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Latitudinal and bathymetric distribution patterns of ophiuroids (Echinodermata: Ophiuroidea) on scallop fishing grounds at the shelf-break frontal system, south-western Atlantic

MARIANA ESCOLAR[1], DANIEL RAÚL HERNÁNDEZ[1] AND CLAUDIA SILVIA BREMEC[1,2]

[1]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo 1, B7602HSA, Mar del Plata, Argentina, [2]Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Dean Funes 3250, Mar del Plata, Argentina

Ophiuroidea represents the dominant invertebrate group in Patagonian scallop fishery by-catch in the south-western Atlantic. This study presents information that brings forward the spatial patterns and abundance of the most abundant species in the benthic community associated with this fishery at the shelf-break front in the Argentine Sea, between 37° and 44°S during the period 2002–2005. Ophiactis asperula, Ophiacantha vivipara, Ophiura (Ophiuroglypha) lymani *and* Gorgonocephalus chilensis *show a latitudinal and bathymetric distribution pattern, explained by their natural distributional ranges and feeding habits. Our results indicate that the abundance and distribution of these species are not related to scallop fishing activities.*

Keywords: ophiuroids, distribution pattern, latitude, depth, scallop fishing grounds, south-western Atlantic Ocean

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INTRODUCTION

Ophiuroids have a worldwide distribution and exploit all kinds of marine benthic habitats from shallow to abyssal depths, often numerically dominating the megafauna (Gage & Tyler, 1982; Summers & Nybakken, 2000; Cranmer *et al.*, 2003). The shallow species are generally associated with sponges, gorgonians and other organisms with erect structures (Gutt & Schickan, 1998; Hendler, 2005; Neves *et al.*, 2007), while those species from shelf and deep areas form dense aggregations covering several kilometres on the sea bed (Piepenburg *et al.*, 1997; Metaxas & Giffin, 2004). Ophiuroids have an important role in the production and ecology of several benthic marine communities due to their high abundance, feeding habits and high activity rates in removing great amounts of organic matter from the seabed. They also represent a significant sink of benthic biomass (Ambrose *et al.*, 2001; Davoult *et al.*, 2009), but their living habits on the sea-floor may be sometimes affected by trawling fisheries on the continental shelves. The most common effects of trawling on these organisms are the direct removal and physical damage (e.g. arm loss and crushing disc) (Bergmann & Moore, 2001; Brooks *et al.*, 2007). Ophiuroids use their arms for feeding and movement, therefore arm loss can have negative effects on them (Pranovi *et al.*, 2001; Harris *et al.*, 2009). However, some ophiuroid species could benefit from an increase in food availability as a result of fishery discards (Gilkinson *et al.*, 2005; Callaway *et al.*, 2007).

Thirty-two species of ophiuroids have been identified in the Argentine Sea (Bernasconi & D'Agostino, 1977; Brogger *et al.*, 2013), but the information about these species is scarce and mainly consists of faunistic records (Lyman, 1882; Mortensen, 1936), taxonomy studies (Bernasconi & D'Agostino, 1971, 1977) and reports from different benthic communities (Roux *et al.*, 1988; Bremec & Lasta, 2002). Nevertheless, it is known that ophiuroids comprise one of the most important groups in the epibenthic invertebrate assemblage from the Patagonian scallop (*Zygochlamys patagonica*) fishing grounds, mainly because of their high contribution in biomass, abundance and production to the community (Bremec *et al.*, 2000; Bremec & Lasta, 2002; Schejter *et al.*, 2008; Escolar, 2010). Ophiuroids represent the first link in the trophic web of this epibenthic community, being the main prey for starfish, snails and echinoids (Botto *et al.*, 2006; Mauna *et al.*, 2011).

The present study aims at providing ecological information about this group in the shelf-break frontal system of the south-western Atlantic Ocean (SW Atlantic Ocean). The analysis of the ophiuroid community in the Patagonian scallop fishing grounds was made on the bases of their composition, spatial

Corresponding author:
M. Escolar
Email: marianaescolar@inidep.gob.ar

distribution and abundance in response to latitude, depth and fishing effort.

MATERIALS AND METHODS

Study site and sampling

Specimens were collected between 36°56′S and 43°30′S and between 80 and 140 m depth (Figure 1), as part of the epibenthic invertebrate assemblage that is dominated by the Patagonian scallop *Zygochlamys patagonica* (King, 1832). This area corresponds to the main Patagonian scallop fishing grounds associated with the Argentine shelf-break front in the SW Atlantic Ocean (Acha *et al*., 2004; Bogazzi *et al*., 2005). This front has been described as a thermohaline shelf-break front (Martos & Piccolo, 1988) produced by the encounter of the sub-Antarctic shelf waters with the cooler and more saline waters of the Malvinas Current (Falklands Current). The permanent feature created by this encounter characterizes the border of the Argentinian shelf with the inner boundary lying between the 90 and 100 m isobaths. This shelf-break front extends from the Burdwood Bank (~55°S) along the shelf break to the east, around the Malvinas Islands (Falklands Islands) and northwards up to the Brazil/Malvinas Confluence (Brazil/Falklands Confluence) (~38°S) (Acha *et al*., 2004).

Benthic samples were collected with a 2.5 m wide dredge fitted with a 10 mm mesh during eight Patagonian scallop's research surveys from 2002 to 2005 on-board the RV 'Capitán Cánepa'. Standard towing time was 10 min and the speed was 3.4 knots during the Patagonian scallop stock assessment surveys. A total of 514 sub-samples (10 l) were taken from each catch and frozen on-board. Once in the Benthos Laboratory at the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), all ophiuroid specimens were sorted, identified and counted.

DATA ANALYSIS

For each species, the frequency of occurrence (number of positive samples for each species/total number of samples) was calculated for all the study area. Abundance (ind m^{-2}) at each station was calculated by the swept area method, as abundance $= c/ae$, where c is the total catch in each tow, a is the area swept by the gear (mean $\pm$ SD: 2722.9 ± 198.9 m^2, tow length = 10 min) and e is gear efficiency estimated at 43% (Valero, 2002).

To study ophiuroids distribution patterns we used a generalized linear model (GLM) (McCullagh & Nelder, 1989). Generalized additive models (GAMs) were fitted preliminarily, taking into account possible non-linear relationships (Wood, 2006). If non-linear relationships were found with GAMs, appropriate terms (e.g. quadratic) were added to the GLM. The abundance (ind m^{-2}) of each species was the response variable while latitude, longitude, year, depth, *Zygochlamys patagonica* abundance ($\log_{10}$) and fishing effort ($\log_{10} + 1$) were treated as explanatory variables. Depth was selected as an explanatory variable because of its influence on ophiuroids distribution (Gage & Tayler, 1982; Piepenburg *et al*., 1997; Summers & Nybakken, 2000). *Zygochlamys patagonica* abundance was also selected because it is the dominant species and it is considered an ecosystem engineer in the study area (Shejter & Bremec, 2007). The fishing effort was estimated as the number of commercial trawls on each sampling station from the beginning of the fishery to the beginning of each conducted research survey (Løkkeborg, 2005). Years

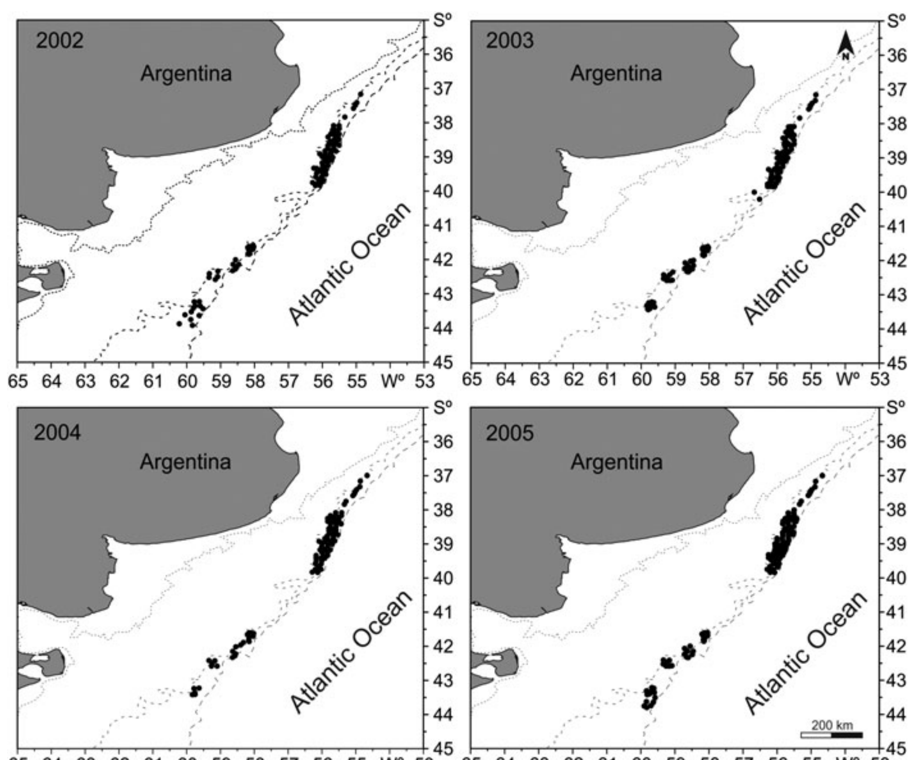

Fig. 1. Positions of the sampling locations in the shelf-break frontal area of the Argentine Sea during the four study years.

were used as a categorical variable. Finally, the longitude was not included in the model because of a strong correlation with latitude.

Abundance (ind m^{-2}) was $\log_{10}(x + 0.1)$ transformed previously to fit the requirements of the statistical tests. The models were fitted using Gaussian errors and identity as link function (Hastie & Tibshirani, 1990). The best model to describe our data was selected using Information Theory, with the lowest Akaike information criterion (AIC) (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). A stepwise backward selection procedure based on minimization of AIC was performed. For each full model containing a combination of explanatory variables, sequential deletion of explanatory variables was conducted until all the possible combinations were tested. The best model was chosen as the one with the lowest AIC. Residual plots were evaluated for violations of model assumptions.

The possible spatial correlation among the GLM residuals was calculated considering experimental semi-variograms. For these analyses we consider distances less than or equal to half the maximum distance among sampling stations and a number of pairs of points in each interval distance more than 50 (Journel & Huijbregts, 1978). We applied a generalized least square (GLS) in those species which presented a residual spatial autocorrelation. This method includes spatial correlation in the regression model through a variance–covariance structure, assuming a parametric correlation function estimated from the semi-variograms (Crawley, 2007; Dormann *et al.*, 2007). All statistical procedures were conducted using the open-source language R, version 2.15.0 (R Development Core Team, 2012).

RESULTS

A total of five ophiuroid species were associated with the shelf-break frontal system: *Gorgonocephalus chilensis* (Philippi, 1858), *Ophiura* (*Ophiuroglypha*) *lymani* (Ljungman, 1871), *Ophiacantha vivipara* Ljungman, 1870, *Ophiomyxa vivipara* Studer, 1876 and *Ophiactis asperula* (Philippi, 1858). The most ubiquitous and dominant species in the samples was *O. asperula* (90.7%). *Ophiomyxa vivipara* was found in 70.6% of the samples, while *O.O. lymani* and *G. chilensis* were recorded in 56.4% and 54.9% of the samples respectively. Among the five mentioned species, *Ophiomyxa vivipara* was considered 'occasional' because of its low frequency of occurrence (1.4%).

Ophiactis asperula abundance ranged from 0.009 to 337.89 ind m^{-2} per sample (mean abundance $\pm$ standard deviation $= 18.83 \pm 41.18$ ind m^{-2}, $N = 514$). This variability can be explained by latitude, *Zygochlamys patagonica* abundance and year (Table 1). The abundance of *O. asperula* showed a positive relationship with *Zygochlamys patagonica* (Figure 2A). *Ophiactis asperula* had a quadratic relationship with latitude; maximum abundances were registered between 41° and 42°S and in southern areas (Figure 2A). The abundance of *O. asperula* was significantly higher during 2004 (Figure 2A; Table 1).

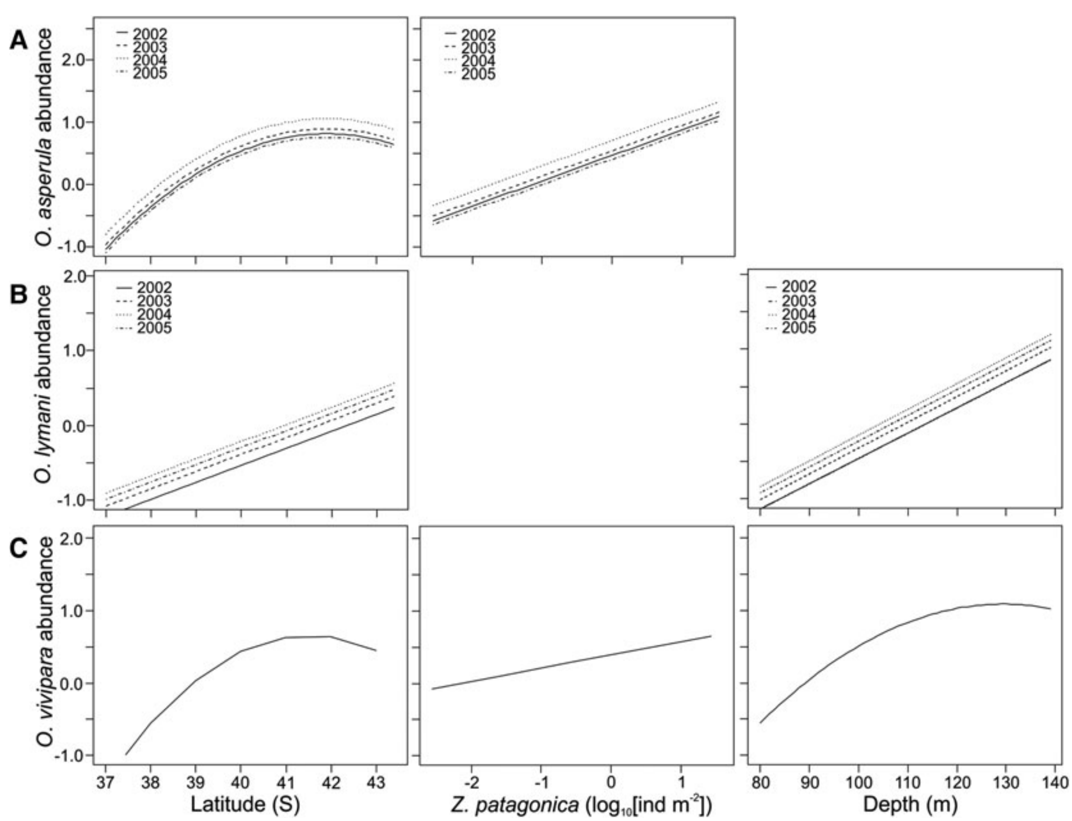

Fig. 2. (A) *Ophiactis asperula*: relationship between abundance ($\log_{10}$ [ind $m^{-2} + 0.1$]) and latitude and *Zygochlamys patagonica* abundance ($\log_{10}$ [ind m^{-2}]), estimated from a generalized least squares (GLS) with normal distribution; (B) *Ophiura (Ophiuroglypha) lymani*: relationship between abundance ($\log_{10}$ [ind $m^{-2} + 0.1$]) and latitude and depth, estimated from a generalized linear model with normal distribution; (C) *Ophiacantha vivipara*: relationship between abundance ($\log_{10}$ [ind m^{-2}]) and latitude, *Zygochlamys patagonica* abundance ($\log_{10}$ [ind $m^{-2} + 0.1$]) and depth (m), estimated from a GLS with normal distribution.

Table 1. Results of generalized linear model among *Ophiactis asperula* abundance ($\log_{10}$ [x + 0.1]) and the variables selected by the Akaike information criterion. A spherical spatial correlation was used with range = 20 km and nugget = 0.3. The model explained 44% of the total variance. *Z. patagonica* = *Zygochlamys patagonica* abundance ($\log_{10}$ [ind m^{-2}]). Significant relationships are in bold typeface.

	Estimate	SE	*t*	*P*
Intercept	−134.538	49.004	−2.745	**0.006**
Year 2003	0.076	0.060	1.259	0.208
Year 2004	0.242	0.062	3.869	**<0.001**
Year 2005	−0.058	0.059	−0.976	0.329
Z. patagonica	0.406	0.043	9.454	**<0.001**
Latitude	6.459	2.432	2.656	**0.008**
Latitude^2	−0.077	0.030	−2.560	**0.012**

Estimate, coefficient estimated; SE, standard error; *t*, observed value; *P*, significance level; ^{2}, quadratic terms.

Ophiura (*Ophiuroglypha*) *lymani* was one of the less abundant species during the study period with a range abundance between 0.002 and 155.53 ind m^{-2} per sample and an estimated mean abundance of 3.76 ± 13.11 ind m^{-2} (N = 514). According to GLM results the variability within samples could be explained by latitude, depth and year (Table 2). *Ophiura* (*Ophiuroglypha*) *lymani* abundance increased with depth and latitude. The lowest abundance values were recorded in 2002 (Figure 2B).

Ophiacantha vivipara had a mean abundance equal to 6.24 ± 11.03 ind m^{-2} in a variable range between 0.001 and 110.14 ind m^{-2} (N = 514). The GLS results are shown in Table 2; *O. vivipara* abundance showed a quadratic relationship with latitude and depth (Figure 2C; Table 3). The highest abundances were recorded at approximately 41° – 42°S and the lowest between 37°S and 38°S (Figure 2C). *Ophiacantha vivipara* also showed a positive relationship with *Zygochlamys patagonica* abundance (Figure 2C; Table 3). In regards to depth, the highest abundance values were recorded between 100 and 130 m (Figure 2C).

As the relationship between abundance and depth was important for the three species, we plotted relative abundance of each station against depth (Figure 3). Although the three species coexist, we observed that *Ophiactis asperula* dominated at depths between 80 and 100 m with a conspicuous decrease in its abundance at depths more than 100 m (Figure 3). On the other hand, the abundance of *Ophiacantha vivipara* and *Ophiura* (*Ophiuroplypha*) *lymani* showed an increase at depths >100 m.

In the case of *Gorgonocephalus chilensis* no model fitted the data. Nevertheless, raw data showed more abundance of this species in northern and shallower areas (Figure 4).

Table 2. Results of generalized linear model among *Ophiura (Ophiuroglypha) lymani* abundance ($\log_{10}$ [x + 0.1]) and the variables selected by the Akaike information criterion. The model explained 46.52% (F = 87.7, $P < 0.01$, N = 510) of the total variance. Significant relationships are in bold typeface.

	Estimate	SE	*t*	*P*
Intercept	−13.083	0.655	−19.945	**<0.001**
Year 2003	0.145	0.072	2.007	**0.045**
Year 2004	0.318	0.076	4.166	**<0.001**
Year 2005	0.237	0.073	3.265	**0.001**
Depth	0.035	0.002	14.135	**<0.001**
Latitude	0.229	0.015	15.278	**<0.001**

Estimate, coefficient estimated; SE, standard error; *t*, observed value; *P*, significance level.

Table 3. Results of generalized least squares among *Ophiacantha vivipara* abundance ($\log_{10}$[x + 0.1]) and the variables selected by the Akaike information criterion. A spherical spatial correlation was used with range = 20 km and nugget = 0.15. The model explained 55.81% of the total variance. *Z. patagonica* = *Zygochlamys patagonica* abundance ($\log_{10}$ [ind m^{-2}]). Significant relationships are in bold typeface.

	Estimate	SE	*t*	*P*
Intercept	−169.341	57.256	−2.958	**0.003**
Depth	0.146	0.058	2.528	**0.012**
Depth^2	−0.001	0.0003	−2.079	**0.038**
Latitude	7.742	2.799	2.765	**0.006**
Latitude^2	−0.093	0.035	−2.684	**0.007**
Z. patagonica	0.172	0.034	5.027	**<0.001**

Estimate, coefficient estimated; SE, standard error; *t*, observed value; *P*, significance level; ^{2}, quadratic terms.

DISCUSSION

Ophiuroids are one of the dominant taxonomic groups on continental shelves, shelf-breaks and abyssal areas worldwide (Metaxas & Giffin, 2004; Chiantore *et al.*, 2006; O'Hara, 2007). *Ophiactis asperula*, *Ophiacantha vivipara* and *Ophiura* (*Ophiuroplypha*) *lymani* are the most abundant species in the benthic community associated with the shelf-break front (Bremec & Lasta, 2002; Schejter *et al.*, 2008; Escolar, 2010), and together with *Zygochlamys patagonica*, account for the major secondary production rates (Bremec *et al.*, 2000).

Ophiactis asperula, *Ophiacantha vivipara* and *Ophiura* (*Ophiuroplypha*) *lymani* were widely distributed in the study area. However, *O. asperula* was present over the full range of latitude and depths studied; this species dominated in terms of abundance. *Ophiactis asperula* and *Ophiacantha vivipara* showed a positive relationship with *Zygochlamys patagonica* abundance, early recognized as a characteristic of the epibenthic fauna associated with the shelf-break front in 1995, previous to the scallop fishery (Bremec & Lasta, 2002). *Ophiactis asperula, Ophiacantha vivipara* and *Z. patagonica* are suspension feeders; therefore, high abundances of these species were recorded in those areas influenced by the high productivity of the shelf-break front (Acha *et al.*, 2004; Botto *et al.*, 2006; Mauna *et al.*, 2011).

The three species of ophiuroids showed a latitudinal distribution pattern increasing significantly southwards. The highest values of *Ophiactis aperula* and *Ophiacantha vivipara* were recorded between 41° and 43°S approximately, while the abundance of *Ophiura* (*Ophiuroglypha*) *lymani* increased beyond the study area; the location of the less abundant samples in this study coincided with the northern boundary of natural distribution of sub-Antarctic species (Bernasconi & D'Agostino, 1977; Bartsch, 1982; Barboza *et al.*, 2011).

Bathymetric distribution patterns are commonly found in ophiuroids (Gage & Tyler, 1982; Summers & Nybakken, 2000; Metaxas & Giffin, 2004) often related to food availability (Metaxas & Giffin, 2004; Booth *et al.*, 2008), oxygen

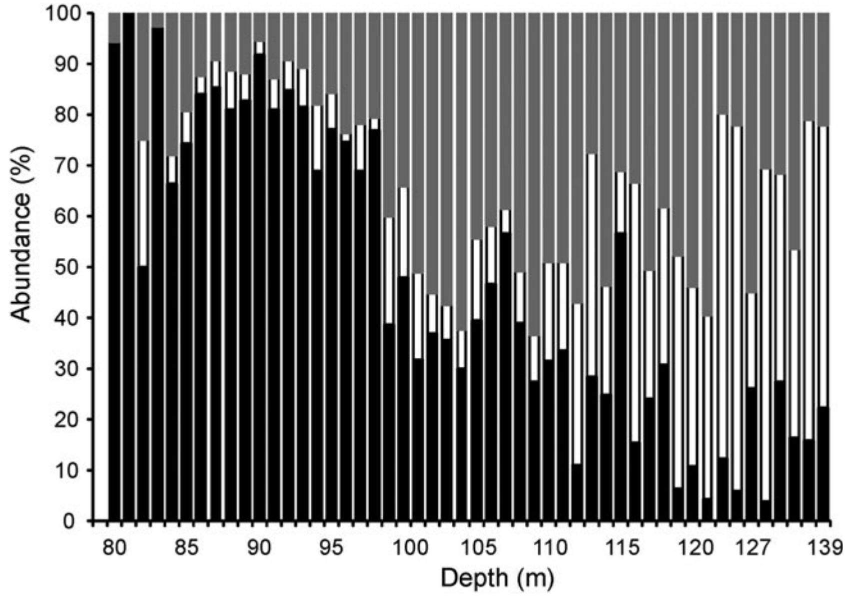

Fig. 3. *Ophiactis asperula*, *Ophiacantha vivipara* and *Ophiura lymani*: relative abundance (%) versus depth (m).

concentration (Summers & Nybakken, 2000), sediment type, salinity, temperature and currents (García *et al.*, 2002; Manjón-Cabeza & Ramos, 2003). In this study, the distribution of *Ophiacantha vivipara* and *Ophiura* (*Ophiuroglypha*) *lymani* was significantly influenced by depth, and although both species increased their abundance toward deeper areas, *Ophiacantha vivipara* reached its highest abundance values between 120 and 130 m.

The analysis of relative abundance per sample showed a depth segregation pattern among the three species: *Ophiactis asperula* was more abundant in samples collected between 80 and 100 m; *Ophiacantha vivipara* dominated in samples collected between 100 and 125 m; and *Ophiura* (*Ophiuroplypha*) *lymani* dominated in deeper samples (>125 m). Similar bathymetric distribution patterns were recorded for *Ophiacantha vivipara* and *Ophiactis asperula* before the Patagonian scallop fishery started (Roux *et al.*, 1993). Our results indicated that scallop fishing activities in the area did not affect the species distribution during the period 2002–2005.

As previously mentioned, niche separation in many species can be explained by different abiotic factors (Ventura & da Costa Fernandez, 1995; Gage *et al.*, 2000; Tuya *et al.*, 2007). It is known that substrates are rather homogeneous in the study area, with predominant soft sediments composed mainly of sand and variable shell content (Parker *et al.*, 1997). Bottom temperatures range between 5° and 8°C with higher values in northern areas (~37.5°S) associated with the presence of the Brazilian Current over the slope (Bogazzi *et al.*, 2005). As the three ophiuroid species studied have omnivorous feeding habits, we propose that the different bathymetric patterns could represent a way of avoiding interspecific competition. *Ophiactis* species show diverse feeding strategies including deposit and suspension feeding (Warner, 1982; Pearson & Gage, 1984; Hendler *et al.*, 1995). *Ophiacantha* species are suspension feeders, although organisms that reside on sediment surface were also recorded in their gut contents (Fell, 1961; Pearson & Gage, 1984). *Ophiacantha vivipara* feeds on copepods and carrion in Antarctica (Fell, 1961; Warner, 1982; McClintock, 1994), while *Ophiura* (*Ophiuroplypha*) *lymani* feeds on detritus, sediment and crustaceans in southern Chile (Dahm, 1999). Clear depth segregation was observed although the bathymetric range of the three species overlaps (Bernasconi & D'Agostino, 1977). This result could be supported by the feeding habits, since suspension feeder species like *Ophiactis asperula* and *Ophiacantha vivipara* were mainly recorded at lower depths influenced by the shelf-break front (Acha *et al.*, 2004; Bogazzi *et al.*, 2005; Mauna *et al.*, 2011). On the other hand, detritivorous species like *Ophiura lymani* would prefer deeper bottoms with higher contents of fine particles (Parker *et al.*, 1997).

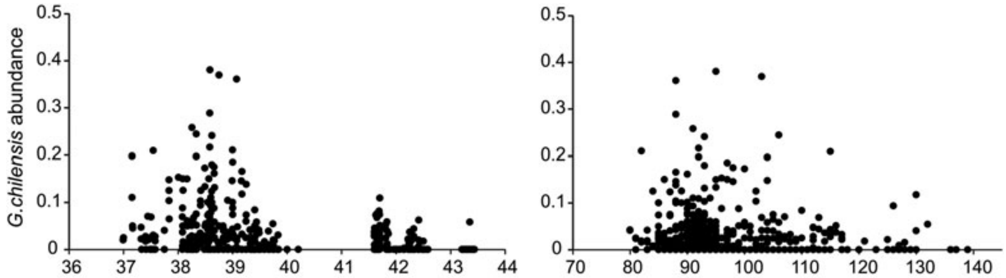

Fig. 4. *Gorgonocephalus chilensis*: abundance (ind m^{-2}) in function of latitude (°S) and depth (m).

O'Hara *et al.* (2011) showed that latitude and depth are two of the variables which contributed substantially to explain the distribution patterns of ophiuroids in the Indian, Pacific and Southern Oceans. According to O'Hara *et al.* (2011), demographic and/or evolutionary processes may have an effect on ophiuroid distribution. In this case, the study area is recognized as transitional between the two biogeographical provinces in the Argentine Sea (Balech & Erlich, 2008). *Ophiactis asperula* is typical of the Argentine province, influenced by the northern Brazil Current, while *Ophiacantha vivipara* and *Ophiura* (*Ophiuroglypha*) *lymani* characterize the Magellan province, influenced by sub-Antarctic waters (Bernasconi & D'Agsotino, 1977; Souto *et al.*, 2011).

In conclusion, the most abundant ophiuroid species at the shelf break front, *Ophiactis asperula*, *Ophiacantha vivipara* and *Ophiura* (*Ophiuroplypha*) *lymani*, showed latitudinal and bathymetric distribution patterns explained partly by their feeding habits, a strategy that possibly helps to avoid interspecific competition. Studies on the biology and ecology of echinoderms are being developed to increase the knowledge about benthic invertebrates in the Argentinean continental shelf with particular emphasis on the productive shelf-break frontal system.

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Correspondence should be addressed to:
M. Escolar
Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo No. 1,
B7602HSA, Mar del Plata, Argentina
email: marianaescolar@inidep.gob.ar