

## Links between marine fauna and oceanic fronts on the Patagonian Shelf and Slope

ALEXANDER ARKHIPKIN, PAUL BRICKLE & VLADIMIR LAPTIKHOVSKY



Arkhipkin, A., P. Brickle & V. Laptikhovskiy 2013. Links between marine fauna and oceanic fronts on the Patagonian Shelf and Slope. *Arquipelago*. Life and Marine Sciences 30: 19-37.

One of the main oceanographic features in the Southwest Atlantic is the transport of cold waters of Sub-Antarctic origin along the Patagonian slope to temperate latitudes (40-42°S) by the Falkland Current. Originating from the Antarctic Circumpolar Current in the Drake Passage, the Current splits into two main northward streams skirting the Falkland Islands from west and east. The strongest eastern branch meanders onto the shelf to the south of Beauchêne Island and north-east of the Falkland Islands and creates four fronts with strong upwellings of the Sub-Antarctic Surface Water Mass (SASW). Extension of SASW to the shelf break and its mixture with shelf waters creates quasi-stationary areas of high productivity. Sub-Antarctic fishes (e.g., southern blue whiting) utilise these areas as their feeding and spawning grounds. Deepwater toothfish and squid (*Onykia ingens*) use them as pathways to migrate from the shelf to deepwater habitats. Temperate fish (e.g., hoki and rock cod) and squid (*Illex argentinus*) feed mainly at the frontal zones with mixture of SASW and Patagonian Shelf waters. The presence of four quasi-stationary meso-scale fronts between the deepwater Falkland Current and shelf waters plays an important role in distribution, migrations and spawning of marine fauna that use them in accordance to their Sub-Antarctic and temperate origins.

Key words: Falkland Current, Falkland Islands, frontal zones, distribution, Sub-Antarctic and temperate marine fauna

Alexander Arkhipkin (e-mail: aarkhipkin@fisheries.gov.fk), Paul Brickle & Vladimir Laptikhovskiy, Directorate of Natural Resources, Fisheries Department, P.O. Box 597, Stanley, FIQQ 1ZZ, Falkland Islands.

### INTRODUCTION

The Patagonian Shelf and Slope are among the most productive areas in the Southwest Atlantic. Two marine ecosystems, the southern temperate ecosystem and sub-Antarctic ecosystem have an ecotone zone here running from the south-western part to the north-eastern part of the Patagonian Shelf through the Falkland (Malvinas) Islands archipelago (Boltovskoy 2000). The abundant pelagic and demersal resources on the Shelf support numerous international trawl and jigging fleets that have been taking annually up to 1 million tonnes of squid, mainly Argentinean squid *Illex argentinus* and Patagonian squid *Doryteuthis gahi* and fish, mainly hakes *Merluccius hubbsi*

and hoki (whiptail hake) *Macruronus magellanicus* (Csirke 1987).

The productivity of the Patagonian Shelf is enhanced by the existence of several year-round tidal mixing fronts (Valdés Front, San Jorge Front and Bahia Grande Front) and seasonal fronts (Patagonian–Magellan Front and Tierra del Fuego Front) originating from cold fresh water inflows from the Straits of Magellan (Belkin et al. 2009). The Patagonian Shelf edge is framed by the Falkland/Malvinas Current Front (FMCF, Belkin et al. 2009) also known as the Argentine shelf-break front (Acha et al. 2004), Patagonian shelf break front (SBF, Franco et al. 2008) and Shelf-break Frontal System (SBFS, Martos & Piccolo 1988). Being a typical example of the western boundary

current fronts, the FMCF runs along the continental slope from 55°S to 37°S and consists of multiple meso-scale fronts parallel to the shelf break (Franco et al. 2008). The main oceanographic feature of this front, the cold-water Falkland (Malvinas) Current, originates from the Antarctic Circumpolar Current (ACC) in Drake Passage and flows northwards (Peterson & Whitworth 1989). The Current reaches the continental slope to the south of the Falklands and splits into two main northward-flowing branches embracing the Islands from the west (the weaker western branch of the Falkland Current) and east (the stronger eastern branch of the Falkland Current) (Bianchi et al. 1982). The upper 300-m water layer of the Falkland Current consists of the Subantarctic Surface Water Mass (SASW) with deeper layers occupied by Antarctic Intermediate Water mass (AIW) (Peterson & Whitworth 1989).

One of the quasi-stationary mesoscale fronts of FMCF is located to the south of the Falkland Islands near the small Beauchêne Island where the Falkland Current meets the continental slope. It causes a strong upwelling of SASW that mixes with the Shelf Water Mass forming the so-called Transient Zone (TZ) at 120-300 m depth (Zyryanov & Severov 1979; Arkhipkin et al. 2004a). This front forms one of the most productive zones that is utilised by various marine squid and fish both as feeding area (squid *D. gahi*, Arkhipkin et al. 2004a; hakes *M. hubbsi* and *M. australis*, Arkhipkin et al. 2003) and spawning grounds (fishes such as southern blue whiting *Micromesistius australis australis*, Falkland herring *Sprattus fuegensis*, Agnew 2002, and red cod *Salilota australis*, Arkhipkin et al. 2010).

It has been shown that the location of the Transient Zone on the shelf fluctuates both seasonally and interannually due to the variation in the intensity and position of the Falkland Current, which in turn influences the distribution of *D. gahi* (Arkhipkin et al. 2004b). The stronger current inflows onto the Falkland Shelf induce stronger offshore outflows of the TZ resulting in farther offshore movements of squid. The position of the front and TZ on the shelf (best identified by near-bottom salinity of 33.85-34.10) might be a useful predictor of the extent of the distribution of *D. gahi* in the area (Arkhipkin et al. 2004b). It has also been shown that the red cod

(or tadpole codling *S. australis*) spawn upstream in upwelling waters of the southern front and then disperse their pelagic larvae downstream in the warmer western branch of the Falkland Current over the entire Patagonian Shelf (Arkhipkin et al. 2010).

Since 1999, the Fisheries Department of the Falkland Islands has been carrying out extensive oceanographic and biological surveys of the marine fauna occurring on the Patagonian Shelf and Slope. In the present study we reveal the presence and characteristics of four quasi-stationary fronts of FMCF that appear at the confluence between the branches of the Falkland Current and shelf waters and analyse their impact on distribution, migrations and spawning of nektonic fishes and squid in accordance to their Sub-Antarctic and temperate origins.

## MATERIAL AND METHODS

### OCEANOGRAPHIC DATA

Oceanographic data were collected at 1,407 stations carried out throughout the year onboard of the Falkland Islands Fisheries Department patrol and patrol/research vessels *Dorada*, *Protegat*, and *Castelo* over the entire Falkland shelf in 1999 – 2011 (Figure 1). Timing and locations of these surveys were chosen according to the distributions of the target species (*D. gahi*, *I. argentinus*, *M. australis*, *S. australis*, Rajidae) around the Falkland Islands. Additionally, monthly oceanographic data were sampled along the transects P1 (749 stations) and P5 (679 stations) running across the western and southern shelf and slope of the Falkland Islands respectively. At each station, a CTDO (conductivity, temperature, depth and oxygen) sealogger SBE-25 (Sea-Bird Electronics Inc., Bellevue, USA) was deployed from the surface to 5–10 m above the bottom to obtain profiles of temperature (°C), salinity, dissolved oxygen (ml/l) and chlorophyll a (mg/l). The standard deployment speed was approximately 1 m sec<sup>-1</sup>. Temperature was measured directly, whereas salinity, density and dissolved oxygen and chlorophyll a were calculated using Seasoftware v. 4.326 software (Sea-Bird Electronics Inc.). All sensors of the CTDO were calibrated annually at Sea-Bird Electronics Inc (Bellevue USA).

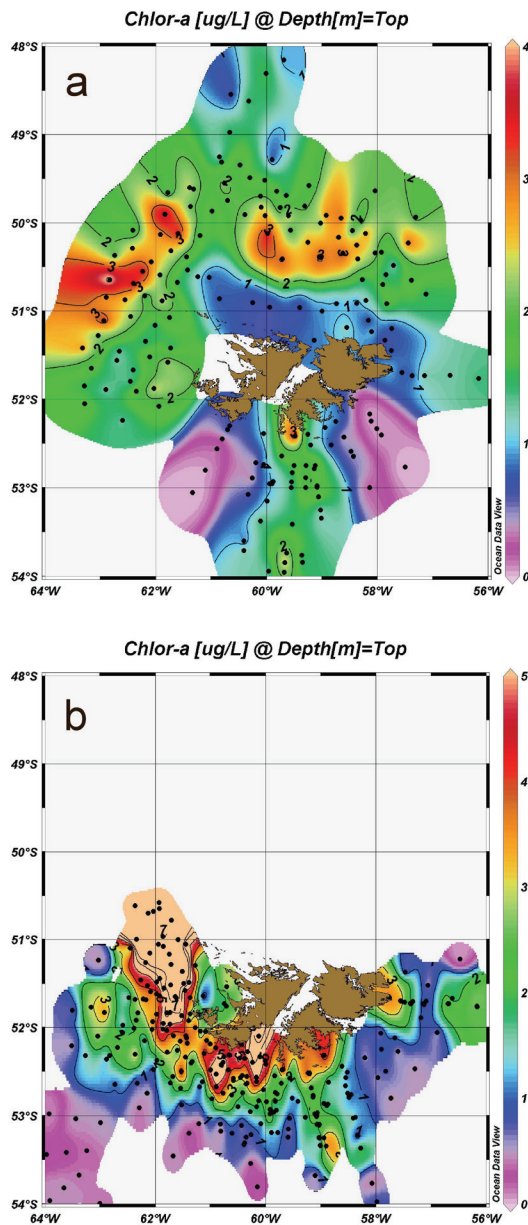


Fig. 1. Oceanographic station locations and mean annual distribution of chlorophyll-a in (a) February and (b) September – October, around the Falkland Islands (Southwest Atlantic). All years combined.

Vertical profiles of temperature, salinity and water density were interpolated along each transect by inverse distance weighing method using Ocean Data View ver. 3.4.3 software (Schlitzer 2009).

BIOLOGICAL DATA

Catch and effort data collected by scientific observers were used to calculate CPUE (tonnes per hour trawled) and this was used as an index of abundance between 1999 and 2010. The catching powers of individual vessels are variable and it was considered impractical to attempt to apply any correction factors or standardisation and therefore the fishing time was used as an index of effort. Data used for plotting the relative abundance of commercial species were taken from 8,750 commercial and 919 research bottom trawls respectively. Additionally, data were also taken from 290 trawls on pelagic vessels targeting southern blue whiting *M. australis*. The observers collected information about the size structure and maturities of the commercial species caught. Due to the volume of data and sizeable catches of rock cod (*Patagonotothen ramsayi*) only catch data from research cruises conducted during 2009, 2010 and 2011 were used for this species. Catch per unit effort (CPUE) of rock cod greater and less than 30 cm total length (LT) were calculated using length frequency, length weight (kg, cm:  $W=0.000005*LT^{3.2276}$ ), catch and trawl duration data. CPUE data were plotted onto a GIS to illustrate the distribution of abundance of various species within the Falkland Islands Conservation Zones.

Data for community analyses within and between frontal systems were taken from the FIFD data base and were queried for catch and effort for the commercial species within four areas surrounding the respective frontal systems and in an area on the northern Falkland Islands shelf away from these areas called ‘no front’ (NoF) (see Table 1) to avoid any border effects with the frontal zones. For this analysis, data collected in austral spring (September – November) between 2000 and 2005 were used in order to reduce any temporal effects that might have an impact on community structure and thus the data analyses.

STATISTICAL METHODOLOGY

Multivariate analyses were employed to examine the differences in fish community structure between the areas within the frontal zones and NoF. The abundance data (tonnes/hr) were 4<sup>th</sup> root transformed to reduce the influence of the most abundant species and then Bray-Curtis similarity

matrices were constructed (Clarke & Warwick 2001). The differences in community structure between fronts and NoF were tested using the one way non-parametric analysis of similarity test (ANOSIM) with a  $H_0$  of no difference of fish community structure between frontal zones and NoF.

The Bray-Curtis similarity matrices were further used to explore fish community structure using non-metric multidimensional scaling (NMDS) and the results are presented as ordination plots. The species that contributed most to the patterns in the analyses were identified using the similarity percentages (SIMPER) on the transformed data set. The SIMPER method compares the average abundances and examines the contribution of each species to dissimilarities between groups or similarities within a group (Clarke & Warwick 2001).

To examine the similarities between fronts and NoF the mean abundance for each species was 4<sup>th</sup> root transformed and Bray-Curtis similarity matrix constructed, a cluster analysis was then performed and the results were presented as a dendrogram. All data analyses were conducted in Primer 6 (PRIMER-E Ltd).

## RESULTS

### OCEANOGRAPHY

Analysis of temperature and salinity on the Falkland shelf and upper slope (30 - 500 m depth) revealed presence of several water masses including Patagonian (PSW) and Falkland Shelf waters (FSW), waters of Transient Zone, western and eastern (WTZ and ETZ, respectively), and waters of western and eastern Falkland Current (WFC and EFC). Western water masses were generally less saline than corresponding eastern water masses (Figure 2).

Four mesoscale frontal zones were revealed around the Falkland Islands, each with its specific water structure (Table 1) and configuration (Figure 3).

The Western Offshore Front (WOF) is situated in a north-western extension of the Falkland Trough that is essentially a broad valley that become narrower and gently more shallow until the shelf break west of the Falkland Islands (Figure 3). This front is oriented longitudinally along 62-64°W. WOF occurs between cold and more saline waters of the western branch of the Falkland Current (WFC) on the eastern and southern sides, and relatively warm and fresher Patagonian shelf waters (PSW) and Falkland shelf waters (FSW) on the western and northern sides (Table 1).

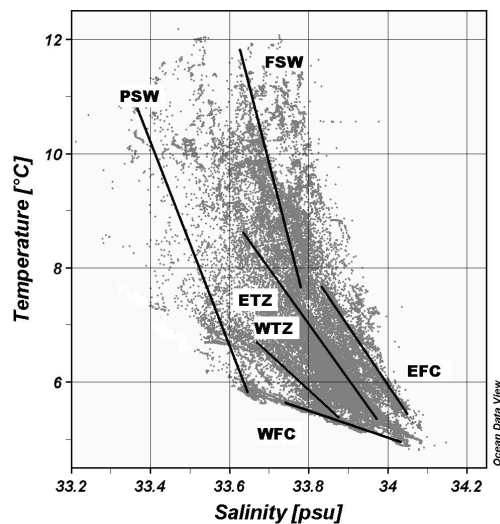


Fig. 2. T-S scatter plot of data collected in February, all years combined. Water masses: PSW, Patagonian Shelf water; FSW, Falkland Shelf Water; WTZ, Waters of the Western Transient Zone; ETZ, Waters of the Eastern Transient Zone; WFC, Western Branch of Falkland Current; EFC, Eastern Branch of Falkland Current.

Table 1. Water masses of the Falkland Shelf (terminology from Arkhipkin et al. 2004a)

Water mass	Parameters of water masses in the frontal zones							
	WOF		WIF		SF		NEF	
	T°C	S ‰	T°C	S ‰	T°C	S ‰	T°C	S ‰
Patagonian shelf waters	5.5-11.5	33.1-33.7						
Falkland shelf waters	6-10.5	33.6-33.7	6.5-11.5	33.6-33.8	5-11.5	33.6-33.8	6-11.5	33.6-33.8
Transient zone	5-7	33.7-33.9	5-7	33.7-33.9	4-7	33.8-34	5-9	33.85-34
West Falkland Current	4.5-7	33.8-34.1	4.5-7	33.8-34.1				
East Falkland Current					3.5-8	33.9-34.1	4-8	34-34.2

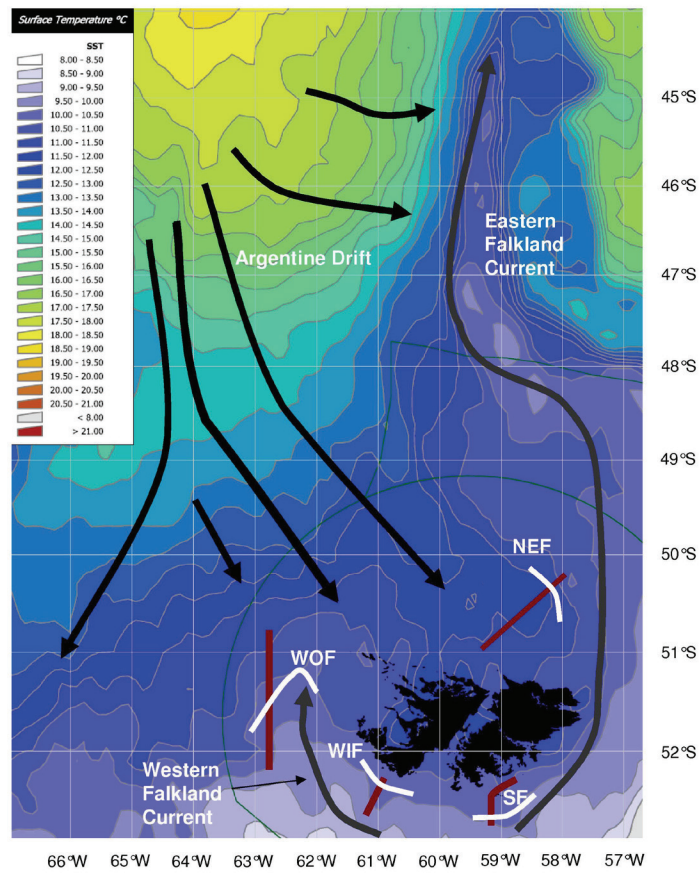


Fig. 3. A schematic illustrating main oceanographic features and frontal systems overlain on SST map from March 2008 (NOAA website). Red bars, oceanographic transects across the frontal systems. WOF = Western Offshore Front; WIF = Western Inshore Front; SF = Southern Front; NEF = North Eastern Front.

Existence of these three water masses is obvious throughout the year. This front represents a highly productive zone situated in the western part of the Falkland waters at depths of 170-250 m (Figure 1). It could be tracked all the way down to the bottom because of strong gradients in salinities (Figure 4).

The Western Inshore Front (WIF) is located along the south-western shores of the Islands that is characterized by an intermediate rise to the shelf from the depth of 350 m. The WIF is occupied by waters of the western branch of the Falkland Current (WFC) on the south-western side, and the Falkland shelf waters (FSW) on the north-eastern side. It is characterized by strong, almost horizontal gradients in salinity (Figure 5).

The Southern Front (SF) is situated in an area that has a very steep shelf slope (from 120 m to 250 m) that rises up from the Falkland Trough to the shelf adjacent to Beauchêne Island. SF is occupied mainly by waters of the Transient Zone situated between FSW and EFC (Table 1). In its northern part, it is characterized by almost horizontal gradients in salinity over the shelf with depths 100-150 m that in deeper waters become vertical and appear near the surface at depths of 500-600 m (Figure 6). There is a high productivity zone where the eastern branch of the Falkland Current meanders south of the East Falkland between 58°30 and 60°W as indicated by chlorophyll a both at the surface and near the bottom (Figure 1).

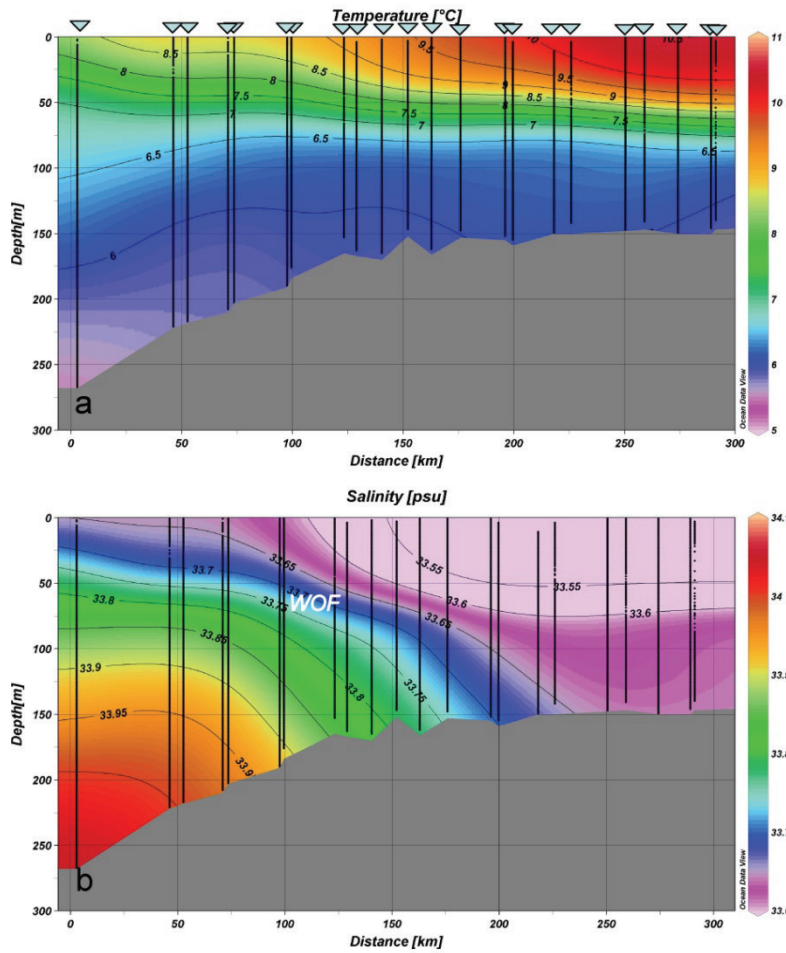


Fig. 4. Distribution of (a) temperature and (b) salinity across the Western Offshore Front in February.

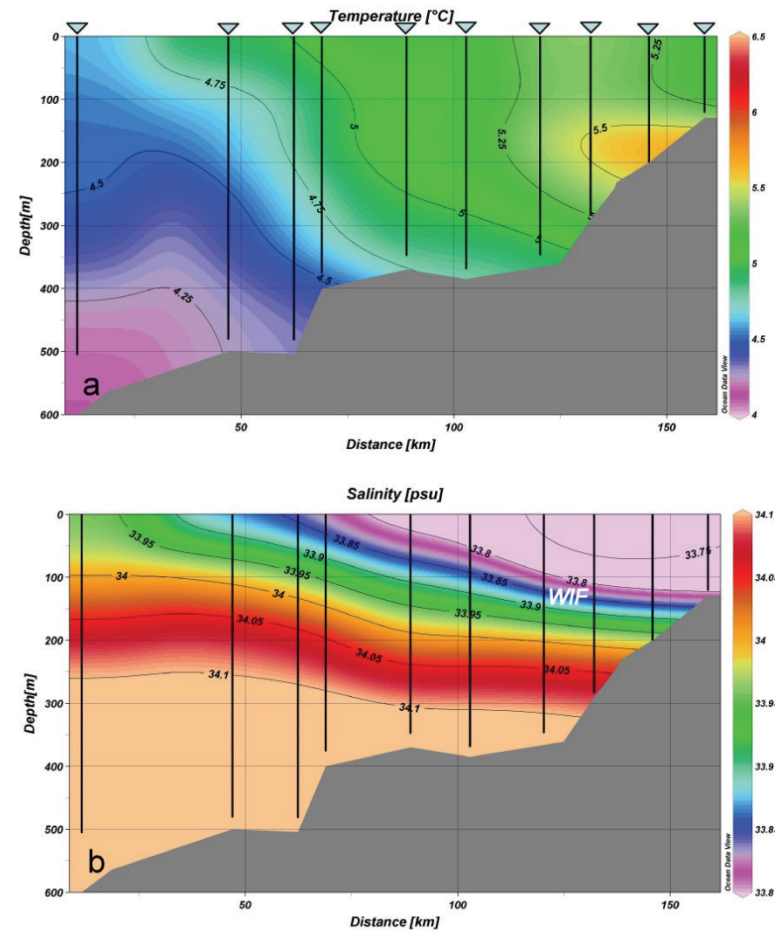


Fig. 5. Distribution of (a) temperature and (b) salinity across the Western Inshore Front in September.

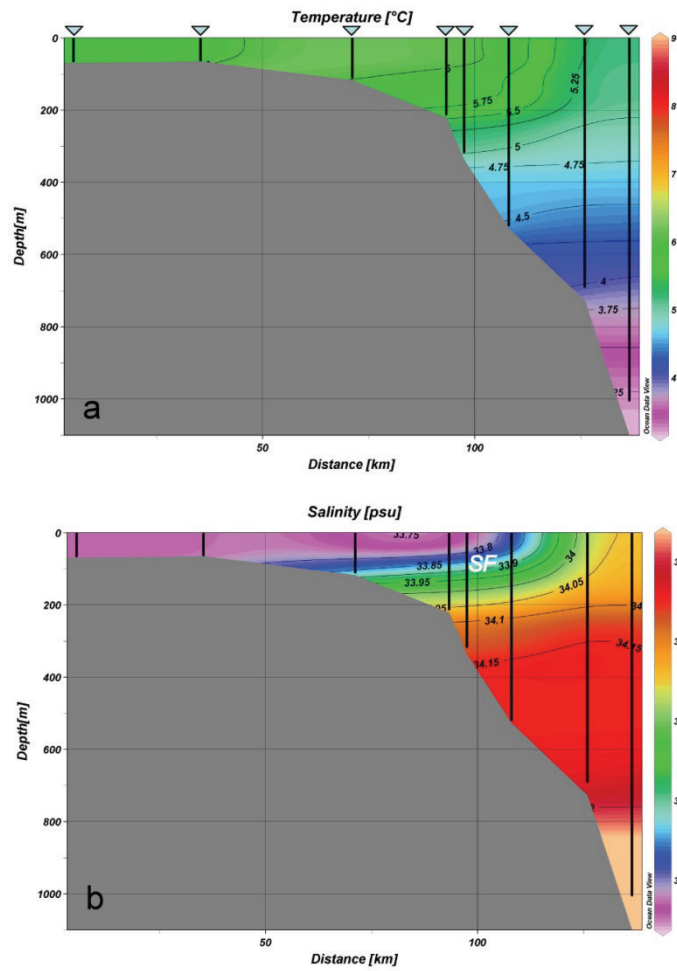


Fig. 6. Distribution of (a) temperature and (b) salinity across the Southern Front in June.

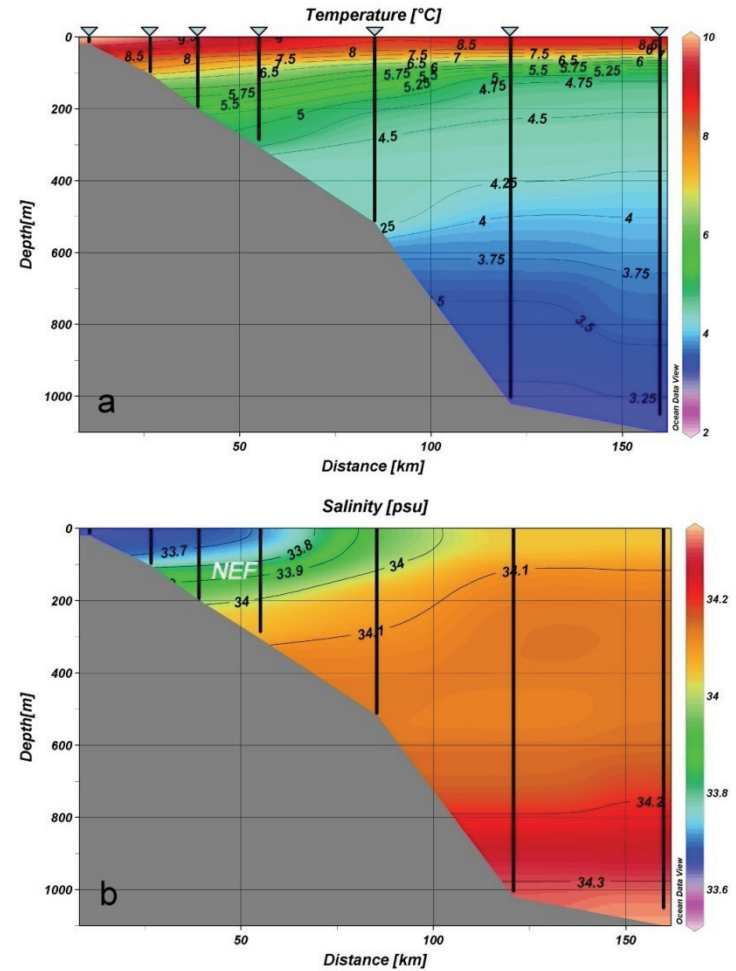


Fig. 7. Distribution of (a) temperature and (b) salinity across the North East Front in January.

The North-eastern Front (NEF) forms on the eastern extremities of the Falkland platform from approximately 51°S and further north up to 50°S that represents the widest point on the Patagonian Shelf. The area to the east of the NEF gives way to a steep slope (130 to 250-280 m depths) which contrasts with the area north of this where the slope is gentle. The NEF has the Falkland shelf waters on its western side and western branch of the Falkland Current on its eastern side. The gradient zone is situated in near-bottom layers along the depth of 200 m and then wedges to the surface at 300-350 m depth (Figure 7). The corresponding productive area with high chlorophyll a content occurs generally between 51°S and 49°S (Fig. 1).

#### DISTRIBUTION OF SUB-ANTARCTIC FAUNA IN RELATION TO FRONTS

As the seas around the Falkland Islands are the ecotone zone between the temperate and sub-Antarctic faunas, the species belonging to both faunas could be found everywhere in the area studied with just few exceptions (see below). However, their abundances (expressed here in terms of catch per hour for bottom and pelagic trawls) were uneven and generally corresponded with the location of fronts in the area.

Southern blue whiting *Micromesistius australis* were found the largest densities in the WIF at depths of 150-200 m, with lower densities in the WOF (Figure 8a). Pelagic trawlers fished for this species in the water column over the shelf break at 200-350 m depths during the post-spawning period (October-December). The largest concentrations of southern blue whiting were encountered in the WIF and NEF, with lower densities observed both in the WOF and SF. In some years, dense aggregations of migrating fish were also observed on their migratory route between SF and NEF (Figure 8b).

Southern (or Patagonian) hake *Merluccius australis* was mainly caught by bottom trawlers as a by-catch during finfish fishery. The fish was most abundant on the southern side of the WIF at 200-300 m depths. It was also found in relatively small quantities in a deeper part of the shelf (300-400 m) occupied by waters of the western branch of the Falkland Current (Figure 8c).

Patagonian toothfish (*Dissostichus eleginoides*) did not create dense aggregations, being mostly

solitary opportunistic predators. This is why these fish were only taken as a by-catch by bottom trawlers. However, relatively large aggregations of immature fish (40-60 cm total length) were encountered in three fronts, namely WOF, SF and NEF at depths of 200-300 m (Figure 9a). Smaller quantities were also observed in the WIF. Similar to toothfish, the great hooked squid *Onychia ingens* was distributed almost everywhere on the Patagonian Shelf, but the highest abundances of this squid were observed in the WOF, SF and NEF at 200-250 m depths (Figure 9b).

The Patagonian longfin squid, *D. gahi* was abundant on the shelf and shelf break to the south and east of the Falkland Islands in areas where the TZ was most pronounced. However, the densest aggregations were encountered in two regions, around the Beauchêne Island (SF) and to the northeast of the Falkland Islands (NEF). In these frontal areas, squid always occurred on the shelf water sides of the fronts (Figure 9f).

Catches of ridge scaled rattail *Macrourus carinatus* were taken into account for our analysis only from depths of < 300 m, as obviously the details in abundance of this deepwater fish in relatively shallow waters would be masked by the much higher abundance in deeper waters. The highest abundance of these grenadiers was observed on the deepwater side of the WIF, with smaller abundances present in all other three fronts (Figure 9c). Another species of grenadiers, banded whiptail *Caelorinchus fasciatus* has been recorded along the 200-m isobath and deeper around the Falkland Islands, with the greatest abundance observed both in WOF and WIF (Figure 8f).

Hoki (*Macruronus magellanicus*) was highly abundant along the shelf edge and continental slope all the way up to 48°S (Figure 8d). The maximum catches were observed at depths of 250-350 m in WOF, WIF, SF and NEF. Similar to another pelagic fish, southern blue whiting, migrating schools of hoki were sometimes encountered in large numbers on their way between SF and NEF. Distribution of red cod *Salilota australis* in the Falkland waters reflected its spawning and feeding migrations, with great abundances of fish encountered during their spawning season over the rocky grounds of WIF (Figure 8e).

Marine fauna and oceanic fronts in Patagonia

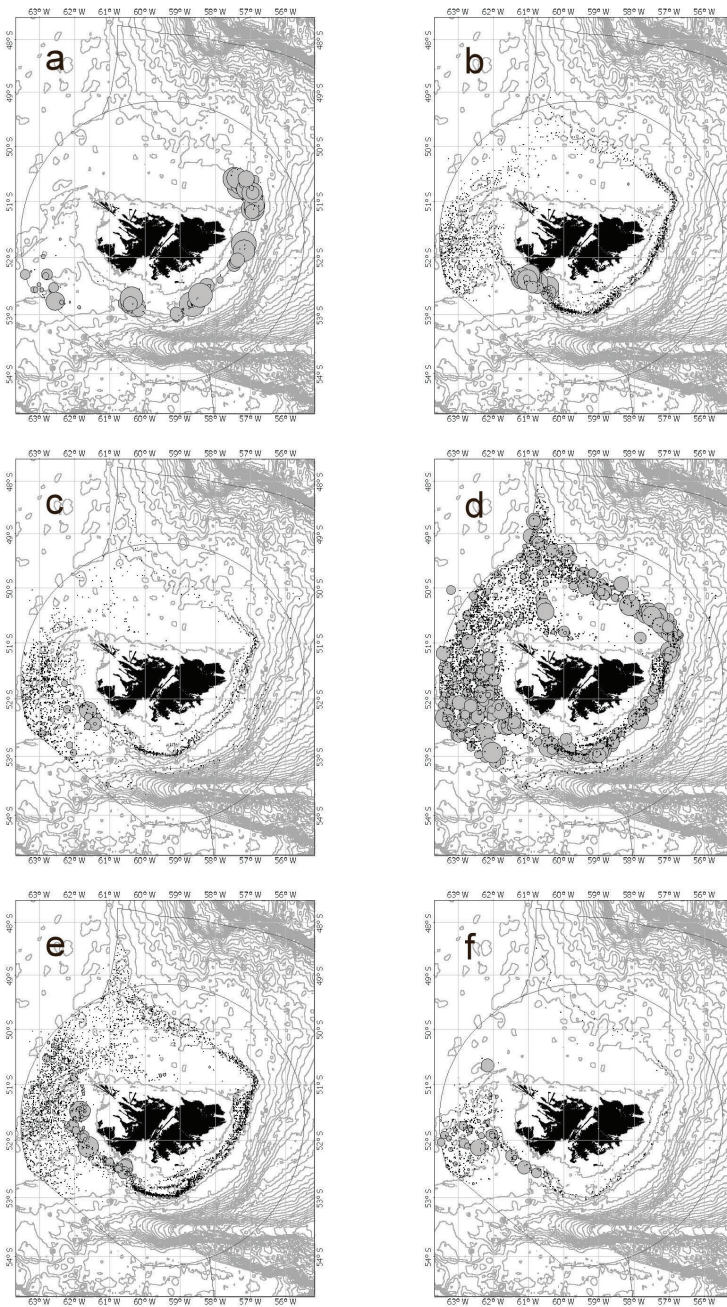


Fig. 8. CPUEs of commercial species. *Micromesistius australis* (max = 186 tonnes/hr) in the pelagic trawl fishery (a), *Micromesistius australis* (max = 371 tonnes/hr) in the finfish fishery (bottom trawls) (b), *Merluccius australis* (max = 1.8 tonnes/hr) (c), *Macruronus magellanicus* (max = 343 tonnes/hr) (d), *Sallitota australis* (max = 510 tonnes/hr) (e) and *Coelorhynchus fasciatus* (max = 1.5 tonnes/hr) (f).

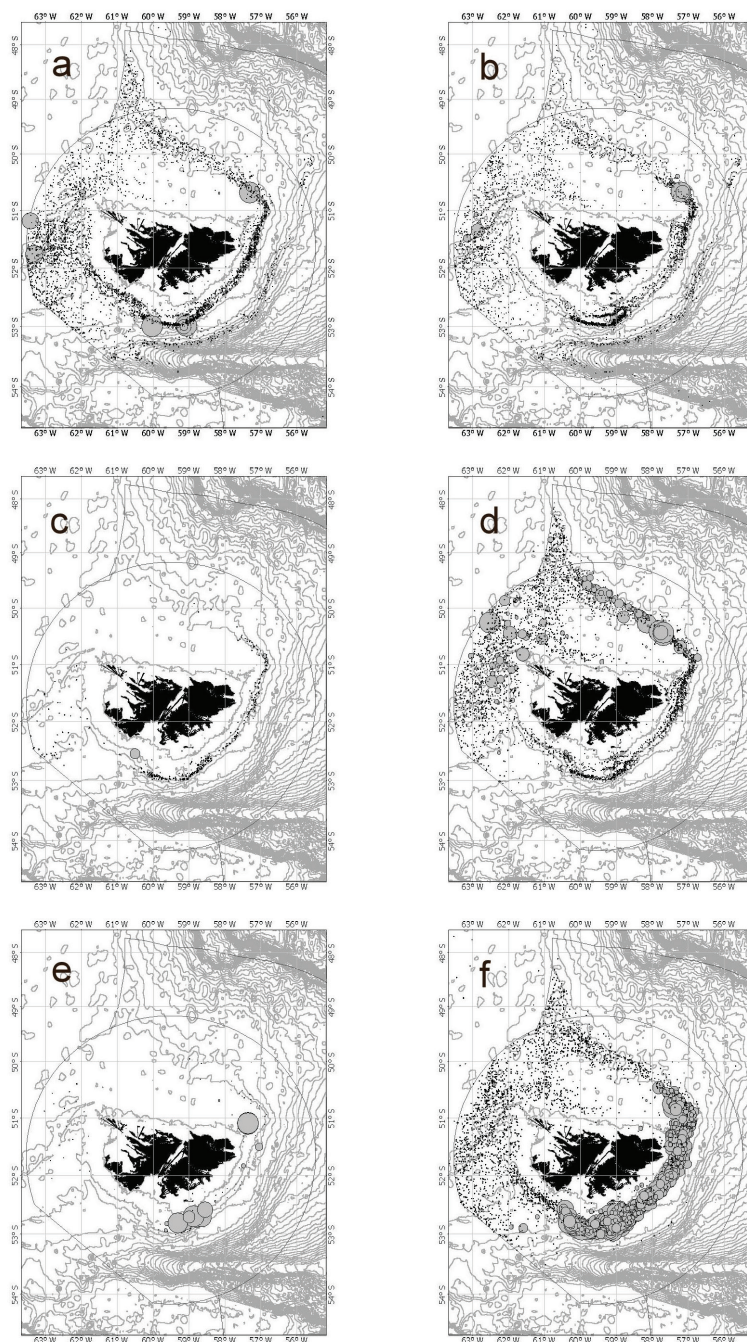


Fig. 9. CPUEs of commercial species (cont'd). *Dissostichus eleginoides* in the finfish fishery (bottom trawls) (max = 1.3 tonne/hr) (a), *Onychia ingens* (max = 1.92 tonnes/hr) (b), *Macrourus carinatus* (max = 0.52 tonne/hr) (c), *Bathyraja griseocauda* (max = 0.75 tonne/hr) (d), *Zygochlamys patagonica* (max = 0.64 tonnes/hr) (e), and *Doryteuthis gahi* (max = 38 tonnes/hr) (f).

Marine fauna and oceanic fronts in Patagonia

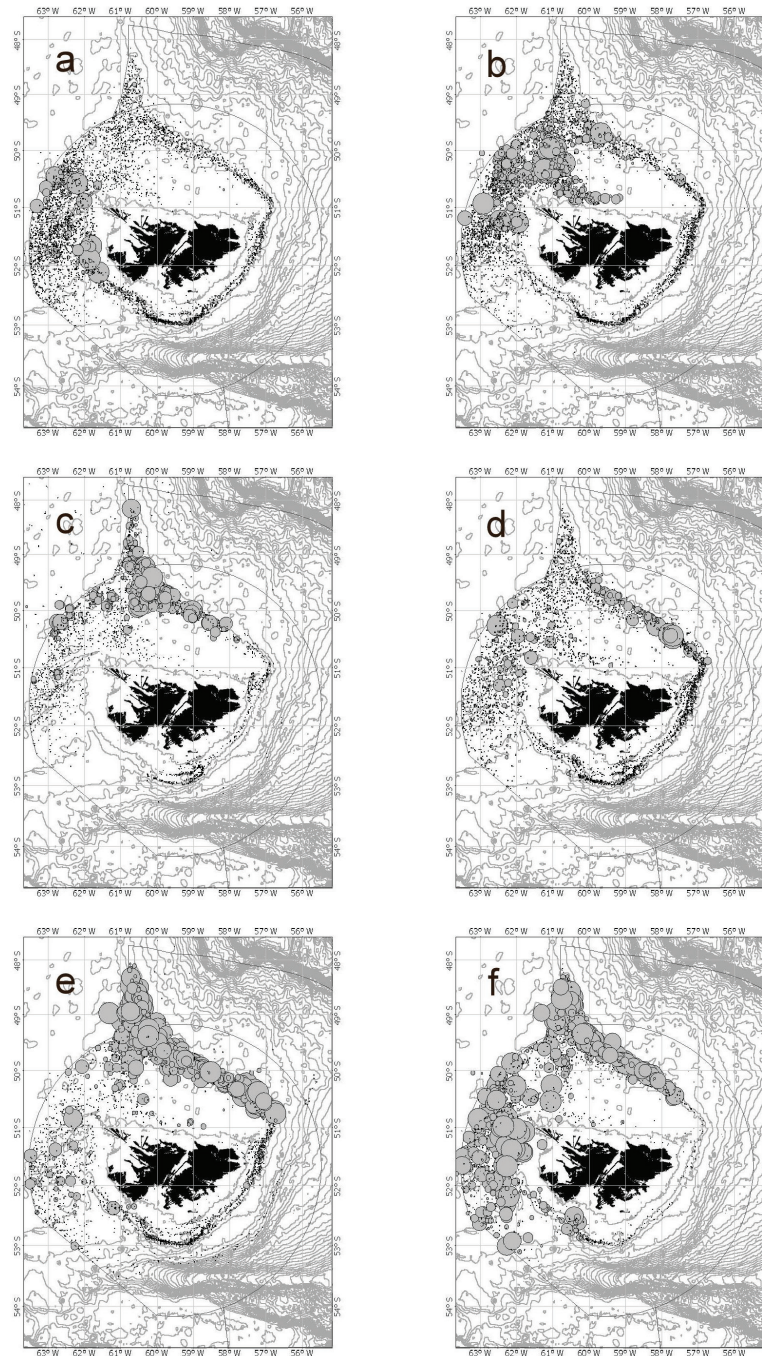


Fig. 10. CPUEs of commercial species (cont'd). *Genypterus blacodes* in the finfish fishery (bottom trawls) (max = 8.80 tonnes/hour) (a), *Merluccius hubbsi* (max = 16.81 tonnes/hr) (b) *Illex argentinus* (max = 1484 tonnes/hr) (c), *Bathyraja brachyurops* (max = 1.23 tonnes/hr) (d), *Bathyraja albomaculata* (max = 0.37 tonnes/hr) (e) and *Dipturus chilensis* (max = 13.51 tonnes/hr) (f).

The grey-tail skate *Bathyraja griseocauda* was the most abundant over the shelf break in the vicinity of WIF, and also abundant in NEF. From NEF, skates followed the FMCF along the upper continental slope up to 48°S (Figure 9d). Patagonian scallop, *Zygochlamys patagonica* was encountered mostly at depths of 100-140 m near SF and NEF, and over several small banks located in-between these fronts (Figure 9e).

#### DISTRIBUTION OF TEMPERATE FAUNA IN RELATION TO FRONTS

Kingclip *Genypterus blacodes* was encountered in the region of quasi-stationary inflow of warm waters of the Argentinean Drift to the north-western part of the Falkland Shelf (Figure 3). Dense aggregations of kingclip were also found on rocky grounds of WOF and WIF (Figure 10a). Similarly to kingclip, common hakes *Merluccius hubbsi* were most abundant both in the middle part of the warm water inflow, and also in its peripheries (in the vicinity of WOF and NEF) (Figure 10b).

The distribution and aggregation of rock cod was analysed separately for small (<30 cm TL) and large (>30 cm TL) fish in two main seasons, October (straight after spawning), and February (middle of the feeding season). In October, the main concentrations of rock cod were observed along the shelf break area. Smaller fish were most abundant near NEF, whereas larger fish were also abundant at WIF. In February, smaller fish were widely distributed in the area of the warm inflow to the northwest of the Falkland Islands, with some concentrations observed in the vicinity of NEF. Larger fish were also encountered in less saline waters of the warm inflow, but main concentrations retained near NEF and WIF (Figure 11).

Dense feeding aggregations of the Argentine

shortfin squid *Illex argentinus* were found near the northern boundary of the warm water inflow to the northwest of the Falkland Islands between February and May. Maximum concentrations were observed near the shelf break to the north of NEF. Sometimes, migrating schools of this squid were encountered as south as WIF (Figure 10c).

The distribution of broad-nose skate *Bathyraja brachiurops* around the Falkland Islands was quite similar to that of shortfin squid, but was not seasonal. Skates were most abundant in an area of the warm water inflow to the northwest of the Islands, and also on the shelf break to the north of NEF (Figure 10d). Another skate, white-spotted skate *Bathyraja albomaculata* was most abundant along the shelf break at 150-250 m depth from NEF up to 48°S. Several big catches were also encountered in the vicinity of both WOF and WIF (Figure 10e). Yellow nose skate *Zearaja chilensis* was most abundant on the shelf break along 200 m isobath north of NEF. Dense concentrations of this skate were also associated with warm water inflow from the Argentinean drift to the northwest of the Falkland Islands. Skates were abundant in the vicinity of WIF and WOF, but encountered only sporadically near SF (Figure 10f).

#### FISH COMMUNITY STRUCTURE

Fish community structure (species composition in conjunction with abundance) within the areas around the frontal systems and in an area on the north shelf not associated with any of the fronts was compared in a pair-wise fashion to examine their similarity. All pair-wise comparisons of community structure between each front and the No Frontal Zone (NoF) using ANOSIM were significantly different and are presented in Table 2. Further, the NMDS analysis (Figure 12) indicated almost all pairs of communities to be significantly different (Table 2).

Table 2. Results of pair-wise comparisons of community structure in different frontal zones using ANOSIM. WOF = Western Offshore Front; NEF = Northeast Front; SF = Southern Front; WIF = Western Inshore Front; NoF = Area on the north Falkland Shelf not adjacent to frontal zones.

	WOF		NEF		SF		WIF		NoF	
	R	P	R	P	R	P	R	P	R	P
<b>WOF</b>	-	-	0.897	0.1%	0.886	0.1%	0.457	0.1%	0.208	0.1%
<b>NEF</b>	-	-	-	-	0.083	0.1%	0.665	0.1%	0.890	0.1%
<b>SF</b>	-	-	-	-	-	-	0.439	0.1%	0.915	0.1%
<b>WIF</b>	-	-	-	-	-	-	-	-	0.557	0.1%
<b>NoF</b>	-	-	-	-	-	-	-	-	-	-

## Marine fauna and oceanic fronts in Patagonia

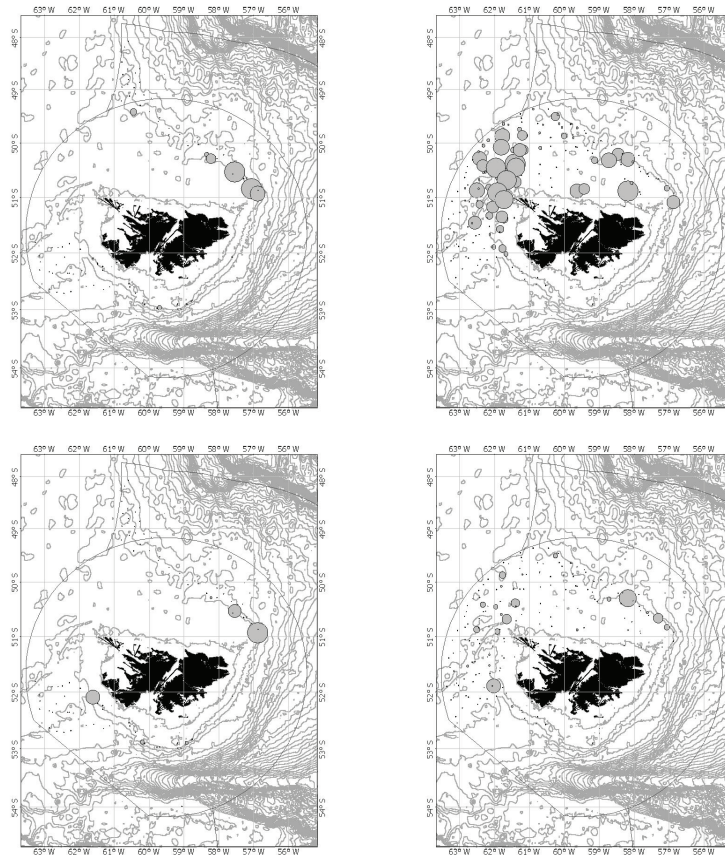


Fig. 11. CPUEs of commercial species (cont'd). *Patagonotothen ramsayi* <math>< 30\text{ cm } L\_T</math> in October (max = 4.71 tonnes/hr) (a), *P. ramsayi* <math>< 30\text{ cm } L\_T</math> in February (max = 14.32 tonnes/hr) (b), *P. ramsayi* <math>\ge 30\text{ cm } L\_T</math> in October (max = 4.36 tonnes/hr) (c) and *P. ramsayi* <math>\ge 30\text{ cm } L\_T</math> in February (max = 3.53 tonnes/hr) (d).

SIMPER indicated that two species *D. gahi* and *M. magellanicus* explained most of the average dissimilarity between WOF and NEF, as well as between WOF and SF, with the former species being more abundant in NEF and SF and latter species being more abundant in WOF. Southern blue whiting and hoki explained most of the dissimilarity between both WOF and WIF, similarly to WOF and NoF. Two community zones, NEF and SF, showed some overlap being however significantly different as indicated by NMDS analysis (Figure 12f), whereas SIMPER showed the average dissimilarity of only 43.8% indicating overlap in community structure.

A cluster analysis using the mean abundance of each species in the frontal zones and in no frontal zones indicated that the NEF and SF had the closest affinities with each other and the WIF, NoF and WOF being more dissimilar. Of the latter the NoF and WOF were more closely related to each other than the WIF (Figure 13).

Species richness at each of the frontal zones was similar. However, the structure of the assemblages was quite different and they were determined by the environmental parameters within and adjacent to the frontal zones, with temperate species dominating the WOF and the WIF, and Sub-Antarctic species generally dominating the SF and NEF.

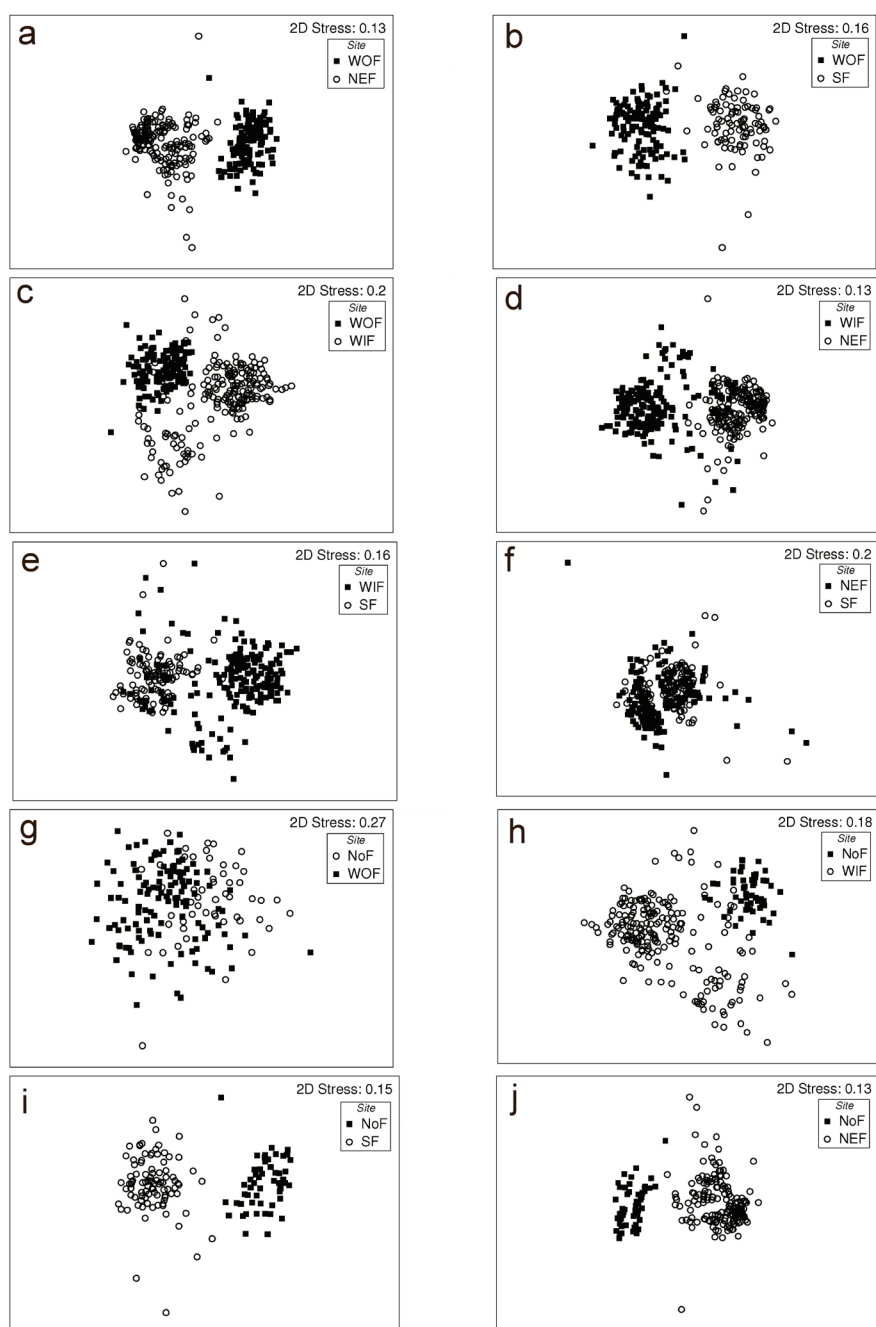


Fig. 12. Non-metric multidimensional scaling plots of fish community structure based on Bray – Curtis similarity measures of 4<sup>th</sup> root transformed abundance data. WOF vs NEF (a), WOF vs SF (b), WOF vs WIF (c), WIF vs NEF (d), WIF vs SF (e), NEF vs SF (f), NoF vs WOF (g), NoF vs WIF (h), NoF vs SF (i) and NoF vs NEF (j).

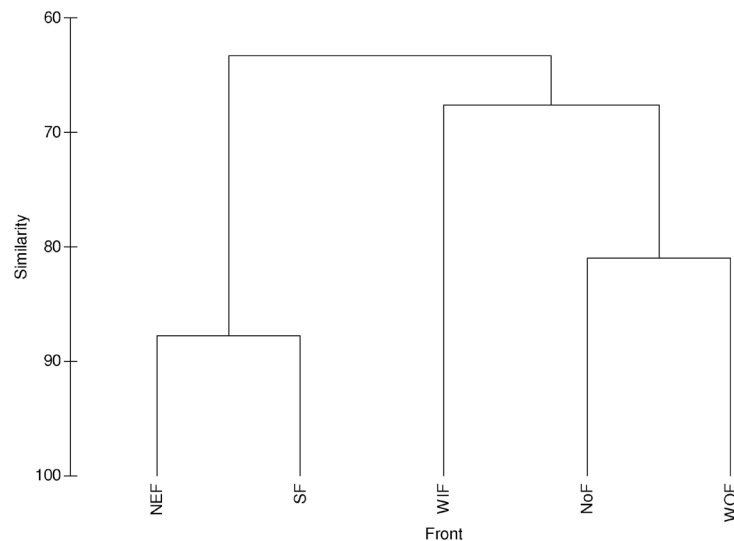


Fig. 13. A dendrogram showing the results of cluster analysis that revealed the similarity of the frontal systems and the non-frontal area (NoF) based on Bray – Curtis similarity measures of 4<sup>th</sup> root transformed mean abundance data.

## DISCUSSION

The results of the present study showed a well-resolved heterogeneity in oceanographic characteristics along the permanent Falkland/Malvinas Current Front (FMCF) in the Southwest Atlantic. One of the reasons of such heterogeneity lies in the latitudinal location of the Front. On its way along the Patagonian shelf break from the Burdwood Bank (54°S) to the region of the Southern Subtropical convergence (40-41°S), the western side of the Falkland Current mixes with various water masses and creates boundary zones with strong gradients of oceanographic variables (Belkin et al. 2009). Another reason of the heterogeneity is variation in topography of the shelf break. In two places, to the south of Beauchêne Island and to the northeast of the Falkland Islands, the shelf drops abruptly from 120-130 m to 260-300 m, resulting in strong upwelling and intrusions of the Falkland Current waters (EFC) onto the shelf. Similar incursions of the slope waters of the FC (up to 150 km from the shelf break) were observed in the northern part of FMCF at 41°S as a result of steering the waters of

the current by curving of the 100-m isobath inshore (Piola et al. 2010).

In the southern part of the FMCF (between 54°S and 48°S) four areas of well-resolved gradients in water temperature and salinity were identified (= fronts), interspersed by areas characterised by relatively smooth gradients (no frontal zones). Two fronts (WOF and W/F) represent the areas of confluence of the western branch of the Falkland current that mixes with either low saline waters of the Patagonian Shelf (33.1-33.7; WOF) or more saline (33.6-33.9) Falkland Shelf waters and Transient Zone. Two other fronts (SF and NEF) appear when the eastern branch of the Falkland Current meanders onto the shelf and mixes with Falkland Shelf waters. Due to different topography of the bottom, the western fronts have lower gradients of oceanographic characteristics than SF and NEF. Unlike the Southern Patagonian Front and Peninsula Valdes tidal front (Alemany et al. 2009), all fronts of the FMCF are quasi-stationary and well-resolved both in winter and summer. Our analysis of the surface water structure did not show the same specific multilayer arrangement of cold water flows parallel to the

shelf break as revealed in the northern part of FMCF (Franco et al. 2008). In fact, in the southern part of the Patagonian Shelf, the Falkland Current does not exactly follow the shelf break, meandering onto the shelf in several locations to the west, south and north-east of the Falkland Islands due to the bottom topography (Zyrjanov & Severov 1979). There is also no major counter-current in the region, unlike the northern part of FMCF, where the Falkland Current ‘collides’ with the warm Brazil Current, creating multiple parallel counterflows along the shelf break (Acha et al. 2004; Belkin et al. 2009).

The northern part of the FMCF (37-38°S) shifts seasonally, offshore in summer and inshore in spring and autumn (Carreto et al. 1995). We have observed similar shifts of at least two fronts (WOF and NEF) in the southern part of FMCF. It is possible that the offshore shifts of those fronts have been a result of seasonal offshore movements of shelf waters. Weakening of the shelf water transport offshore in spring resulted in spreading of the saline Falkland Current waters near the bottom onto the shelf with the front becoming nearly horizontal as indicated by almost horizontal gradients in salinity. Intensification of offshore shelf water transport in summer resulted in pushing out the FC waters to the shelf break with the front becoming nearly vertical as indicated by almost vertical gradients in temperature and salinity. Two other fronts were quasi-stationary throughout the year (WIF and SF).

Mixing of shelf waters with Subantarctic waters on the western side of the Falkland Current creates a band of increased primary productivity, indicated by higher concentrations of chlorophyll-a (chl-a) especially in spring and summer, called Patagonia High Chlorophyll Band (PHCB). Distribution of chl-a in PHCB is patchy and depends on seasonal variability of upwelling intensity along FMCF (Romero et al. 2006). Elevated concentrations of chl-a have been observed in spring at all fronts, but in summer the WIF front had a minimum chl-a. Maximum concentrations of chl-a ( $>12 \text{ mg/m}^3$  in spring and  $>3 \text{ mg/m}^3$  in summer) were associated with the region of maximum stratification to the north of WOF, where the waters of the western branch of the Falkland Current meet the warm inflow of

Patagonian Shelf waters (=Argentinean Drift) to the northwest of the Falkland Islands, similar to Cape Blanco and Peninsula Valdes fronts in the western part of the Patagonian Shelf (Bianchi et al. 2005).

Patchiness in distribution of sedentary fauna is closely correlated with variability in bottom habitat types (determined largely by bottom geomorphology and sediments) and near-bottom circulation. Relative stability of oceanographic fronts to the north of 45°S on the Patagonian shelf provided necessary environmental conditions for locations of the Patagonian scallop beds *Z. patagonica* (Bogazzi et al. 2005). Outside of the highly productive inshore bights with semi-closed circulation the distribution of scallop beds is correlated with frontal areas of increased primary productivity indicated by higher concentrations of chl-a (Ciocco et al. 2006). Our results confirmed these findings, at least for two fronts, SF and NEF. Elevated chl-concentrations (especially in spring) near the shelf break area were good indicators of the presence of dense scallop beds in SF and NEF. There were no scallop beds near WIF where the chl-a concentrations were low. The near absence of scallop beds in the northern part of WOF that was characterized by the maximum oceanographic gradients and maximum concentrations of chl-a seemed controversial at first. However, the bottom depth of this front (200-250 m) exceeds the optimum depths of *Z. patagonica* occurrence in offshore waters (50-195 m, mainly 80-140 m, Ciocco et al. 2006) that might explain their almost complete absence near the front despite other favourable environmental and nutritional conditions. Bottom depths at both NEF and SF (120-150 m) are within the optimal depth range for scallop banks (Bogazzi et al. 2005).

Unlike sedentary organisms, both demersal and pelagic fish and squid may actively or passively migrate between fronts and non-frontal zones, with their movements being influenced but not completely obstructed by strong gradients of the frontal zones. However, macro-scale analysis of the Patagonian Shelf frontal and non-frontal zones revealed a negative relationship between the fish diversity and primary production in macro-scale fronts. The species richness was higher in the non-frontal zone of the Patagonian

Shelf compared with that of the southern part of the FMCF (Alemany et al. 2009). It was suggested that among the main reasons of decreased fish diversity could be a domination of a few species in the resource-rich environment of the frontal system, or partial consumption of food resources by sedentary fauna that could potentially decrease the food availability to pelagic organisms. On the contrary, no difference has been found in the northern part of the FMCF with neighbouring non-frontal part of the Argentinean Shelf (Alemany et al. 2009). In the southern part of FMCF, we have not found any difference in fish and squid richness between frontal and non-frontal zones where various species were encountered with equal probabilities.

However, the abundance of fish and squid varied greatly, being generally much higher in frontal zones. Possibly, fish and squid concentrated near seasonally moving or quasi-stationary frontal regions, taking advantage of their higher water productivity, similarly to the observed behaviour of pelagic fish near Peninsula Valdez Tidal Front (Alemany et al. 2009). These results contradicted macro-scale observations of distribution of demersal fish fauna on the Patagonian Shelf, where either no difference in biomass were found in the southern part of FMCF and non-frontal zones, or the biomass in non-frontal zones was even greater than near the fronts in the northern part of FMCF (Alemany et al. 2009). However, it is possible that the macro-scale observations by Alemany et al. (2009) were skewed by the presence of abundant common hake that migrates seasonally between shelf break (feeding area) and inner shelf (spawning area) (Podesta 1990).

Intrusions of the SASW of the Falkland Current onto the shelf favoured migrations of deep-water fish and squid in relatively shallow waters near frontal zones. Adult Patagonian toothfish *D. eleginoides*, great hooked squid *O. ingens*, deep-water grenadiers *M. carinatus* were all observed in greater abundances along the offshore side of all fronts. Similar biomass distribution was observed in shelf and shelf-break fishes belonging to the Sub-Antarctic fauna, which distribution was mainly associated with SASW as well, such as southern blue whiting *M. australis*, Patagonian hakes *M. australis*, red cod *S. australis* and the

grenadier, banded whip-tail *C. fasciatus*. Large pelagic hoki *M. magellanicus* was sometimes encountered in dense schools outside frontal zones, but main concentrations of this fish were also associated with frontal zones. The most polar of all loliginid squid *D. gahi* was concentrated mainly in frontal zones between relatively cold shelf waters and eastern branch of the Falkland current, avoiding productive but warmer areas in the vicinity of WIF and WOF with the impact of warmer waters of the Argentinean drift from the northwest.

On the contrary, temperate fauna of the Patagonian Shelf was most abundant near fronts between the Falkland Current and temperate waters of the Argentinean drift, with main concentrations found near the warm side of these fronts. Typical examples of this fauna were common hake *M. hubbsi*, kingclip *G. blacodes* and shortfin squid *I. argentinus*. Patagonian rock cod *P. ramsayi* used the fronts during their spawning period in winter, providing their larvae that hatched in spring with abundant food resources during maximum productivity in these areas. In summer, these fish disperse in temperate waters outside the fronts, where they are preyed upon by large demersal predators such as hakes and kingclip.

The results of this study have shown for the first time that the longest macro-scale hydrological front in the Southwest Atlantic, Falkland/Malvinas Current Front consists of several meso-scale fronts of varying productivity. Fish and squid richness (total number of species) did not change between the meso-scale frontal zones and adjacent regions, however the fish and squid abundance was greater near the frontal zones due to increased productivity and food availability (Olson et al. 1994). Sub-Antarctic and temperate fish and squid fauna were more abundant in the frontal zones albeit mainly encountered at the side of the front occupied by the waters that that fauna was associated with. The Sub-Antarctic and deepwater fish are abundant in SASW, whereas the temperate fauna was abundant in shelf waters of the Argentinean Drift. Therefore, the presence of several quasi-stationary fronts between the deepwater Falkland Current and shelf waters plays an important role in distribution, migrations and spawning of marine fauna that use them in

accordance with their Sub-Antarctic and temperate origins.

## ACKNOWLEDGEMENTS

We are grateful to the generations of Falkland Islands Fisheries Department Scientific Observers who participated in collection of the data presented in this paper. Our thanks are also extended to the Masters and crews of the RVs *Dorada*, *Protegat* and *Castelo* and the commercial vessels that helped to collect oceanographic, biological and fisheries data. We thank the Director of Natural Resources John Barton for supporting this work.

## REFERENCES

- Acha, E.M., H.W. Mianzan, R.A. Guerrero, M. Favero & J. Bava 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *Journal of Marine Systems* 44: 83–105.
- Agnew, D.J. 2002. Critical aspects of the Falkland Islands pelagic ecosystem: distribution, spawning and migration of pelagic animals in relation to oil exploration. *Aquatic Conservation* 12, 39–50.
- Aleman, D., E.M. Acha & O. Iribarne 2009. The relationship between marine fronts and fish diversity in the Patagonian Shelf large marine ecosystem. *Journal of Biogeography* 36: 2111–2124.
- Arkhipkin, A.I., D.A.J. Middleton, J.M. Portela & J.M. Bellido 2003. Alternative usage of common feeding grounds by large predators: the case of two hakes (*Merluccius hubbsi* and *M. australis*) in the Southwest Atlantic. *Aquatic Living Resources* 16 (6): 487–500.
- Arkhipkin, A., R. Grzebielec, A.M. Sirota, A.V. Remeslo, I.A. Polishchuk & D.A.J. Middleton 2004a. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fisheries Oceanography* 13: 1–9.
- Arkhipkin, A.I., D.A.J. Middleton, A.M. Sirota & R. Grzebielec 2004b. The effect of Falkland Current inflows on offshore ontogenetic migrations of the squid *Loligo gahi* on the southern shelf of the Falkland Islands. *Estuarine, Coastal and Shelf Science* 60: 11–22.
- Arkhipkin, A.I., P. Brickle & V.V. Laptikhovskiy 2010. Usage of the island water dynamics by spawning red cod, *Salilota australis* (Pisces: Moridae) on the Falkland Islands shelf (Southwest Atlantic). *Fisheries Research* 105: 156–162.
- Belkin, I.M., P.C. Cornillon & K. Sherman 2009. Fronts in large marine ecosystems. *Progress in Oceanography* 81: 223–236.
- Bianchi, A., M. Massonneau & R.M. Olevera 1982. Analisis estadístico de las características T–S del sector austral de la Plataforma Continental Argentina. *Acta Oceanologica Argentina* 3: 93–118.
- Bianchi, A.A., L. Bianucci, A.R. Piola, D. Ruiz Pino, I. Schloss, A. Poisson & C.F. Balestrini 2005. Vertical stratification and air sea CO<sub>2</sub> fluxes in the Patagonian shelf. *Journal of Geophysical Research*, 110: C07003.
- Bogazzi, E., A. Baldoni, A. Rivas, P. Martos, R. Reta, J.M. Orensanz, M. Lasta, P. Dell’Arciprete & F. Werner 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the southwestern Atlantic. *Fisheries Oceanography* 14: 359–376.
- Boltovskoy, D., ed. 2000. *South Atlantic zooplankton*. Backhuys Publishers, Leiden, 1706 pp.
- Carreto, J.I., V.A. Lutz, M.O. Carignan, A.D. Cucchi Colleoni & S.G. De Marco, 1995. Hydrography and chlorophyll a in a transect from the coast to the shelf-break in the Argentinian Sea. *Continental Shelf Research* 15 (2/3): 315–336.
- Ciocco, N.F., M.L. Lasta, M. Navarte, C. Bremec, E. Bogazzi, J. Valero & J.M. Orensanz 2006. Chapter 26, Argentina. Pp. 1251–1293 in: Shumway, S.E. & G.J. Parsons (Eds). *Scallops: Biology, ecology and aquaculture*. Development in Aquaculture and Fisheries Science 35. Elsevier, Amsterdam, 1460 pp.
- Clarke, K.R. & R.M. Warwick 2001. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth: PRIMER-E, 2<sup>nd</sup> edition, 172 pp.
- Csirke, J. 1987. The Patagonian fishery resources and the offshore fisheries in the South-West Atlantic. *FAO Fisheries Technical Paper* 286, 75 pp.
- Franco, B.C., A.R. Piola, A.L. Rivas, A. Baldoni & J.P. Pisoni 2008. Multiple thermal fronts near the Patagonian Shelf break. *Geophysical Research Letters* 35: L02607.
- Martos, P. & M.C. Piccolo 1988. Hydrography of the Argentine continental shelf between 38° and 42°S. *Continental Shelf Research* 8: 1043–1056.
- Olson, D.B., A.J. Mariano, C.J. Ashjian, G. Peng, R.W. Nero & G.P. Podesta 1994. Life on the edge: marine life and fronts. *Oceanography* 7: 52–60.
- Peterson, R.G. & T. Whitworth III 1989. The

- Subantarctic and Polar fronts in relation to deep water masses through the Southwestern Atlantic. *Journal of Geophysical Research* 94: 10817–10838.
- Piola, A.R., N. Martinez Avellaneda, R.A. Guerrero, F.P. Jardon, E.D. Palma & S.I. Romero 2010. Malvinas-slope water intrusions on the northern Patagonia continental shelf. *Ocean Science* 6: 345–359.
- Podesta, G.P. 1990. Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the Southwestern Atlantic Ocean. *Fishery Bulletin* 88: 167–177.
- Romero, S.I., A.R. Piola, M. Charo & C.A. Eiras Garcia 2006. Chlorophyll-*a* variability off Patagonia based on SeaWiFS data. *Journal of Geophysical Research* 111: C05021.
- Schlitzer, R. 2009. Ocean data view, <http://odv.awi.de>.
- Zyrjanov, V.N. & D.N. Severov 1979. Water circulation in the Falkland-Patagonian region and its seasonal variability. *Okeanologiya* 29: 782–790.
- Received 17 Oct 2012. Accepted 14 Dec 2012,  
Published online 25 Feb 2013.