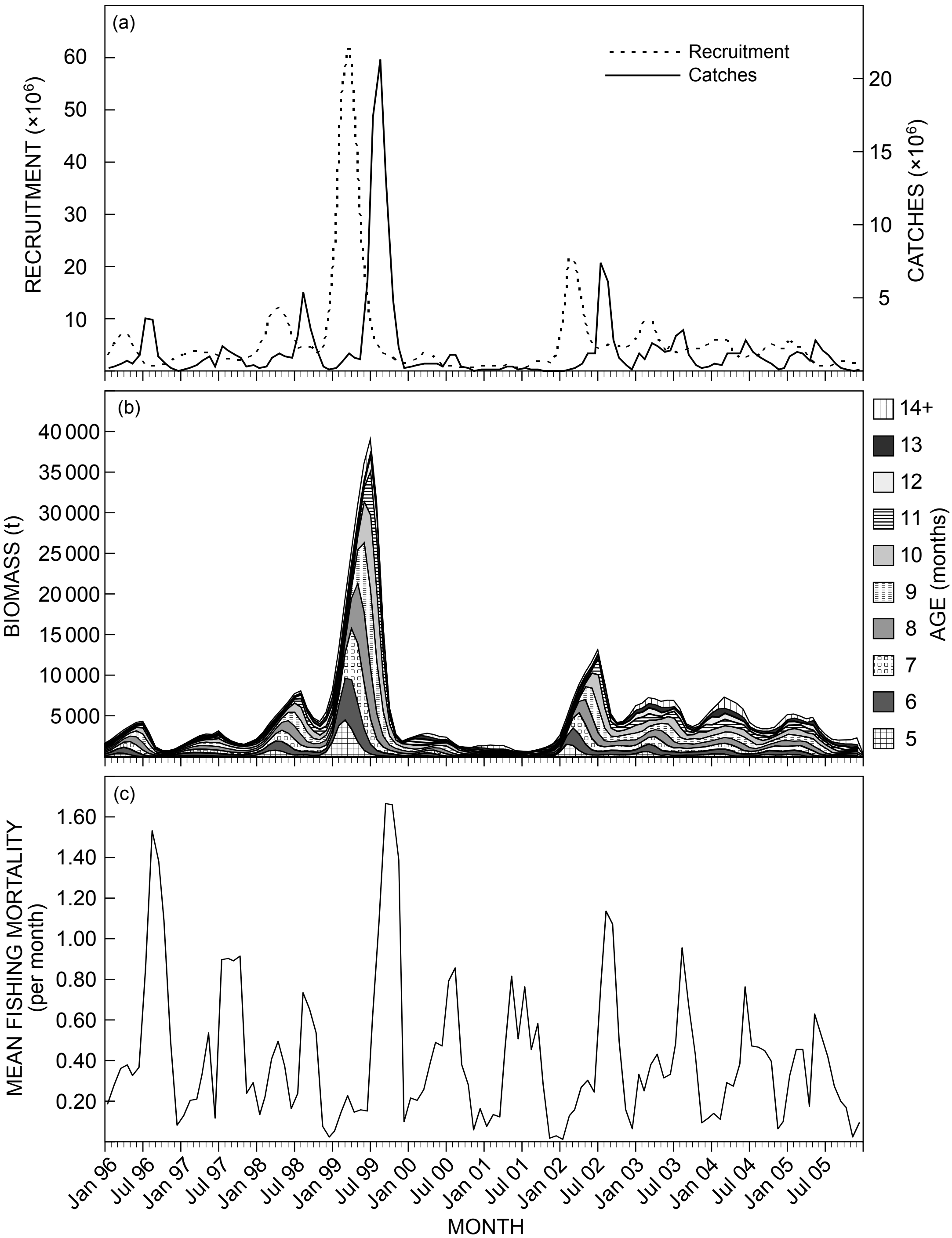

Figure 2: Monthly catches and cohort analysis estimates of (a) octopus recruitment, (b) biomass and (c) mean fishing mortality (*F*, from age 9 to 13 months), from January 1996 to December 2005

by the death of post-spawning individuals and a relatively long pre-recruitment period (5 months long) compared to the total life expectancy (estimated to be 12–14 months on average in Senegal, Domain et al. 2000).

Results from catch data indicate that octopus recruitment (number of individuals at age 5 months) varied considerably between years and seasons (Figure 2a). In addition, recruitment was continuous all year but peaked in spring and declined in summer. The average number of recruits was 5.6 million per month with a high coefficient of variation of 160% (minimum = 0.4 million in March 2001 and maximum = 61.8 million in March 1999). Recruitment also fluctuated widely between yearly cohorts, but no real trend in recruit abundance was observed during the study period (Table 3). Values varied between 13 million recruits (cohort 2001) and 243 million (cohort 1999) per year.

The biomass also varied considerably between years and seasons (Figure 2b). High interannual biomass variability was likely due to the simultaneous presence of a unique annual cohort (i.e. no overlapping between successive annual cohorts because of the short lifespan). The minimum biomass was observed in August 2001 (696 t) and the maximum in July 1999 (39 187 t). Biomass by age revealed that the summer peak was composed of juveniles (6–9 months) and adults, whereas the spring peak consisted of recruits (5 months) and juveniles (6–9 months).

In Senegal, the octopus fishery is characterised by marked interannual and seasonal exploitation with a high fishing mortality in summer and low mortality in winter, spring and autumn (Figures 2c, 3). Fishing pressure peaks in July or August to take advantage of maximum biomass. Mean annual fishing mortality varied from 0.32 to 0.70 month^{-1} from year to year (Table 3).

Figure 3 illustrates that fishing mortality was highest for the last six age classes and lowest for the youngest age classes during the first months after recruitment. Mortality increased progressively throughout the lifespan of individuals within a cohort, and reached a maximum for older octopuses that were most abundant in summer. The seasonal pattern of exploitation for *O. vulgaris* was relatively similar for all seasons (same profile along age class, Figure 3) but differed in intensity throughout the year and peaked in summer.

Environmental effects on octopus recruitment

Correlation coefficients for the relationship between the number of recruits and environmental parameters showed that the coastal upwelling intensity has a positive influence on recruitment (Table 4). Highly significant negative correlations were found between recruitment and SST (Figure 4).

Annual recruitment exhibited a significant negative correlation with an annual mean of SST (r^2 = 0.63, p < 0.05, Figure 4). Thus, more than 60% of the year-to-year variability in the octopus recruitment success can be explained by interannual fluctuations in SST that is linked to coastal upwelling (Table 4). The year 1999 was characterised by very strong upwelling, which may explain the particularly high observed recruitment that led to biased correlations (Figure 4). Nevertheless, a significant correlation remained for the spring SST when the data for 1999 were removed from the dataset. Other regressions with seasonal environmental indices showed that annual recruitment of octopus was significantly correlated with winter and spring coastal upwelling indices, suggesting that winter and spring conditions strongly influence early life survival rates.

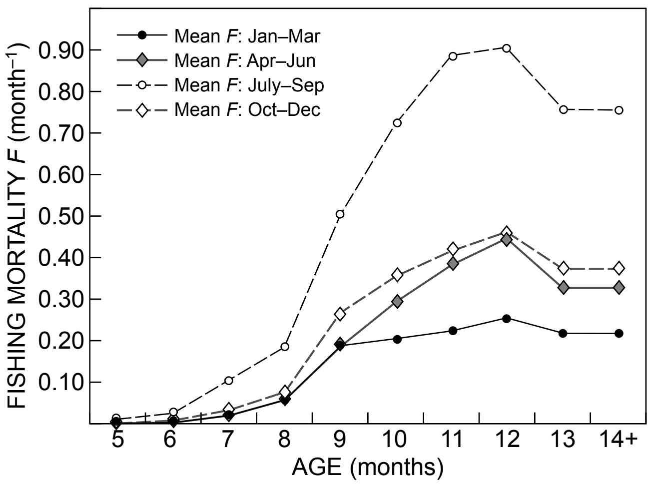

Figure 3: Cohort exploitation patterns for four periods: January–March, April–June, July–September and October–December

Table 3: Results of cohort analysis for *O. vulgaris* between 1996 and 2005

Year	Recruitment (× 10^3)	Catch (t)	Biomass (t)	SSB (t)	Mean $F_{9–13}$
1996	38 480	6 111	2 466	214	0.57
1997	33 178	4 688	2 231	175	0.46
1998	82 204	9 484	5 340	467	0.29
1999	243 216	45 080	19 318	1 673	0.70
2000	17 860	4 195	2 127	377	0.37
2001	13 680	1 175	1 176	316	0.29
2002	102 347	13 860	7 289	552	0.46
2003	64 995	11 375	5 956	905	0.37
2004	49 940	8 489	5 228	1 145	0.36
2005	26 703	6 954	3 568	822	0.32

Table 4: Correlation between octopus recruitment and different mean values of coastal upwelling index (CUI) and SST

r^2	CUI (m^3 s^{-1} m^{-1})			SST (°C)		
	Yearly mean	February–April	Mean CUI > 3.5	March–May	March–April	Yearly mean
Yearly recruitment	0.315***	0.554***	0.496***	0.428***	0.524***	0.626***
Recruitment without 1999	0.231**	0.269***	0.418***	0.520***	0.275**	0.306***

** p > 0.05
*** p < 0.05

Annual exploitation diagnosis

Yield-per-recruit curves suggest that increasing current fishing efforts would result in a slight decrease in yield per recruit, and that decreasing fishing efforts would not result in a significant increase in yield per recruit (Figure 5). For the 1996, 1997 and 1999 cohorts, the octopus population seems to have been slightly overexploited, whereas the 2001 cohort appears to have been underexploited. The exploitation diagnosis for the 1998, 2000, 2002, 2003 and 2004 cohorts is that the stock was fully exploited (Table 5). Yields per recruit expressed as a function of fishing mortality were very similar from one year to another and showed that for all cohorts, full exploitation was reached for F_{max} close to 0.4 month^{-1}, providing an average of 180 g recruit^{-1}. Year 2001 was an exception due to a particular seasonal pattern of the fishing efforts and a low mean yearly fishing effort (Table 5).

Yield per recruit and spawning potential ratio curves expressed for a 'mean' fishing season (Figure 6) showed that the stock has been, on average, fully exploited from 1996 to 2004. The multiplier factor corresponding to the maximum yield per recruit was close to 1. The current level of SPR, corresponding to a fishing mortality close to F_{max}, is equal to 22% of the pristine level. Thus, increasing fishing effort would decrease the spawning potential ratio

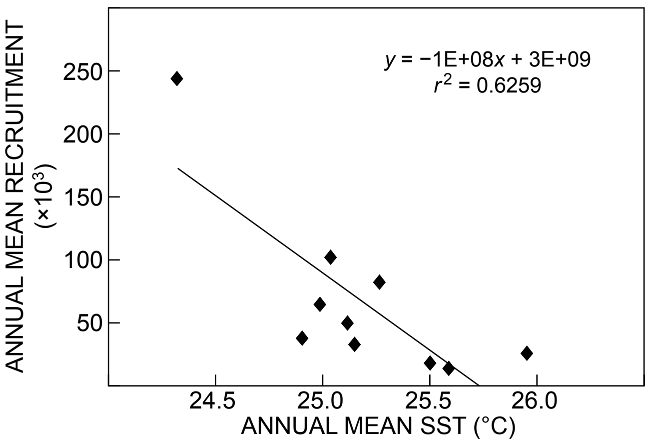

Figure 4: Effects of yearly mean SST on octopus recruitment in Senegalese waters

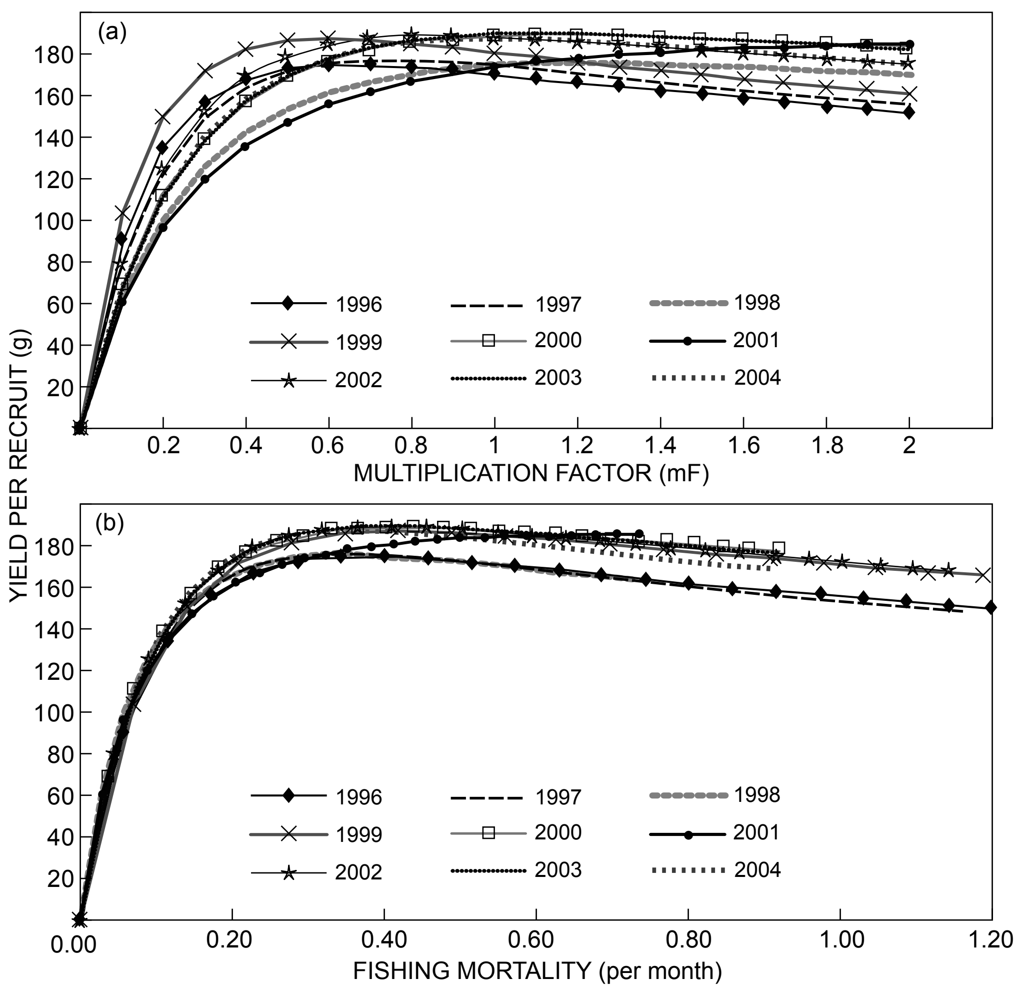

Figure 5: Relationship between yield per recruit and (a) multiplier factor and (b) fishing mortality for octopus in Senegalese waters between 1996 and 2004

Table 5: Estimates of fishing mortality (*F*), yield per recruit (Y/R) and spawning potential ratio (SPR) reference points for *O. vulgaris* taken in Senegal

Cohort	$F_{current}$ ($month^{-1}$)	$F_{25\%}$ ($month^{-1}$)	F_{max} ($month^{-1}$)	$Y/R_{current}$ (g)	$Y/R_{25\%}$ (g)	Y/R_{max} (g)	$SPR_{current}$	SPR_{max}
1996	0.57	0.34	0.40	169.97	172.82	174.37	0.13	0.21
1997	0.46	0.30	0.33	173.94	175.86	176.44	0.13	0.23
1998	0.29	0.32	0.35	174.31	174.83	175.34	0.29	0.23
1999	0.70	0.35	0.42	180.32	184.17	186.79	0.09	0.20
2000	0.37	0.37	0.44	188.13	188.13	188.70	0.24	0.19
2001	0.29	0.73	0.71	173.59	184.87	185.43	0.44	0.25
2002	0.46	0.34	0.41	188.65	188.43	189.20	0.17	0.20
2003	0.37	0.37	0.41	189.08	189.08	189.44	0.25	0.23
2004	0.36	0.31	0.36	186.87	186.00	186.87	0.20	0.20

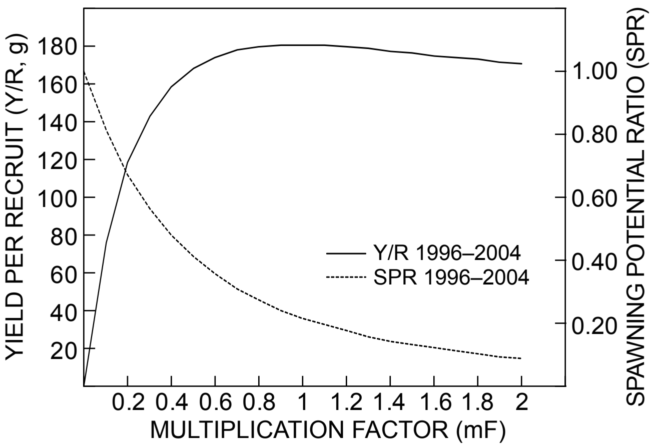

Figure 6: Relationship between yield per recruit and spawning potential ratio versus multiplier factor for the cohorts, 1996–2004

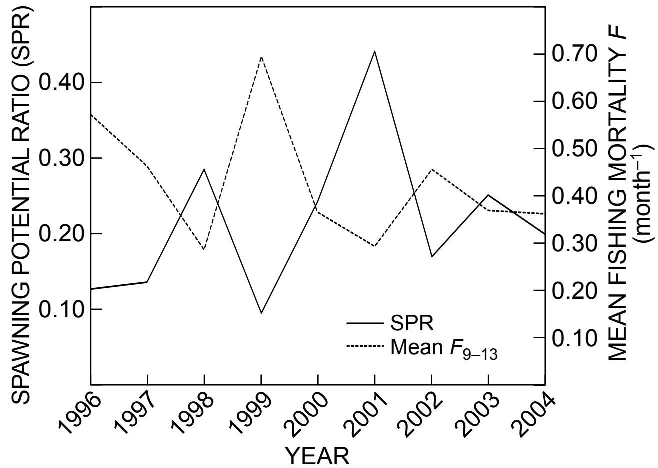

Figure 7: Annual variability of spawning potential ratios and fishing mortality (from age 9 to 13 months), 1996–2004

to lower than 22% of the pristine condition and may have some effect on octopus recruitment. However, from 1996 to 2004, the spawning potential ratio exhibited high year-to-year variability, and during several years SPR values were lower than 15%. No effects were found for related recruitment and no trends were observed (Figure 7).

In the context of environmental variability, the usual indicators such as F_{max}, SPR_{max} and Y/R_{max}, remain useful for fisheries management purposes (Table 5). Five yearly cohorts (among the nine included in our dataset) have been overexploited ($F > F_{max}$), leading to a yield per recruit close to Y_{max} (because of the flat Y/R curve) and catches close to the maximum sustainable yield (MSY) for the cohort. Nevertheless, the SPR of these cohorts was severely affected, with values lower than 15% (and even 10% for the 1999 cohort). Even if recruitment is strongly dependent on environmental conditions, such a value should not be considered sustainable in a precautionary approach.

We also observed that exploiting cohorts that have a fishing mortality equal to F_{max} leads to spawning potential ratios that are always lower than 25% (except for the unique 2001 cohort). A more precautionary approach based on the SPR = 25% target would lead to fishing mortalities ($F_{25\%}$) that are lower than F_{max} (on average $F_{25\%}$ = 0.38 and F_{max} = 0.43), whereas the related yield per recruit would be very close to Y/R_{max}.

Discussion

Results from this study will help identify the relationships between variability in octopus recruitment and coastal upwelling intensity, and evaluate the status of the octopus stock relative to fishing efforts.

Effects of upwelling on octopus

Results showed that the population structure and abundance of octopus varied greatly from year to year and seasonally. Biomass varied according to season, reaching its highest level in July and lowest in October. High interannual fluctuations in recruitment were also observed. These large variations in recruitment and in biomass have been described or suspected for most cephalopod stocks (Beddington et al. 1990, Pierce and Guerra 1994, Agnew et al. 1998, Young et al. 2004, Otero et al. 2008), including octopus stocks in other West African areas such as Mauritania (Jouffre et al. 2006, Gascuel et al. 2007), in the Sahara Bank near Dakhla (Faraj and Bez 2007) and in the Canary Islands (Caballero-Alfonso et al. 2010).

The present study allows us to quantify the seasonal recruitment of the Senegalese octopus stock using a monthly VPA. This quantification is particularly important for estimating recruitment because it concerns a variable that is difficult to estimate directly or using absolute values, and is of special interest to the relationship between resources and the environment. For example, in our study there was a 20-fold difference between the maximum and the minimum values of annual recruitments estimated throughout the 10-year study period. Results also confirmed that recruitment occurred mainly in spring, although the length of the peak period varied annually. Recruitment estimates supported the results of the previous stock assessment for octopus in Senegalese waters (Jouffre et al. 2002), and our study extends these assessments to include a larger time period (4 vs 10), a significant improvement when considering the levels of temporal variability. In addition, our study brings new insights into the causes of this variability, which was not explained by variations in fishing activity, and there was no relationship between spawning stock size and recruitment. Changes in recruitment between years were mainly attributable to fluctuations in environmental conditions.

The relationship between annual octopus recruitment and annual mean SST was significant (63% of the total variance explained). Coastal upwelling intensity was shown to be the source of interannual fluctuations observed in the recruitment of *O. vulgaris* in West Africa, as shown previously for the population along that coast (Caverivière and Demarcq 2002, Faure 2000, Laurans et al. 2002) and on populations in Mauritania (Demarcq and Faure 2000). This pattern is also in accordance with the dynamics exhibited by other important resources in the area (e.g. *Sardinella* sp. and *Farfantepenaeus notialis*), which have similar periodicity (Fréon et al. 1992, Oliver 1993, Cole and McGlade 1998, Carbonell et al. 1999, Thiaw et al. 2009). Changes in recruitment from year to year that are due to fluctuations in environmental conditions are thought to especially affect the early life stages of several cephalopod populations (Dawe and Warren 1993, Bakun and Csirke 1998, Waluda et al. 1999, Caballero-Alfonso et al. 2010), an idea first suggested for English Channel loliginids that were affected by SST (Robin and Denis 1999, Agnew et al. 2000). This conclusion indicates that the physical environment or food availability may be the primary controlling factor for larval octopus survival, and this bottom-up control is likely driving octopus recruitment.

The fishing impact — diagnosis on the stock status

The exploitation patterns at each relative age indicated that the older animals are subjected to the highest levels of fishing mortality. The increase in fishing mortality in adults could be explained by a seasonal change in the behaviour of fishers. Larger octopus may be the preferred target in spring when they spawn along the coast, and in summer when octopus numbers have greatly increased. However, the lowest fishing mortalities were observed in winter and spring when the catchability of the stock was lowest, and in autumn when abundance had declines. This type of exploitation pattern was also observed for the same stock (Jouffre et al. 2002) and for squid stock in the English Channel (Royer et al. 2002, 2006).

Octopus cohorts were generally fully exploited or slightly overexploited, and, with the exception of the 2001 cohort, the current rate of fishing mortality was always higher or close to the F_{max} and $F_{25\%}$ thresholds. This high fishing mortality leads to high catch rates with yields per recruit that are close to the maximum value Y/R_{max}, but it can also lead to low biomass with an observed SPR of <10% (the recruitment overfishing empirical threshold generally accepted for fish stocks) for one of the 10 studied cohorts. Managing the fishery with the goal of maintaining mortality around the $F_{25\%}$ threshold would be a more precautionary approach and would lead to higher biomass, thus increasing the global resilience of the stock. In this case, fishing mortality would be slightly lower than the F_{MSY} target, and catches would then be close to the maximum sustainable yield.

A monthly age-based assessment approach

The following two options for the present stock assessment approaches should be addressed:

1. The use of an age-based modelling approach. Indeed, size-based (or weight-based) methods exist. These methods use 'pseudo-cohorts' (i.e. the catch or biomass for the entire stock over a given period of time is considered equivalent to those of a single cohort over its entire life) and assume constant recruitment and unchanged levels of exploitation for all cohorts in the pseudo-cohort (Gascuel et al. 1994b). Such assumptions are inappropriate in the present study, which focuses on typical seasonal exploitation and a recruitment pattern also known to be strongly seasonal.
2. The use of a one-month resolution option. This option is unusual within the field of stock assessment studies, where traditional age-based models usually involve years. The use of months is required for species characterised by a short life and a very fast growth rate, and appears to be a very powerful approach for species such as *O. vulgaris*.

Conclusion

This paper emphasises that the high year-to-year variability of octopus recruitment caused by upwelling intensity is a key issue for the analysis of cephalopod fisheries. The results also show that the octopus stock has been fully exploited or slightly overexploited over the past decade. Status of octopus stock appears relatively constant, contrasting with the annual variability in catches. A similar pattern has also been observed in the exploitation of octopus off Mauritania, as described by Jouffre et al. (2006). These authors suggested that the Mauritanian octopus fishery seems to adapt to the current fishing efforts targeting this cephalopod, sometimes reporting the largest part of their fishing effort on other demersal resources with longer lifespans, such as Sparidae fish. Fishing efforts in these fisheries seem to be driven by the annual local abundance of the resource (rather than the reverse). Therefore, adaptive management plans involving more frequent and periodical assessments are needed to optimise these environmentally constrained and short-term fisheries (Beddington et al. 1990, Pierce and Guerra 1994, Agnew et al. 1998, Young et al. 2004, Guerra et al. 2010). Short-step stock modelling techniques like the one proposed here should be a useful tool to achieve this goal.

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Appendix: Age-specific monthly catches (in numbers) of *Octopus vulgaris* in Senegalese waters from January 1996 to December 2005

Fishing year	Age group	January	February	March	April	May	June	July	August	September	October	November	December
1996	5	1 964	3 785	11 789	15 275	10 297	34 110	85 338	67 313	9 362	4 944	1 653	436
	6	3 853	7 183	22 181	28 852	19 497	63 517	160 961	127 831	18 764	9 760	3 227	847
	7	17 550	2 9645	89 174	117 505	80 012	246 537	652 067	528 980	90 663	45 209	14 462	3 731
	8	29 272	41 056	114 337	154 860	107 745	288 321	852 589	730 581	164 118	77 864	23 898	5 912
	9	56 250	64 521	146477	205 405	151 499	298 580	1 130 779	1 089 761	330 897	155 020	47 376	10 972
	10	38 902	48 863	65807	83 659	76 038	97 955	490 207	601 834	202 389	105 443	36 808	7 995
	11	24 628	38 979	36651	36 373	41 344	44 740	182 140	275 120	100 498	48 831	19 276	4 497
	12	15 378	28 366	25589	19 605	22 277	26 126	54 693	86 810	40 411	14 947	7 448	1 785
	13	6 929	15 009	16913	12 431	11 827	16 642	12 265	17 763	14 525	4 338	1 663	479
	14+	1 679	6 643	10121	8 508	8 070	13 900	3 015	3 106	4 027	985	163	124
1997	5	734	2 961	7 036	14 493	16 499	3 088	27 891	27 158	21 615	14 988	6 224	2 311
	6	1 736	5 643	13 417	27 453	31 577	6 077	52 926	51 228	40 987	28 478	11 785	4 746
	7	11 859	23 620	56 289	112 825	134 064	27 968	218 340	207 432	168 982	118 019	48 278	24 223
	8	28 755	33 437	79 547	152 045	193 751	46 956	302 014	273 251	229 920	164 037	65 441	48 627
	9	62 214	52 171	119 793	210 926	299 814	87 577	469 344	384 301	328 887	251 063	95 907	113 430
	10	17 512	32 227	57 908	93 007	146 121	48 787	327 303	235 741	167 147	155 553	54 972	90 880
	11	6 618	20 225	24 113	41 887	70 930	21 215	200 264	141 055	90 042	85 436	24 683	47 546
	12	3 583	11 699	9 618	22 949	41 986	8 125	90 301	62 459	42 679	33 180	7 807	17 500
	13	1 580	5 831	4 474	14 950	25 457	3 895	27 917	18 247	14 356	7 745	2 227	4 580
	14+	424	2 004	1 588	11 324	15 579	2 428	4 975	4 011	4 602	1 834	495	736
1998	5	1 485	788	13 862	29 584	25 245	25 827	69 856	92 764	33 952	15 472	3 114	2 538
	6	3 079	1 756	26 596	55 513	47 466	48 347	130 526	175 817	65 500	30 120	6 009	4 780
	7	16 162	10 673	113 776	221 240	190 406	191 205	512 525	719 672	283 215	134 049	26 081	19 248
	8	32 604	25 521	166 953	276 857	242 414	233 686	619 006	999 655	440 660	217 686	40 333	25 077
	9	71 632	66 307	264 540	334 038	303 543	262 047	694 993	1 627 115	827 625	423 866	73 446	34 589
	10	45 312	59 424	135 227	131 835	123 510	76 264	250 090	1 181 435	643 813	345 384	54 392	20 137
	11	23 919	48 245	72 053	69 428	55 613	28 222	90 074	458 318	350 225	239 002	30 411	10 349
	12	11 805	34 987	43 061	45 650	27 955	15 394	27 141	132 253	184 512	143 597	14 352	5 010
	13	4 459	16 250	23 657	31 995	16 423	9 353	11 460	33 209	50 987	51 367	7 149	3 475
	14+	869	6 432	11 318	22 630	11 983	5 262	3 420	6 163	13 548	12 893	3 001	1 178
1999	5	886	5 408	18 197	13 475	5 531	186 899	194 734	57 118	47 915	19 104	11932	3 879
	6	1 747	10 465	34 819	25 644	10 965	349 343	374 798	126 933	101 762	41 190	23 979	7 589
	7	8 041	45 865	147 677	106 901	51 429	1 374 341	1 603 940	748 407	553 877	232 235	116 357	34 467
	8	14 220	71 756	213 499	149 424	90 238	1 658 645	2 505 241	1 921 720	1 266 368	538 444	216 825	55 447
	9	32 677	132 592	334 648	224 884	185 482	1 813 233	5 029 047	5 968 794	3 553 155	1 453 589	480 780	93 212
	10	36 484	107 993	180 163	123 297	145 282	517 962	4 724 668	7 037 135	3 886 863	1 399 265	412 544	35 106
	11	31 282	88 161	102 437	72 936	101 597	173 604	2 320 282	3 932 676	2 396 218	774 291	258 919	12 387
	12	24 168	63 949	67 350	52 914	65 572	64 747	603 424	1 253 861	1 048 475	288 199	91 666	3 532
	13	16 446	35 229	46 800	46 750	49 659	21 414	77 403	222 511	297 843	72 523	22 448	1 077
	14+	9 052	15 094	32 448	64 637	71 542	13 333	7 486	35 773	76 158	19 516	5 902	250
2000	5	482	596	748	498	681	501	2 846	2 991	487	370	36	109
	6	1 082	1 408	1 935	1 227	1 786	1 273	7 373	7 817	1 058	893	79	258
	7	6 176	9 104	14 772	8 650	13 966	9 436	56 329	60 573	5 587	6 026	411	1 698
	8	18 414	26 551	41 326	24 934	38 903	26 511	156 427	167 607	17 262	17 434	1 271	5 027
	9	71 873	92 857	113 674	81 540	103 853	75 095	411 293	429 580	77 401	58 419	5 723	18 708

Appendix (cont.)

Fishing year	Age group	January	February	March	April	May	June	July	August	September	October	November	December
	10	104 314	125 845	97 066	109 024	83 009	66 775	267 393	249 390	135 498	76 184	10 161	30 629
	11	54 282	80 215	74 074	95 358	70 043	44 945	115 607	102 511	73 199	52 005	7 615	26 851
	12	24 335	35 302	51 924	66 920	54 678	31 551	37 195	38 338	15 646	22 430	7 029	16 752
	13	5 821	9 903	32 654	44 575	44 220	22 947	7 181	11 343	4 855	5 348	4 034	8 720
	14+	566	3 713	24 598	20 363	46 333	18 675	2 025	7 371	5 193	2 724	1 704	2 717
2001	5	57	62	31	542	707	123	335	116	76	8	12	23
	6	122	135	69	1 408	1 770	267	765	271	167	18	27	49
	7	624	743	397	10 827	12 768	1 406	4 551	1 716	927	108	147	247
	8	1 922	2 310	1 245	30 156	35 936	4 347	13 458	5 070	2 883	338	455	759
	9	8 566	10 520	5 763	80 622	103 305	19 534	50 565	18 809	13 116	1 555	2 060	3 372
	10	14 282	20 368	12 271	60 430	89 565	34 646	71 391	28 558	25 418	3 262	3 847	5 462
	11	7 865	18 172	14 123	39 911	45 773	22 619	38 966	19 146	19 889	2 710	2 365	2 677
	12	5 905	14 131	13 654	27 197	27 117	12 483	16 147	7 896	9 557	2 064	388	1 984
	13	7 688	5 953	7 220	17 249	19 600	5 890	2 750	3 913	2 684	4 067	13	2 963
	14+	3 758	1 035	1 648	5 292	11 931	1 433	114	1 122	436	1 543	0	1 504
2002	5	7	165	481	6 134	43 875	38 316	24 477	21 299	2 596	1 271	642	148
	6	15	377	1 207	11 721	80 687	71 058	50 812	43 694	6 411	2 899	1 555	358
	7	81	2 249	8 744	49 363	299 104	271 935	251 113	216 105	45 382	17 318	10 540	2 438
	8	250	6 701	24 651	72 112	309 217	305 369	620 915	484 078	130 863	51 689	30 281	7 054
	9	1 136	25 946	71 524	125 285	235 026	282 096	2 209 207	1 544 374	429 008	201 504	98 041	23 644
	10	2 159	39 884	65 966	103 703	99 470	78 575	3 003 755	2 137 002	581 823	314 016	115 847	32 402
	11	1 649	26 242	39 610	70 509	65 292	43 465	1 069 672	1 200 599	505 745	197 684	71 003	31 885
	12	867	14 254	20 814	38 834	49 374	31 817	131 030	363 985	277 263	74 382	30 202	24 896
	13	700	7 114	6 499	21 551	34 442	23 394	11 811	62 510	75 873	14 177	7 954	9 244
	14+	3 959	2 062	1 302	9 375	18 817	8 988	2 395	8 161	14 229	1 221	2 806	6 705
2003	5	6 918	3 501	30 978	26 798	25 119	27 632	5 980	4 476	1 591	336	204	446
	6	13 858	7 116	59 016	51 107	47 418	52 089	14 961	10 380	3 695	746	443	1 066
	7	66 526	35 247	246 987	214 452	192 739	210 784	107 676	64 302	23 025	4 184	2 330	7 057
	8	124 526	70 991	347 169	304 433	253 633	274 181	302 906	189 040	67 856	13 025	7 202	20 650
	9	293 071	185 825	524 172	471 655	342 927	361 426	868 630	688 955	249 649	59 495	32 320	73 058
	10	305 977	219 345	287 564	271 867	172 147	174 605	733 695	963 726	363 350	118 821	56 847	106 494
	11	229 142	171 768	182 046	161 531	103 084	111 006	303 036	561 328	241 309	108 226	35 342	76 522
	12	122 831	103 849	117 773	108 846	62 451	70 096	80 247	220 763	119 900	69 712	15 936	31 825
	13	42 053	39 384	61 595	76 357	61 889	43 455	22 656	60 584	39 514	35 095	3 491	7 535
	14+	6 179	8 838	24 756	47 506	59 474	40 316	5 784	16 999	7 419	14 131	243	382
2004	5	673	2 735	13 152	13 681	1 946	4 202	3 300	1 621	1 001	672	101	303
	6	1 698	5 360	25 309	26 623	4 889	10 486	8 368	3 775	2 318	1 513	231	773
	7	12 439	24 316	109 352	118 863	35 507	75 223	61 640	23 603	14 351	8 749	1 397	5 757
	8	35 193	40 906	164 522	188 578	100 286	212 410	172 386	69 212	42 365	26 353	4 156	16 200
	9	103 993	83 261	283 669	330 518	293 789	622 412	475 947	249 207	157 183	106 771	15 932	46 319
	10	108 925	72 007	219 229	192 867	286 144	578 645	358 849	342 668	230 926	173 179	24 256	43 843
	11	95 277	58 269	186 951	133 974	196 627	305 578	152 427	195 252	150 251	112 441	15 178	32 786
	12	69 824	55 703	115 702	100 885	125 590	143 261	63 600	70 257	70 573	54 153	8 733	19 361

Appendix (cont.)

Fishing year	Age group	January	February	March	April	May	June	July	August	September	October	November	December
	13	20 813	39 286	54 952	56 850	69 543	86 980	29 289	25 040	36 175	21 979	9 607	6 638
	14+	2 855	14 463	25 265	29 789	47 489	69 145	12 505	11 610	19 911	11 172	7 778	7 111
2005	5	4 459	3 772	2 847	1 925	5 782	3 698	3 941	1 196	370	234	21	100
	6	9 683	8 936	7 447	5 162	15 360	9 795	9 679	2 997	873	617	53	258
	7	56 115	60 260	57 848	41 612	122 262	77 509	69 245	21 846	5 790	4 864	389	1 940
	8	126 156	154 724	160 356	114 256	335 242	213 497	180 404	59 638	15 452	13 489	1 098	5 441
	9	301 619	399 956	415 630	276 166	817 391	528 956	439 222	158 538	44 849	34 843	3 202	15 248
	10	215 555	293 351	266 029	12 1419	377 224	261 192	220 680	109 704	45 793	24 118	3 109	13 784
	11	137 525	175 797	142 963	53 875	178 081	108 471	81 336	51 856	34 021	24 634	2 277	11 902
	12	74 365	99 957	74 900	27 143	142 166	69 096	39 472	30 529	27 196	31 293	2 311	9 182
	13	23 252	52 071	45 308	8 647	100 030	63 837	25 950	18 683	21 878	12 670	3 581	5 788
	14+	5 817	27 904	16 236	4 105	49 368	37 369	6 554	17 301	19 175	713	3 027	8 627