



Original Article

Evaluation of determinants of *Xiphopenaeus kroyeri* (Heller, 1862) catch abundance along a Southwest Atlantic subtropical shelf

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Generalized linear models were applied to identify factors affecting the capture rates (catch per unit effort, cpue) of *Xiphopenaeus kroyeri* and to estimate time-series data with standardized abundance indices. The adjusted models revealed that the most powerful vessels (with greater HP) were up to 3.5 times more efficient than vessels with less powerful engines. The seasonal variation of the resource changed from year to year, most likely due to variations in the recruitment season and the timing of temporary fishing bans. The variation of cpue was similar between the northern and southern sectors of the study area. In these, *X. kroyeri* abundances increased in the years 1996, 1997, 2001 and 2002, while in the central sector, the cpue fluctuated with a period duration of approximately two years. During the period, the relative abundance of the species displayed neither a decreasing nor an increasing trend, indicating that this has been harvested at stable levels. However, *X. kroyeri* stock was reduced by overfishing during the 1980s and exhibits variations in abundance that may occur in response to environmental fluctuations; thus, the harvesting of this species should be managed with extreme caution.

Keywords: abundance indices, catch per unit effort, generalized linear models, time-series.

Introduction

Determining the degree to which the physical and operational characteristics of vessels and environmental factors influence catch yield is important for the evaluation of variations observed in fishery yields. This analysis also benefits fisheries management by allowing more effective conservation of the resource and the fishing activity itself (Maunder and Punt, 2004).

Penaeid shrimp are of great importance for coastal fisheries worldwide. The high commercial value of these shrimp and their distribution along continental shelves make them highly vulnerable to fishing, which has led to the overexploitation of most of these resources. Currently, penaeid shrimp are considered to be the most valuable fishing commodity in the global market (Gillett, 2008). Fishing of the Atlantic seabob, *Xiphopenaeus kroyeri* (Heller, 1862), warrants special attention because, among the top ten exploited shrimp species, *X. kroyeri* had the highest percentage catch increase between 1995 (18 802 t) and 2005 (52 411 t) (Gillett, 2008).

In Brazil, *X. kroyeri* is one of the most important resources for the fishing industry and for the community structure of coastal marine species. The species was the primary crustacean caught in 2010 and represented 26.7% of the total commercial catch of crustaceans

reported in the country (MPA, 2012). *Xiphopenaeus kroyeri* is caught throughout the coastal region, particularly along the subtropical shelves (Ibama, 1993; Dias Neto and Dornelles, 1996; Paiva, 1997; Ibama, 2008). Furthermore, *X. kroyeri* represents the lowest trophic level among the commercially exploited species in this region (Vasconcelos and Gasalla, 2001).

The capture of *X. kroyeri* is typically performed by artisanal fleets with vessels <15 m in length that operate with one or two trawl nets and specifically target this species. This shrimp fishery is important economically and socially to many coastal communities (Perez *et al.*, 2001; Graça-Lopes *et al.*, 2007; Kolling *et al.*, 2008).

Xiphopenaeus kroyeri is a benthic species that ranges from the continental shelf of the western Atlantic from North Carolina (USA) to the State of Rio Grande do Sul (Brazil) and is most abundant at depths up to 30 m (Boschi, 1963; Iwai, 1973; Holthuis, 1980; Santos and Ivo, 2000). The species spends its entire life cycle in the same environment, and it does not depend on estuaries for the development of juveniles (Holthuis, 1980; Castro *et al.*, 2005).

The *X. kroyeri* fishery and the biology of the species have been well studied in Brazil, with several studies conducted in the northeastern (Coelho and Santos, 1993; Santos and Coelho, 1998; Santos and Ivo,

2000; Santos *et al.*, 2001; Santos and Freitas, 2006; Silva and Santos, 2006, 2007; Santos and Silva, 2008), southeastern (Nakagaki and Negreiros-Fransozo, 1998; Castro *et al.*, 2005; Graça-Lopes *et al.*, 2007; Simões *et al.*, 2010) and southern (Branco *et al.*, 1999; Branco and Moritz, 2001; Branco, 2005; Pezzuto *et al.*, 2008; Campos *et al.*, 2009) parts of the country.

Fisheries are primarily managed using time area closures in waters along southeastern and southern Brazil (18°20'S to 33°45'S). Initiated in 1984, the designated period has already undergone several changes. The closure was initially implemented to manage the fishing of the shrimp species *Farfantepenaeus brasiliensis* and *F. paulensis*, but it also prohibited the fishing of other shrimp species, including *X. kroyeri*, in the same area. Only in the years 2006 and 2007 was the period of closure directed specifically at managing the fishing of *X. kroyeri* (Franco *et al.*, 2009).

Several biological characteristics of *X. kroyeri*, including its reproductive capacity, lack of dependence on estuaries and short life cycle, allow the species to efficiently recover from fishing mortality. Despite this potential for recovery, however, there has been considerable concern since the 1970s about the stress on the population caused by commercial fisheries of the species (Santos *et al.*, 1973; Graça-Lopes *et al.*, 2007; Pezzuto *et al.*, 2008). Variations in *X. kroyeri* catch rates over the years and a decrease in population size observed in stock assessments led to its inclusion in the National List of Species of Aquatic Invertebrates and Fish Overexploited or Threatened with Overexploitation ("Lista Nacional das Espécies de Invertebrados Aquáticos e Peixes Sobreexploradas ou Ameaçadas de Sobreexploração") (D'Incao *et al.*, 2002; MMA, 2004; Graça-Lopes *et al.*, 2007).

Catch and effort data from commercial and recreational fishing are commonly used as an index of population trend when reported as cpue. This represents one of the most easily accessed sources of information for analysing fisheries stocks in exploitation (Gulland, 1956; Gavaris, 1980; NRC, 2000). However, the use of these data as an index of abundance necessitates methods for filtering out variations caused by factors other than abundance, such as technological changes in the fleet, season and area. This process has been widely performed in fishery studies using multiplicative models for the standardization of catch rates (Large, 1992; Goni *et al.*, 1999; Punt, 2000; Maynou *et al.*, 2003; Battaile and Quinn, 2004; Tascheri *et al.*, 2010).

The coefficients of multiplicative models are typically estimated by fitting generalized linear models (GLMs), which allows for the identification of factors that influence catch rates as well as the calculation of standardized indices of abundance (Maunder and Punt, 2004; Venables and Dichmont, 2004; Xiao *et al.*, 2004).

Although *X. kroyeri* fisheries and the biology of the species are well studied, no attention has been given to the standardization of *X. kroyeri* catch rates along the Brazilian coast. This step is of the utmost importance for the development of indices of relative abundance, which can be used as a basis for management of the fishery and adjustment of the models for stock evaluation (Maunder and Punt, 2004).

To better understand the fishing dynamics of *X. kroyeri*, the present study aimed to (i) identify the factors that influenced the catch rates of *X. kroyeri* by double-rig trawling in the State of São Paulo from 1990–2009, (ii) estimate a time-series with standardized indices of abundance for the species, (iii) identify patterns of *X. kroyeri* cpue, and (iv) assess whether the variation in species abundance in different fishing areas was associated.

Data and methods

Data

Data from the landings of double-rig trawlers in the fishing ports of Cananéia, Santos and Ubatuba in São Paulo State (Figure 1) were used. A lengthy time-series of data is available for these ports. The information was collected using the census method, which involves interviews with fishermen at the time of landing as part of the Fishing Activity Monitoring Program of the São Paulo Fisheries Institute (FAO, 1999; Ávila-da-Silva *et al.*, 2007).

For the present analysis, we considered vessel (length and engine power) and travel data along with complete data for catch, effort and fishing area. The Brazilian rule for seabob trawlnets limits the buoy line to maximum 12 m length and the mesh to at least 24 mm (SUDEPE, 1984). Possible variations in the sizes of fishing nets per boat or trip were not taken into account.

The fishing area was divided into three sectors, defined by the radius of activity of the fleets based in each of the ports: (a) the northern sector, the area of operation of Ubatuba fleets, bounded by latitudes 23°00'S and 23°50'S; (b) the central sector, the primary area of operation of Santos fleets, extending from parallel 23°50'S to 24°30'S; and (c) the southern sector, with trips recorded in Cananéia, between latitudes 24°30'S and 25°35'S. The latitudinal limits designate the area from the coastline with a perpendicular extension until the 50 m isobath (Figure 1).

Analysis of the northern sector included data from 31 522 trips made by 172 vessels, which captured 2034.3 t of *X. kroyeri* between 1990 and 2009. For the central sector, the analysis included data from 3242 trips made by 96 vessels, which captured 5842.3 t of the species. For the southern sector, the analysis included data from 3651 trips made by 121 vessels, which captured 3442.1 t of the species during the period. Total effort was 50 738, 19 699 and 11 304 fishing days for Northern, Central and Southern regions, respectively.

The fishing boats were categorized according to vessel length and engine power. The length categories were as follows: (i) small scale 1 (s-1) for vessels <10 m; (ii) small scale 2 (s-2) for vessels between 10 and 12 m; (iii) intermediate scale 1 (i-1) for boats between 12 and 15 m; and (iv) intermediate scale 2 (i-2) for vessels >15 m in length. These categories were determined using the fisheries legislation regulating the trawler fleets catching shrimp in the region as a reference. Vessels that are 10 m or longer are legally required to complete and submit catch maps for all fishing trips, while boats that are 12 m or longer are not designated as artisanal for fishing licences. Vessels that are 15 m or longer are included in the Fishery Vessel Satellite Tracking Program ("Programa de Rastreamento de Embarcações Pesqueiras por Satélite" – PREPS) (SEAP/PR *et al.*, 2006; MPA and MMA, 2010; MPA and MMA, 2011). The horsepower classes were (i) <18 HP, (ii) 18–99 HP, (iii) 100–179 HP and (iv) ≥180 HP.

For the years 1990–2009, the months during which a fishing ban was enforced were identified. The months immediately following these periods were classified as opening months for fishing (Table 1).

Statistical analysis

Generalized linear models and effort standardization

Estimation of the magnitude of influence of year, month (January–December), length class (s-1, s-2, i-1, i-2), HP class (<18, 18–99, 100–179, ≥180) and opening-month status (variable indicating whether the month was one open to fishing following a period of

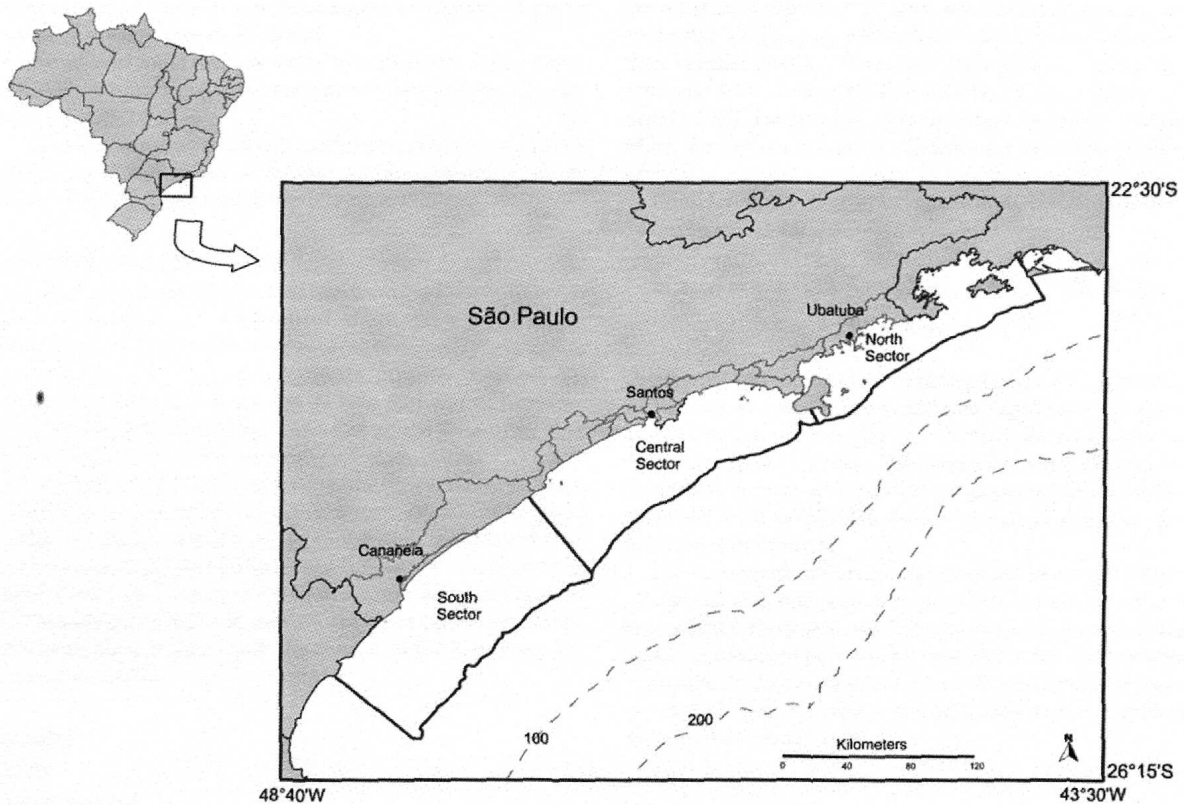


Figure 1. Geographic location of the fishing sectors and main fishing ports where *X. kroyeri* is landed in the State of São Paulo (Ubatuba, Santos and Cananéia).

Table 1. Closed periods (temporary bans on trawling) in the southeastern and southern regions of Brazil from 1990–2009.

Year	Closed periods
1990–1992	15 February–15 May
1993–1996	No closure
1997	15 February–15 May
1998	1 March–31 May
1999–2000	15 February–15 May
2001–2005	1 March–31 May
2006–2007	1 October–31 December
2008	No closure
2009	1 March–31 May

closure) on fishing cpue was carried out for each sector using analysis of deviance for GLM fit (McCullagh and Nelder, 1989; Lindsey, 1997; Venables and Ripley, 1997; Quinn and Deriso, 1999). Catch rate, or cpue, was measured as the landed catch (kg) per effective fishing days of each trip.

The cpue distribution for all sectors showed asymmetry, with lower values being the most frequent, mainly in the northern and southern sectors. For these sectors a log-normal distribution was the best fit for the cpue, while a gamma distribution was assumed for the central sector. Thus, the GLM technique was used to identify the magnitude of influence of the explanatory factors on the cpue of the species. The Gaussian family and the identity link function on log transformed cpue were used for the northern and southern

sectors, while a gamma distribution and a logarithmic link function on raw cpue data were used for the central sector.

First the models were fitted considering all variables, without concern for their order and with no interactions. The effect of dropping terms from the models was explored by examining the Akaike Information Criterion (AIC) (Akaike, 1974) of each single term. In a second step, variables were ordered based on their AIC value. The definition of the final model terms with first-order interactions was performed using the stepwise method (backward and forward) based on AIC values (Venables and Ripley, 1997). Previous estimates were not fixed when one more effect was added.

The models were based on the following pattern, with changes in the order of the factors and the inclusion of first-order interactions, according to the models fitted for the fishing sectors:

$$\ln \mu_{ymhlc} = \alpha + \beta_y + \theta_m + \varepsilon_h + \rho_l + \gamma_c \quad (1)$$

In the above equation, μ_{ymhlc} is the expected cpue for month m of year y for a vessel of HP class h and length class l and takes into consideration whether the month was an opening month for fishing or not. α is the observed cpue of a vessel belonging to HP class < 18 and length class $s-1$ in January 1990 for the northern and central sectors and from 1995 for the southern sector. β_y is the abundance in year y relative to 1990 for the northern and central sectors and relative to 1995 for the southern sector. θ_m is the abundance during month m relative to January. ε_h is the efficiency of a vessel of class h with respect to the HP class < 18 . ρ_l is the efficiency of a vessel of class l

relative to length class $s-1$. γ_c is the change in the capture rate in the case of an opening month for fishing.

The adjustment of the final model for each of the areas is exemplified by means of graphs for the type of vessel with greater temporal coverage by area.

Excluding the year and month coefficients, all of the coefficients in the interaction model were used for the calculation of the standardized effort per fishing trip (Quinn and Deriso, 1999).

Exploratory time-series analysis

The monthly and annual cpue time-series were calculated by sector based on estimates of standardized effort. An autocorrelation analysis was used for the monthly series to verify variation patterns at given time-lags. The autocorrelation function measures the relationship between a series and its own past and is calculated using the Pearson correlation coefficient of the time-series with itself by applying a lag of k months (Zuur *et al.*, 2007).

To quantify the association between the time-series of different sectors and to determine whether *X. kroyeri* abundance followed similar trends by considering temporal lags, cross-correlation functions were applied for the annual time-series of standardized cpues. The cross-correlation function is also calculated based on the Pearson coefficient and assesses the correlation between the cpue of sector A at time t with the cpue of sector B at time $t + k$ (Zuur *et al.*, 2007).

Results

GLMs

Northern sector

Of the total trips, 12 431 (39%) were made by vessels with <18HP; 18 867 (60%) were made by vessels with 18–99 HP; and only 221 (1%) were made by vessels with ≥ 100 HP. The shortest vessels (class $s-1$) were responsible for 31 003 trips (98%), and the other classes accounted for the remaining 516 trips (2%).

The following model was selected:

$$\ln \mu_{myhl} = \alpha + \theta_m + \beta_y + \varepsilon_h + \gamma_c + \rho_t \quad (2)$$

All factors included in this model were significant, explaining 22.4% of the total variation in cpue. Month was the most important factor, explaining 8.8% of the variation, followed by year, HP class, opening-month status and length class (Table 2).

Vessels of HP class 18–99 (HP-B) were 1.4 times ($e^{0.341}$) more efficient than HP class <18 (HP-A). The model indicated two increases in cpue during any given year, one occurring in June and

Table 2. Analysis of deviance for the GLM (family = gaussian, link = identity) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the northern sector.

Source of variation	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				31 518	14 290
Month	11	1257.3	8.8%	31 507	13 033
Year	17	959.5	6.7%	31 490	12 073
HP class	3	906.3	6.3%	31 487	11 167
Opening month	1	72.7	0.5%	31 486	11 094
Length class	3	4.1	0.0%	31 483	11 090
Total explained			22.4%		

the other in November. The catch rate during an opening month (following a temporary fishing ban) was 1.3 times higher ($e^{0.240}$) than in other months. There were sharp peaks in species cpue in 1997 and 2005, both with cpues about 1.9 times greater ($e^{0.64}$) than in 1990. The variation was significant for vessels of class $i-1$, which showed an increase in efficiency 1.5 times that of class $s-1$ ($e^{0.431}$).

Considering the first-order interactions between factors, the following model was selected:

$$\ln \mu_{myhl} = \alpha + \theta_m + \beta_y + \varepsilon_h + \rho_t + \theta\beta_{my} + \varepsilon\beta_{hy} + \beta\rho_{yt} + \varepsilon\rho_{ht} + \theta\rho_{ml} + \varepsilon\theta_{hm} \quad (3)$$

This model had a coefficient of determination (r^2) of 36.0%. All interactions included in the model were significant, and the year:month interaction accounted for 13.2% of the total variation in the species cpue (Table 3). The cumulative normalized deviance residuals (q-q plot) of this model is represented in Figure 2a and the model fitted to cpue data from $s-1$ length class and 18–99 HP class vessels in Figure 3a.

The year:month interaction revealed that most years had two cpue peaks, with one peak more pronounced than the other. The timing of the sharp peak was between May and June, and that of the less pronounced peak was between November and December.

Despite the low explanatory power, all interactions of year and month with the HP class and length class factors significantly explained variation in cpue.

Central sector

The trip distribution by HP class was as follows: 19 trips (1%) in vessels of HP class <18; 1029 (32%) in HP class 18–99; 1982 (61%) in HP class 100–179; and 210 (5%) in HP class ≥ 180 . A total of 223 (7%) trips were made in length class $s-1$ vessels; 621 (19%) in class $s-2$; 2241 (69%) in class $i-1$; and 155 (5%) in class $i-2$.

The following model was selected:

$$\ln \mu_{mych} = \alpha + \theta_m + \beta_y + \gamma_c + \varepsilon_h \quad (4)$$

Table 3. Analysis of deviance for the GLM (family = gaussian, link = identity) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the northern sector with first-order interactions.

Factor	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				31 518	14 290
<i>Main effects</i>					
Month	11	1257.3	8.8%	31 507	13 033
Year	17	959.5	6.7%	31 490	12 073
HP class	3	906.3	6.3%	31 487	11 167
Length class	3	4.3	0.0%	31 484	11 163
<i>Interactions</i>					
Month:Year	146	1883.3	13.2%	31 338	9 280
Year:HP class:	34	73.6	0.5%	31 304	9 206
Year:Length class	18	19.7	0.1%	31 286	9 186
HP class:Length class	1	4.1	0.1%	31 285	9 182
Month:Length class	29	18.4	0.1%	31 256	9 164
Month:HP class:	18	12.7	0.1%	31 238	9 151
Total explained			36.0%		

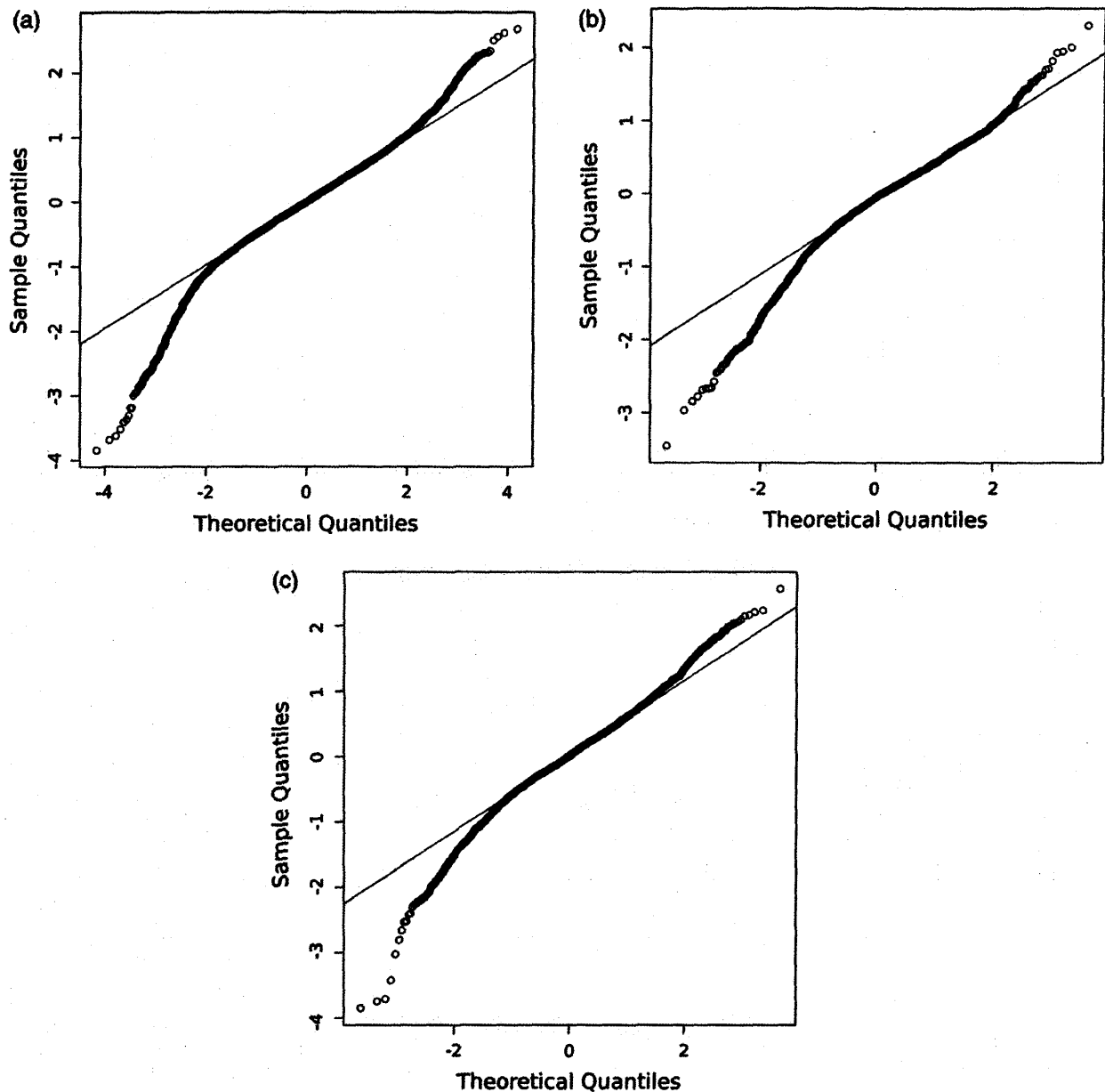


Figure 2. Cumulative normalized deviance residuals for the GLM fitted to cpue (kg/day of fishing) for *X. kroyeri* in the northern (a), central (b) and southern (c) sectors.

The coefficient of determination indicated that the fitted model explained 19.5% of the variation in *X. kroyeri* cpue. Most of the variation was explained by the month factor (13.1%), followed by year, opening-month status and HP class (Table 4).

The cpue was significantly higher in the months of May and June when compared with January. The cpue in between August and December was low relative to other months. The lowest cpue was observed in 1991, when it was 58.2% of that in 1990. The highest cpue occurred in the years 1997 and 2004 when catch rates were, respectively, 1.5 and 1.3 times higher than in 1990. For opening months, catch rates were 1.4 times higher than in other months.

Vessels of HP class ≥ 180 were 1.1 times more efficient than vessels of HP class < 18 .

Considering the first-order interactions between factors, the following model was selected:

$$\ln \mu_{myh} = \alpha + \theta_m + \beta_y + \varepsilon_h + \theta\beta_{my} + \beta\varepsilon_{yh} \quad (5)$$

The coefficient of determination (r^2) for this model was 36.9%, and the year:month interaction explained 15.3% of the total variation (Table 5). Figure 2b shows the q-q plot of this model and Figure 3b the model fitted to cpue data from 18–99 HP class vessels.

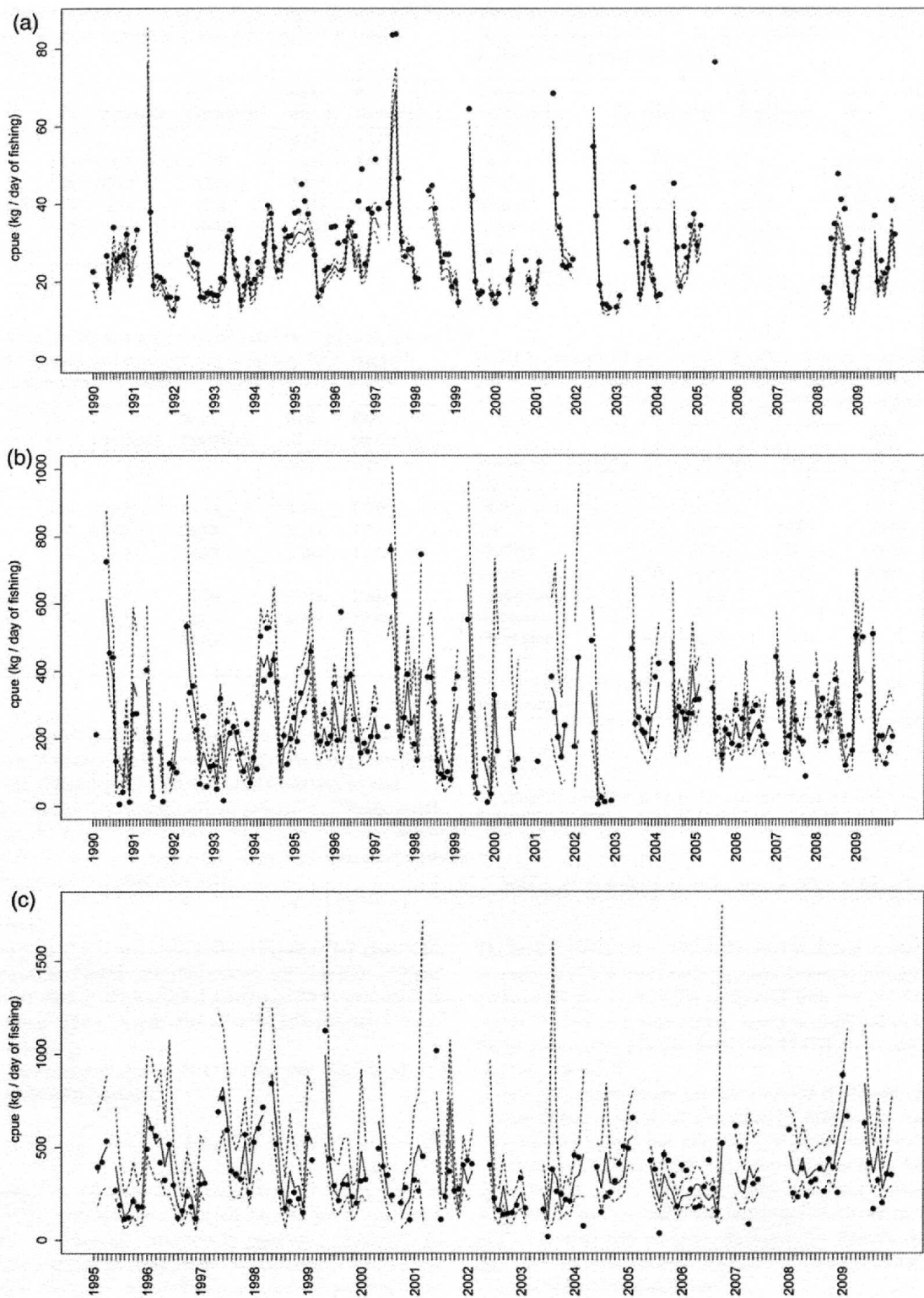


Figure 3. GLM fitted to cpue (kg/day of fishing) for *X. kroyeri* in the northern sector by vessels of < 10 m and with engines of 18–99 HP (a), in the central sector by vessels with engines of 18–99 HP (b), and in the southern sector by vessels with engines of 100–179 HP (c). Points represent the observed cpue per month; the line indicates the estimated cpue and the dashed lines their confidence intervals of 95%.

Table 4. Analysis of deviance for the GLM (family = gamma, link = log) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the central sector.

Source of variation	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				3 241	2 127
Month	11	279.7	13.1%	3 230	1 848
Year	19	105.7	5.0%	3 211	1 742
Opening month	1	20.4	1.0%	3 210	1 722
HP class	3	9.6	0.5%	3 207	1 712
Total explained			19.5%		

Table 5. Analysis of deviance for the GLM (family = gamma, link = log) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the central sector with first-order interactions between factors.

Factor	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				3 241	2 127
<i>Main effects</i>					
Month	11	279.7	13.1%	3 230	1 848
Year	19	105.7	5.0%	3 211	1 742
HP class	3	8.9	0.4%	3 208	1 733
<i>Interactions</i>					
Month:Year	169	325.7	15.3%	3 039	1 408
Year:HP class	42	64.7	3.0%	2 997	1 343
Total explained			36.9%		

The year:month interaction indicated that the seasonal pattern of cpue was not consistent in all years. Generally, there were two peaks per year, with variation in the peak months from year to year.

The HP class:year interaction indicated that in most years, vessels of HP classes 18–99 and 100–179 were more efficient than vessels of HP class <18. However, the magnitude of influence was exceptionally high for years 1994, 1996 and 2004.

Southern sector

Of the total trips, 359 (10%) were made in vessels of HP class <18; 2364 (65%) in HP class 18–99; 832 (23%) in HP class 100–179; and 78 (2%) in HP class ≥180. A total of 2656 trips (73%) were made in vessels of class s-1; 241 (7%) in class s-2; 680 (19%) in class i-1; and 56 (2%) in class i-2.

When interactions between factors were not considered, the following model was selected:

$$\ln \mu_{yhmkl} = \alpha + \beta_y + \varepsilon_h + \theta_m + \rho_l + \gamma_c \quad (6)$$

The adjusted model showed a coefficient of determination (r^2) of 40.7% and indicated that all factors were significant ($p < 0.05$) in explaining variation in cpue of *X. kroyeri*. The most important factor was year, explaining 21.3% of the model, followed by HP class, month, length class, and opening-month status (Table 6).

The efficiency of vessels in HP class ≥180 was 3.5 times that of vessels in HP class <18. The cpue peaked in May, then decreased substantially from June onward. The length classes s-2 and i-1 had a capture efficiency 1.4 and 1.9 times that of class s-1 vessels, respectively. The cpue during opening months was 1.2 times greater than in other months.

Table 6. Analysis of deviance for the GLM (family = gaussian, link = identity) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the southern sector.

Source of variation	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				3 633	3 483
Year	14	739.1	21.2%	3 619	2 744
HP class	3	480.5	13.8%	3 616	2 263
Month	11	164.2	4.7%	3 605	2 099
Length class	3	23.9	0.7%	3 602	2 075
Opening month	1	4.5	0.1%	3 601	2 071
Total explained			40.5%		

Table 7. Analysis of deviance for the GLM (family = gaussian, link = identity) fitted to log values of cpue (kg/day of fishing) for *X. kroyeri* in the southern sector with first-order interactions.

Source of variation	df	Deviance	% Explained	Res. df	Res. Deviance
NULL				3 633	3 483
<i>Main effects</i>					
Year	14	739.1	20.3%	3 619	2 744
HP class	3	480.5	13.2%	3 616	2 263
Month	11	164.2	4.5%	3 605	2 099
Length class	3	23.9	0.7%	3 602	2 075
<i>Interactions</i>					
Year:Month:	128	281.6	7.8%	3 474	1 794
Year: HP class	34	109.1	3.0%	3 440	1 685
HP class:Length class	3	15.0	0.4%	3 437	1 670
Total explained			52.1%		

Considering the first-order interactions between factors, the following model was selected:

$$\ln \mu_{yhmkl} = \alpha + \beta_y + \varepsilon_h + \theta_m + \rho_c + \beta\theta_{ym} + \beta\varepsilon_{yh} + \varepsilon\rho_{hc} \quad (7)$$

The model explained 52.1% of the total variation in the cpue. The year:month interaction was the most important factor and increased explanatory power by 8.0% compared with the previous model (Table 7). The q–q plot of this model is displayed in Figure 2c. The adjustment to cpue data from 100–179 HP class vessels is represented in Figure 3c.

The year:month interaction showed that the lowest cpue in the months from August to December (observed in the model without interaction) did not occur in the same way for all the years. In some years catch rates were exceptionally low during these months (1997, 2004 and 2008). Two cpue peaks occurred every year. However, there was variation in both the month when peaks occurred and in peak amplitude. In general, the highest cpue peak occurred between May and July, and the lowest occurred between September and November.

The interaction model indicated that the HP class factor differentially influenced catch rates during the analysed period. In most years, the expected pattern was observed, and vessels of higher HP classes had a higher efficiency. In 1998, HP class had an exceptionally high influence on cpue. In 1996, 1997, 2001 and 2002, however, the reverse of the general pattern was observed, with lower cpue in higher HP classes.

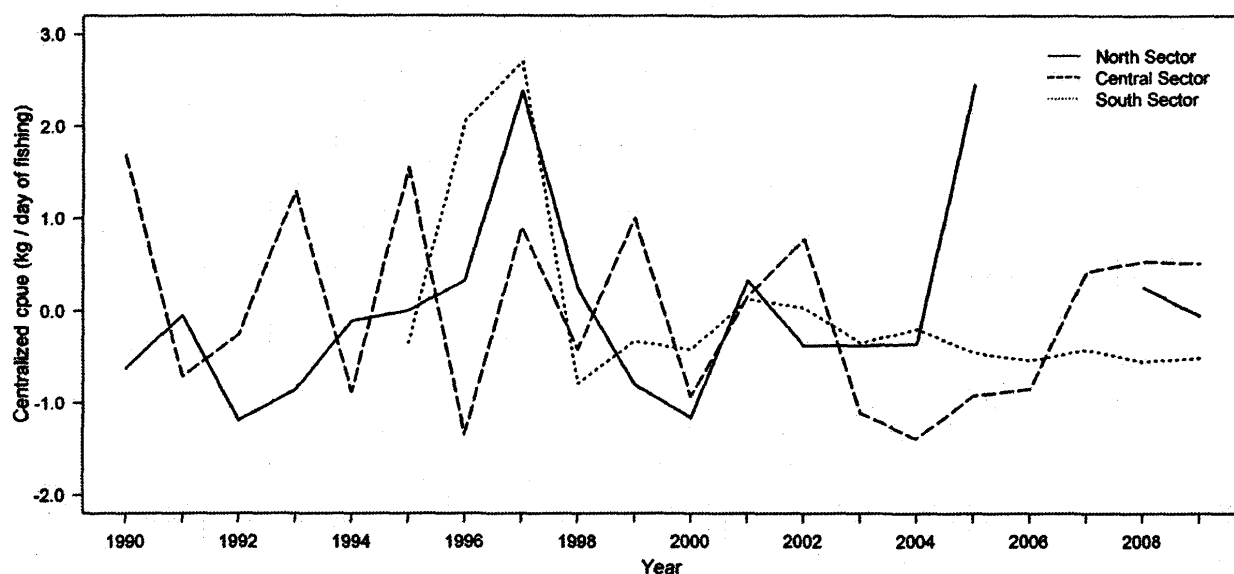


Figure 4. Time-series of standardized annual cpue for *X. kroyeri* between 1990 and 2009 in the northern, central and southern sectors. The values are centred to zero mean and 1 standard deviation.

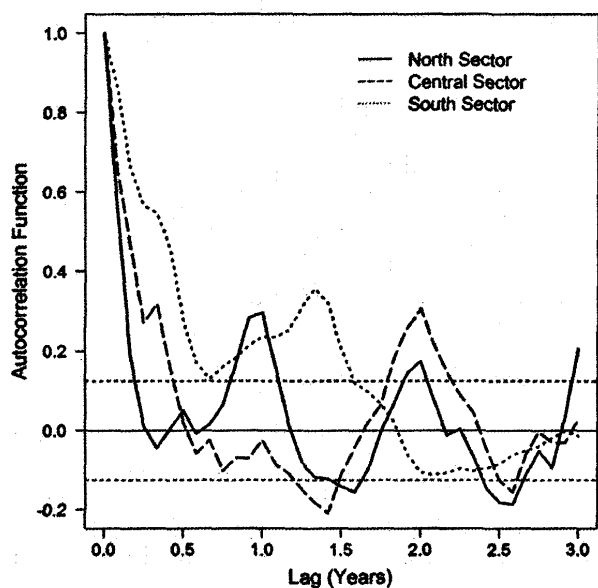


Figure 5. Autocorrelation of the standardized monthly cpue time-series (kg/day of fishing) for *X. kroyeri* in the northern, central and southern sectors. The time-lag is in years, and the dashed lines represent 95% confidence intervals.

Exploratory time-series analysis

In the northern sector, *X. kroyeri* abundance showed a similar pattern for the two decades in the study period. Two peaks occurred every ten years: a minor peak at the beginning (1991 and 2001) and a more pronounced peak in the middle of the decade (1997 and 2006, Figure 4).

In the central sector, the standardized cpue followed a general pattern with one- or two-year periods of high abundance followed by approximately two-year periods of low cpue. There was only one exception, between 2003 and 2006, when the cpues were low

for four years. Additionally, the magnitude of the peak decreased over the 20-year period.

In the southern sector, the *X. kroyeri* cpue increased substantially in 1996 and 1997. In 1998, the abundance dropped to very low levels then increased slightly from 1999 to mid-2002. From 2003–2009, the abundance tended to be stable, with a slight decrease (Figure 4).

The autocorrelation function applied to the series from the northern sector showed generally high values at time t , low values at time $t + 6$ and high values again at $t + 12$, indicating a strong intra-annual pattern with a 12-month period (Figure 5). For the central and southern sectors, the autocorrelation function revealed similar patterns, although they were not as clear as those observed for the northern sector. In general, negative correlation values were obtained at a lag of 6–7 months, returning to positive correlations after 11–12 months (Figure 5).

The cross-correlation function between the series of standardized cpues highlighted a seasonal variation pattern with periods of positive correlation of 12 months between the three sectors, indicating that the dynamics of this fishery follows similar temporal pattern in the whole study area. A weaker correlation was obtained between the central and southern sectors (Figure 6).

Discussion

Among the factors used in models to determine the magnitude of the influence of vessel characteristics on *X. kroyeri* catch rates, engine power (HP) was the most important and was a significant factor ($p < 0.05$) in all three fishing sectors. Several studies have found that engine power is one of the major contributors to the increased power of trawling vessels (Goni *et al.*, 1999; Rijnsdorp *et al.*, 2000; Marchal *et al.*, 2002; Maynou *et al.*, 2003; O'Neill *et al.*, 2003; O'Neill and Leigh, 2007; Lopes *et al.*, 2008). Engine power influences the speed at which the trawl net can be towed, which in turn affects the vertical and horizontal opening, effective area and sweep volume of the net (Gulland, 1956; Weinberg and Kotwicki, 2008).

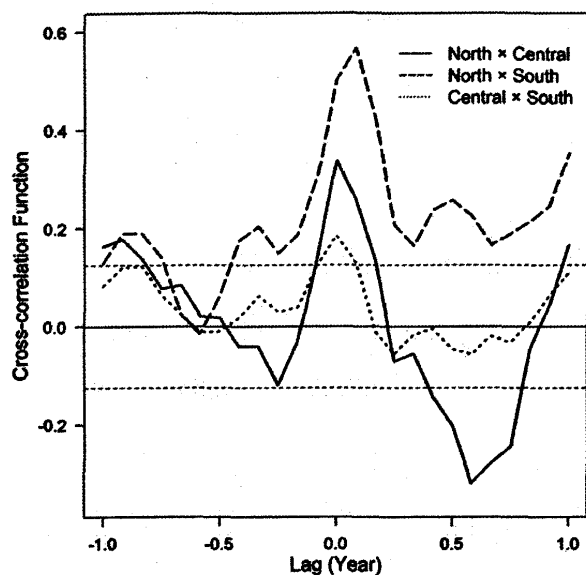


Figure 6. Cross-correlation of the standardized time-series of *X. kroyeri* cpue for different sectors: central and northern, southern and northern and southern and central. The time-lag is in years, and the dashed lines represent 95% confidence intervals.

Although vessel length had a significant influence in the northern and southern sectors, length was never one of the most influential factors. Among vessels of similar lengths, changes in other physical characteristics, such as engine power, had a greater influence on fishing power.

The results on the significance of the effects of engine power and length of the vessel were important to time-series analysis. A variation in fishing power implies a variation in catchability and hence in a change on the proportionality between cpue and stock density (Marchal *et al.*, 2002). Commercial catch and effort data are observational datasets and standardization is necessary to minimize bias due to the confounding of apparent abundance patterns with fishing power (Bishop, 2006).

When the interactions between factors were not considered, the fitted models for the three sectors indicated a pattern of seasonal variation in the cpue of *X. kroyeri*. A sharp peak occurred in the austral fall, specifically in the month of June for the northern sector, in May and June for the central sector, and in May for the southern sector. In all three sectors, cpue dropped sharply during the second half of the year, with a small increase during the austral spring. For the northern, central and southern sectors, this smaller peak occurred in November, October and September, respectively.

The inclusion of first-order interactions in the three models, particularly the year:month interaction, substantially improved the explanatory power of the total variation in *X. kroyeri* cpue. The importance of the year:month interaction indicates that the seasonal pattern was not the same in all years. More specifically, both the intensity and month of occurrence of the abundance peaks varied from year to year in a window of about three months (May to July). This could be verified on GLM and time-series analysis.

Studies have shown that *X. kroyeri* reproduces throughout the year. Female maturation occurs twice annually, from August–October and from February–April. These peaks result in an influx of juveniles during the austral spring and autumn (Nakagaki and

Negreiros-Fransozo, 1998; Branco, 2005; Castro *et al.*, 2005). However, we observed variations in the months when these peaks occurred, indicating that the time of onset of recruitment varied from year to year, as these studies considered distinct periods (Nakagaki and Negreiros-Fransozo, 1998; Branco *et al.*, 1999; Fransozo *et al.*, 2000; Branco, 2005; Castro *et al.*, 2005).

The opening-month status was a significant factor only in those models that did not consider interactions. This was due to variations in or the absence of a closed fishing period from year to year. Thus, the year:month interaction accounted for the variability caused by this factor. Fishery closure during the main recruitment season is a common method used for the protection and restoration of shrimp stocks worldwide (Garcia, 1989). The present findings suggest that temporary fishing bans had positive effects on the *X. kroyeri* stock in southeastern Brazil.

A sharp drop in catch rates in the second annual semester was observed across the three fishing sectors. This decrease was most likely due to the coincidence of the fall recruitment season at the fishery with the opening of the fishing season, typically in June. Thus, an intensive fishing effort on the species may have resulted in a drop in cpue in the second half of the year.

Although the month of peak cpue varied from year to year, it generally followed a latitudinal pattern. Both autumn and spring peaks occurred first in the southern sector, then in the central sector and finally in the northern sector. One possible explanation for this latitudinal pattern is that the peaks of reproduction and/or recruitment are linked to oceanographic variables that follow the same pattern. The life cycle and spatial and temporal distribution patterns of penaeid shrimp are influenced by several environmental factors (Boschi, 1963; Dall *et al.*, 1990; Fransozo *et al.*, 2002; Costa and Fransozo, 2004; Castro *et al.*, 2005; Costa *et al.*, 2005, 2007). However, there is no consensus in the literature regarding the factors that effectively trigger the increase in reproductive activity (Fransozo *et al.*, 2002; Castro *et al.*, 2005; Costa *et al.*, 2007).

The results indicate that the observed variation in the catch pattern from year to year must have occurred because of temporal variations in both the onset of recruitment and the timing of fishing bans.

The cross-correlation between the time-series for annual standardized cpue indicated that the interannual variation was similar for the northern and southern sectors but different for the central sector, possibly due to differences in fleet characteristics. The majority of vessels in the central fleet belonged to the length class i-1 and HP class 100–179, while the majority in the northern and southern sectors belonged to the length class s-1 and HP class 18–99.

Larger vessels with more powerful engines have a wider radius of action and are capable of altering their fishing area in response to local variations in the abundance of the target species. In the central sector, variation in the preferred capture area of *X. kroyeri* was observed. Between 1990 and 1997, an average of 36% of the annual *X. kroyeri* catch was from the area between 24°20'S and 24°30'S, and 18% was from the area between 24°00'S and 24°10'S. From 1998–2002, captures in the former area represented only 5% of the annual total, while the latter area represented 45%. Between 2003 and 2009, 45% of the total catch was obtained from the former area, and 6% was from the latter. In the northern and southern sectors, variations in preferred fishing areas were not identified.

Local variations in species abundance likely influenced the central sector fleet, resulting in a shifted operating area from 1998–2002 towards the more northern latitudinal range. On the

basis of the lower mobility observed for the northern and southern fleets, these sectors are more directly affected by regional changes.

For the northern and southern sectors, a marked increase in *X. kroyeri* cpue was observed in 1996 and 1997 along with a less prominent peak in 2001 and 2002. In the central area, cpue oscillated with a period duration of approximately two years. Time-series graphs of cpue with standardized effort did not reveal any clear trends over the 20 years analysed. This result indicates that cpue has remained stable, with random variations that may have occurred in response to environmental variations.

Two evaluations of the species stock in the southeastern and southern regions of Brazil were previously reported. The first study found that during the 1980s, the fishing effort was generally above the estimated maximum sustainable effort (Valentini *et al.*, 1991). The second study found that in 1990, there was a significant reduction in the maximum sustainable yield, maximum sustainable effort and maximum relative abundance; however, the fishing effort for those years was at or below the estimated maximum sustainable effort (D'Incao *et al.*, 2002).

Although populations of this species were reduced in the 1980s due to excessive harvesting, the fishing effort levels from 1990–2009 allowed stocks of *X. kroyeri* to remain at stable levels, with oscillations that may have occurred in response to local environmental variations. In Brazil, *X. kroyeri* is considered an overexploited stock (Paiva, 1997; MMA, 2004). However, a stock in this condition can be re-established at lower population levels and remain stable indefinitely, without the collapse of the fishery (Hilborn and Hilborn, 2012).

The *X. kroyeri* fishery and stocks should be carefully managed. The necessary precautions include a restriction of the fishing effort because the stock is sensitive to environmental variations and populations have been reduced by excessive fishing activity in the past. Additionally, the identification of key environmental factors that influence the abundance of this species is of utmost importance and should be incorporated into the management of the *X. kroyeri* fishery.

It was concluded that the variations in the relative abundance of *X. kroyeri*, measured by cpue, were primarily due to fluctuations in population size that resulted from the reproductive cycle and recruitment patterns of the species. This effect was amplified by the closed fishing season, which reduced fishing mortality during an important period of the life cycle. The physical characteristics of vessels also contributed significantly to the variation in cpue. This finding highlights the importance of effort standardization to ensure that catch rates are adjusted in response to oscillations in population size. In particular, vessel engine power should be considered for the purposes of fisheries planning and management. Despite significant variations, the estimated relative abundance of *X. kroyeri* neither increased nor decreased from 1990–2009, indicating that the species has been harvested at stable levels. However, the stock should be managed with extreme caution. Its population was reduced by overfishing and undergoes significant annual variations in abundance, which most likely occur in response to environmental variations.

Supplementary data

The following supplementary data are available at *ICES Journal of Marine Science* online:

- (i) coefficients estimates of the GLM without interactions for *X. kroyeri* in the northern, central and southern sector; and

- (ii) stepwise model results of the GLM for *X. kroyeri* in the northern, central and southern sector with first-order interactions between factors.

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