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Important readjustments in the biomass and distribution of groundfish species in the northern part of the Kerguelen Plateau and Skiff Bank

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Abstract

The recent changes in the conservation status (establishment and extension of a marine reserve) and the long history of fishing in the Kerguelen Islands exclusive economic zone (EEZ) (Indian sector of the Southern Ocean) justified undertaking a fish biomass evaluation. This study analysed four groundfish biomass surveys (POKER 1–4) conducted from 2006 to 2017 across depths ranging from 100 to 1 000 m. Forty demersal species were recorded in total and density distributions of twenty presented. However, only seven species account for the majority of the biomass (96%). Total biomass was 250 000 tonnes during the first three surveys (POKER 1–3), and 400 000 tonnes for POKER 4 due to a high catch of marbled notothen (*Notothenia rossii*) and mackerel icefish (*Champsocephalus gunnari*) (accounting for 44% and 17% of the 400 000 tonnes biomass respectively). Across survey years, Patagonian toothfish (*Dissostichus eleginoides*) catch rates were consistently uniform in terms of biomass. However, as a representation of the estimated biomass for the Kerguelen region, the biomass reported herein is estimated to be a small portion of a larger biome. Overall Kerguelen fish diversity is likely linked to the extension of deep-sea and coastal species range outside the studied bathymetric area. Therefore, species trends and density distributions are tentatively explained from hypothesised drivers: namely, fishery history and the hydrological/productivity factors of the region.

Réajustements importants de la biomasse et de la distribution des espèces de poissons de fond dans la partie nord du plateau de Kerguelen et sur le banc Skiff

Résumé

Une évaluation actualisée de la biomasse ichtyologique dans la Zone Economique Exclusive (ZEE) des îles Kerguelen (secteur indien de l'océan Austral) était nécessaire à la suite d'une longue période d'exploitation et du changement de statut de conservation de l'aire considérée (création puis extension d'une réserve marine). Cette étude analyse quatre campagnes d'évaluation de biomasse des poissons démersaux (nommées POKER 1 à 4). Ces campagnes ont été réalisées de 2006 à 2017 et dans la gamme de profondeur 100–1 000 m. Quarante espèces sont répertoriées et la distribution géographique de vingt d'entre elles est présentée. Cependant seulement sept espèces représentent le plus grand pourcentage de la biomasse (96%). Cette dernière atteint 250 000 tonnes lors des trois premières campagnes et 400 000 tonnes lors de la dernière campagne en raison d'une exceptionnelle contribution du colin de Kerguelen (*Notothenia rossii*) et du poisson des glaces (*Champsocephalus gunnari*) (représentant respectivement 44% et 17% de ces 400 000 tonnes). L'uniformité des taux de captures de la légine australe (*Dissostichus* *eleginoides*), en termes de biomasse, est à signaler sur la période cernée. Cependant si l'on veut considérer l'ensemble de la zone de Kerguelen qui représente un plus vaste biome, cette évaluation de biomasse reste encore une estimation partielle. L'extension de l'aire de distribution tant des espèces côtières que profondes au-delà de la strate bathymétrique de ces campagnes contribue à un ajout substantiel de biomasse pour aboutir à la diversité totale en poisson de la zone. Des tentatives d'explication des tendances de l'évolution des biomasses des espèces et de la distribution géographique des densités sont avancées en considérant deux facteurs potentiels : à savoir l'historique de la pêche et les conditions hydrologiques et de productivité spécifiques de la zone.

Keywords: fish, *Notothenia rossii*, *Champsocephalus gunnari*, *Dissostichus eleginoides*, biomass, Kerguelen Island, French EEZ, Southern Ocean

Introduction

The Kerguelen Islands are situated in the northern part of the Kerguelen Plateau south of the Sub-Antarctic Front (SAF) and the main branch of the Antarctic Circumpolar Current (ACC) but the Polar Front (PF), a major hydrographic structure in the Indian Ocean sector of the Southern Ocean, crosses the Plateau between the Kerguelen Islands and Heard Island shelves (Park and Vivier, 2011). The shelf surrounding these islands is the largest of the Southern Ocean (104 300 km^2 between coastline and the 500 m isobath). The relatively large Skiff bank (3 120 km^2), rising to 300 m, is isolated from the main shelf to the South West. The inshore and offshore areas host a diverse fish community of 110 species, including 60 pelagic, 28 neritic and 22 deep-sea species (Duhamel et al., 2005, 2014). Some of these species (mainly the neritic ones) have been regularly exploited since the 1970s both by bottom/pelagic trawls and bottom longlines (Duhamel and Williams, 2011).

Ichthyological studies at Kerguelen began with the description of species (Richardson, 1844; Günther, 1880, 1887) collected during the British expeditions of HMS *Erebus* and *Terror* visiting in 1840 and HMS *Challenger* during the 1872–1876 circum-navigation (Hureau, 2011). Later, with the opportunity for land-based expeditions after the construction of the French research station at Port-aux-Français, Kerguelen Islands, some coastal at-sea surveys, including scuba diving, became feasible in a limited depth range (0–40 m). This led to studies on the life cycles of some shallow fish species (Hureau, 1970; Moreau and Duhamel, 1997). These fish surveys expanded to the shelf and deep-sea during the *Marion-Dufresne 1* oceanographic cruises MD 03/ICHTYO (1974) and MD 04/BENTHOS (1975) (Hureau, 1976; Guille, 1977). However, the major step change in the acquisition of knowledge on bottom shelf/slope trawled species occurred when legal commercial fisheries began in 1979 after the exclusive economic zone (EEZ) was declared in 1978. The historic fishery data are described in Duhamel et al. (2011) and the known fishery trends were those obtained from commercial catches focusing on the past data of the trawl-exploited stocks (Hennemuth et al., 1988). The emergence of deep-sea longline techniques in 1992 extended the bathymetric coverage (500–1 500 m: 128 410 km^2) of the fishery and consequently added new fish species caught and studied. The legal longline fishery has been regulated under sustainability protocols since its beginning. An episode (1997–2004) of illegal, unreported or unregulated (IUU) longline fishing is to note. The fishery rules and associated on-board monitoring protocols and surveys (i.e. the SKALP surveys, see Duhamel, 1993) greatly increased our biological knowledge. Fishing regulation in the Kerguelen waters is in line with protecting fragile benthic ecosystems (move-on rules), avoiding by-catch species (fish, birds, marine mammals) by using scaring devices, night setting, weighted lines, seasonal or areal closure. The pelagic realm (from ichthyoplanktonic stages of demersal species to the true meso/bathypelagic species) was the last domain (addition of 326 900 km^2 from the shelf break to the limit of EEZ) to be studied (Koubbi et al., 1990, 1991, 2000, 2001, 2003; Duhamel and Hulley, 1993) due to limited access with scuba gear (shallows), rare use of any midwater trawl during scientific cruises (over and off the shelf) and a gap from the bottom trawl fishery (which targeted fish only 6/10 m over the bottom) up to this point. Dedicated research programs on predator–prey interactions (marine mammals and seabirds) opened up this realm of research with at-sea cruises on board vessels (*La Curieuse*, *Marion-Dufresne II*). These studies greatly increased our holistic understanding of the Kerguelen marine region (Duhamel, 1998; Duhamel et al., 2000; Guinet et al., 2001; Koubbi et al., 2001; Bost et al., 2002; Loots et al., 2007) culminating in the creation of the Kerguelen Marine Reserve in 2006 which has since been extended to incorporate the whole EEZ during 2016 and 2017. However, a lack of biomass monitoring of the Kerguelen bottom fish populations, both the fished and the unfished ones, remains an issue for conservation and definition of sustainable catch limits. To fill this gap of knowledge, groundfish biomass surveys named POKER (POissons de KERguelen) were undertaken in 2006, 2010, 2013 and 2017 over the Kerguelen Islands extended shelf (up to 1 000 m) and adjacent banks. These surveys were designed to evaluate fish biomass and abundance with a focus on species which were overfished throughout the 1970s in the region, such as marbled rockcod (*Notothenia rossii*), grey rockcod (*Lepidonotothen squamifrons*) or mackerel icefish (*Champsocephalus gunnari*) (Duhamel et al., 2011) and recruitment of Patagonian toothfish (*Dissostichus eleginoides*), the species targeted by the longline fishery operating more recently. POKER surveys were also designed to provide key information on groundfish composition, biological parameters (sex, maturity, age, diet) and spatial distribution.

The aim of our study was to present the results of the four POKER surveys and interpret these results in light of historical and recent commercial fisheries and environmental conditions. Historical data collected on the abundance of juvenile *N. rossii* in their known coastal nursery areas were reanalysed and presented here to provide additional information on the recovery trend of the adult population, overfished on the slope in the 1970s.

Material and Methods

POKER cruises: groundfish biomass surveys.

Four cruises were conducted over a 10-year period: POKER 1 (2006), POKER 2 (2010), POKER 3 (2013) and POKER 4 (2017) (Table1; Figure 1) with the same chartered trawler (FV *Austral*, 77 m) in an area representing 183 000 km^2 and a depth range of 100 to 1 000 m over the northern part of the Kerguelen Plateau.

Survey design

The POKER surveys were carried out during the austral spring (September–October) to avoid the known annual spawning aggregative behaviour of the main species, except *L. squamifrons* which spawn in spring (Duhamel, 1987). The POKER surveys consisted of 200 stations separated by 5 n miles (3 n miles at Skiff bank) selected randomly within five strata: shelf (100–500 m) and deep-sea (500–1 000 m) strata to the north and south of 49°S and another one at the top of Skiff Bank (see protocol in Duhamel and Hautecoeur, 2009). Skiff Bank was surveyed to 1 000 m depth during the first survey, and then limited to the top of the bank (300–500 m depth) due to difficulties to fish in deeper rough grounds. The limit for shelf and deep water was set at 500 m considering the major change in the fish fauna occurring at this depth (Duhamel et al., 2005). The 200 stations selected randomly on the first survey (POKER 1, 2006) were revisited at similar locations during the following cruises. However, when a selected station revealed grounds not suitable for trawling, another randomly selected one (backup station) was used in the same stratum. The minimum depth (100 m) corresponds to the average external limit of the 2006 Marine Reserve. The maximum depth limit (1 000 m) was determined by the ability of the trawler (engine power and the maximum length of warps) to effectively deploy the bottom trawl (35 m headline/39 m footrope, reference: G2035013 from Le Drezen: www.ledrezen.com). A warp tension controller (Marelec SM 2-D) allowed the avoidance of major damage to the gear with an automatic release in case of unforeseen events. Trawl duration was set at 30 minutes on ground (to limit catch and bottom trawl footprint) at a speed of 2 to 3 knots. We used a codend mesh size of 40 mm, except during POKER 3 where 90 mm was used. Scanmar® sensors tied on the gear were used to determine the exact start and end time of trawling on the ground and the mouth opening of the gear. MaxSea® software (linked to a global positioning system (GPS)) gave the opportunity to compute the ground track of the trawl and subsequently to obtain the swept area at each station. Finally, trawling was conducted during the day (as defined from the nautical ephemerids) for the shelf stations to avoid bias due to diel migrations of *C. gunnari*, a semi-pelagic species (Duhamel, 1991).

Table 1: Characteristics of the POKER cruises (* mackerel icefish additional stations).

Cruise	POKER 1	POKER 2	POKER 3	POKER 4
Dates	06/09–09/10/2006	28/08–28/09/2010	30/08–30/09/2013	31/08–30/09/2017
Stations (n)	204	208	202	209 (+9*)
Species (n)	36	37	30	35
Specimens (n)	67 735	157 584	77 406	189 548
Weight (kg)	18 911	48 492	31 850	46 208
Mesh size (codend) (mm)	40	40	90	40

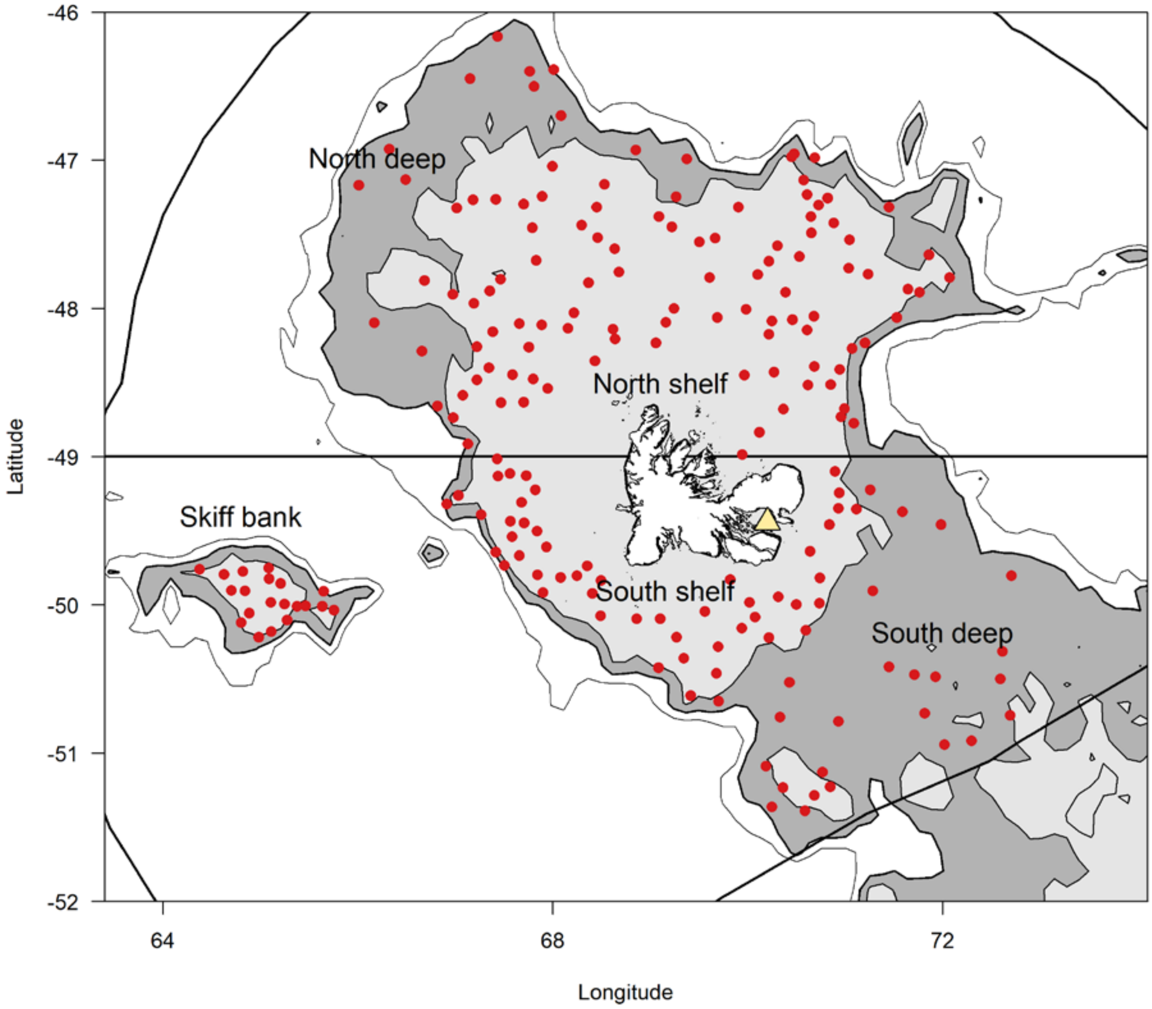

Figure 1: Map of the sampling stations of the bottom trawl surveys (POKER) in the Kerguelen Islands EEZ. The same stations were sampled over four years (2006, 2010, 2013 and 2017). Depths contours correspond to 500 m (light grey region, shallow <500 m), 1 000 m (dark grey region, 500 m to 1 000 m) and 1 500 m (not sampled). External black lines: French EEZ limits. Bathymetry source: Gebco (2014). (Δ Morbihan Bay trammel nets monitoring, 1982–1992).

Data collection

At each station, the scientific team on board sorted all the fish caught by species (field guide used: Duhamel et al., 2005) before counting the number of individuals and weighing the catch using an electronic scale (Marelec W10/15D4 0–15 kg and 0–60 kg). When the catch was too large (rare cases!), a sub-sample was weighed and counted in some baskets and the total was estimated after counting all the baskets. The most abundant fish species were measured (total length (TL) in cm) at each station to determine length-frequency distributions (LFD) and biological parameters such as sex and maturity stage were determined following the Everson scale (Everson, 1977). Fish were also examined for stomach contents and fullness index (except species regurgitating stomach contents), and dominant species in the catch had their otoliths subsampled for ageing. Stomach contents analysis was performed at each station during POKER 4 (2017) to investigate the spatial differences on stomach fullness/diet composition. Two of the dominant species, *C. gunnari* and *N. rossii*, had their diet composition and density mapped over the Kerguelen Plateau. When *C. gunnari* and *N. rossii* were caught at the same station, the digested state of *C. gunnari* was accounted for to correct for potential feeding of *N. rossii* inside the trawl.

All these data were registered in an electronic logbook, together with the characteristics of the station (coordinates, depth, date, trawl duration, speed of the vessel, weather conditions). For data analyses, we removed trawl events <15 min or <1.5 km long (n = 24) from the analyses because they were not comparable to the average trawl of 30 min covering an average distance of 2.9 km. One very large trawl of *N. rossii* in 2013 was also removed because the catch was too large to be hauled on board.

Fish species composition

The observed fish species composition was compared between years, geographical and bathymetric strata in order to show temporal and spatial trends in groundfish community composition and biomass.

Fish density and biomass estimations

Fish density (in kg km^{-2}) was calculated for each haul by dividing the total catch value by the swept area (in km^2). The swept area corresponded to the haul distance multiplied by the width of the gear mouth. Fish density per haul was compared between years and strata using boxplots. We used a log-scale for the density comparisons because of occasional extremely high densities encountered in dense fish aggregations.

Mean biomass of each species and its confidence interval values were computed using a bootstrap stratified non-parametric procedure (Efron and Tibshirami, 1986). The bootstrap method was used to estimate uncertainties around biomass estimates and stratification was used to account for spatial variations in fish density and strata size (Kerguelen north shelf, Kerguelen north deep, Kerguelen south shelf, Kerguelen south deep and Skiff Bank). The biomass estimate was obtained by multiplying the density observed in a strata by the total seafloor area of each strata (see Duhamel and Hautecoeur, 2009, for surface calculations). Mean biomass and its confidence intervals (5 and 95%) were determined using a bootstrap resampling procedure with 10 000 subsamples (Belchier et al., 2017). Skiff Bank mean density and total biomass had to be estimated separately because hauls/stations were separated by 3 n miles whereas stations on the Kerguelen Plateau were separated by 5 n miles. For five species which tend to aggregate in dense schools (*D. eleginoides*, *L. squamifrons*, *N. rossii*, Antarctic horsefish (*Zanclorhynchus spinifer*) and Unicorn icefish (*Channichthys rhinoceratus*)), we replaced the maximum catch of the dataset by the second-largest catch value of the given year to limit the influence of these extreme values on biomass estimations. Then, total biomass was estimated for each species by summing up the biomasses estimated in each strata.

Fish distribution

Species distributions were mapped for all POKER surveys using R software (package ggplot2, Wickham, 2016) or QGIS® for the diet composition. In distribution maps, observed density at each station was represented by a dot, the size of which was proportional to the observed density. Densities were also colour-coded to help interpretation and extreme values were set to the maximum values in the scale and displayed by a dot with a black contour line. Density maps per species provided useful information on temporal trends and spatial patterns highlighting the importance of strata in biomass estimate and showing species co-occurrences.

Juvenile fish monitoring in coastal areas

Notothenia rossii was the predominant commercial fish species in the 1970s and 1980s and was substantially overfished during this period (Duhamel and Williams, 2011). We reanalysed juvenile fish monitoring surveys conducted in coastal areas from 1982 to 1992 to monitor the juvenile part of the population after the trawl overfishing of adults (Duhamel, 1987) and the total fishery closure in1986. These surveys complement the results of the POKER surveys for this important species. They were carried out in the Morbihan Bay (eastern sector of the islands, Figure 1) where six stations were regularly sampled with a 90 × 1.5 m long trammel net (mesh size 230 and 60 mm) set at the kelp limit from 5 to 25 m depth (setting at dusk, hauling at dawn) (see Moreau and Duhamel, 1997). Four stations (Port aux Français, Molloy Cape, Suhm Island and Antares Island) of the six described above were selected (Chi2 contingence table) as representative for the catches of the juvenile *N. rossii* population (age 2–3) (see Duhamel et al., 2005, for a comprehensive description of its life cycle). We calculated the catch per unit effort (CPUE) of *N. rossii* juvenile fish to monitor fish recovery during this period and analysed these results in light of the POKER surveys.

Commercial catches in longline and trawl fisheries

Additional information on the deeper bathymetric range and levels of current fishing exploitation (annual catches) of species caught during the POKER surveys were obtained from the PECHEKER database (Pruvost et al., 2011). It must be kept in mind that the level of commercial catches of a species can interfere with the POKER survey results and the observed trends. There was no IUU fishing to be added to the legal catches in the Kerguelen EEZ (see Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) annual Scientific Committee reports) during the survey period (2006–2017).

Marine environmental conditions.

Oceanographic conditions from satellite-derived data, for example, sea-surface temperature (SST), in the Kerguelen region were used to detect any recent variations related to global changes which could potentially have an effect upon ecosystems and fish populations. Empirical Orthogonal function (EOF) was used to perform the analysis on the SST variable that has a combination of spatial and temporal trends. The extended reconstructed SST (ERSST) version 4 having a 2 × 2° spatial resolution for the 1981–2017 period was used (Huang et al., 2015). For the location of the PF (defined as the northernmost 2°C isotherm of the subsurface temperature minimum near 200 m; Park et al., 2014), we analysed all available historical hydrographic data in the study area. In addition, we have also used the satellite altimetry-derived mean dynamic topography by CLS/CNES: MDT CNES-CLS13.

Results

In each POKER survey, 30 or up to 37 different species of groundfish were observed (Table 1), resulting in 40 different species in total across surveys.

Species composition and biomass

Northern Kerguelen Plateau: shelf and deep waters

Over the Kerguelen Plateau, only six species dominated significantly (96% of the total catch across the four surveys) in terms of number and seven species in terms of weight (Figure 2), among the 22 commonly recorded species. Eleven other finfish species were commonly recorded but less abundant as well as five species of shark and skate (Figures 2 and 3). The 19 other species were rare or recognised as ‘out of their range’ (inshore or deepest-living species). These species totalled 480 individuals and 36.34 kg of biomass and were excluded from the species composition representations but summarised in Table 2.

The six dominant species in numbers were always: *C. gunnari*, *Z. spinifer*, *C. rhinoceratus*, *L. squamifrons*, *N. rossii*, and *D. eleginoides* (Figure 2) but their respective proportion varied through years. In 2017, species composition was dominated by *C. gunnari* in number but *N. rossii* in weight, while the contributions of *Z. spinifer*

Table 2: Rare species not included in the POKER cruise's rank species analysis due to their weak contribution to number or weight in the total catch.

Family	Species	Cruise:	1	2	3	4	
		Year:	2006	2010	2013	2017	All years
Notacanthidae	*Notacanthus chemitzii*	Number	0	1	0	0	1
		Weight (kg)	0	1.08	0	0	1.08
Macrouridae	*Coryphaenoides* sp.	Number	1	1	0	0	2
		Weight (kg)	0.1	0.02	0	0	0.12
Moridae	*Guttigadus kongi*	Number	1	5	1	1	8
		Weight (kg)	0.05	0.29	0.02	0.12	0.48
	Harlargyreus johnsonii	Number	5	3	2	0	10
		Weight (kg)	1.73	0.55	0.58	0	2.86
	Lepidion ensiferus	Number	4	8	8	2	22
		Weight (kg)	0.24	0.65	1.3	0.16	2.35
Oreosomatidae	*Pseudocyttus maculatus*	Number	0	0	0	1	1
		Weight (kg)	0	0	0	0.16	0.16
Liparidae	*Paraliparis copei*	Number	5	1	1	17	24
		Weight (kg)	0.2	0.01	0.05	0.3	0.56
	Paraliparis neelovi	Number	12	5	2	7	26
		Weight (kg)	0.66	0.35	0.1	0.23	1.34
	Paraliparis operculosus	Number	30	15	2	17	64
		Weight (kg)	0.3	0.35	0.03	0.26	0.93
	Paraliparis thalassobathyalis	Number	0	3	0	2	5
		Weight (kg)	0	0.08	0	0.04	0.12
Zoarcidae	*Lychenchelys hureaui*	Number	2	1	0	1	4
		Weight (kg)	0.06	0.02	0	0.04	0.12
	Lycodapus antarcticus	Number	24	10	0	41	75
		Weight (kg)	0.25	0.08	0	0.54	0.86
Nototheniidae	*Indonotothenia cyanobrancha*	Number	1	16	0	1	18
		Weight (kg)	0.22	4.98	0	0.26	5.46
	Notothenia magellanica	Number	2	0	2	1	5
		Weight (kg)	0.46	0	0.6	0.36	1.42
	Harpagifer spinosus	Number	0	3	0	1	4
		Weight (kg)	0	0	0	0.01	0.01
	Bathydraco antarcticus	Number	14	38	8	23	83
		Weight (kg)	0.47	2.03	0.3	0.7	3.50
Centrolophidae	*Icichthys australis*	Number	4	8	2	6	20
		Weight (kg)	2.69	6.03	0.64	3.37	12.73
Achiropsettidae	*Achiropsetta tricholepis*	Number	0	1	0	0	1
		Weight (kg)	0	0.46	0	0	0.46
	Mancopsetta milfordi	Number	7	0	0	0	7
		Weight (kg)	1.78	0	0	0	1.78

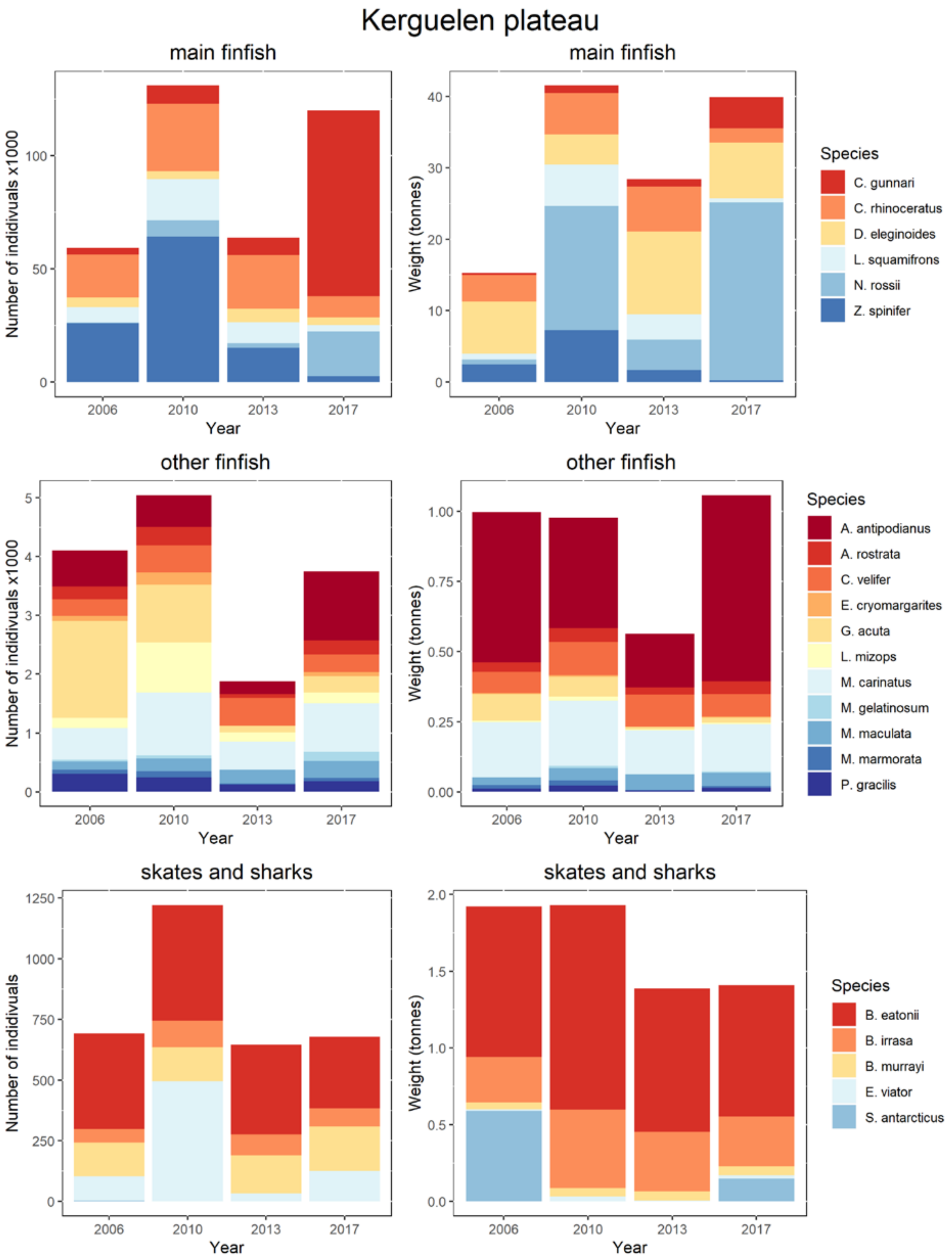

Figure 2: Fish species composition in number (left) and weight (right) at the POKER stations located on the shelf and deep strata of the Kerguelen Islands EEZ (northern Kerguelen Plateau). Rare species (<100 individuals over the four surveys) are not included but summarised in Table 2.

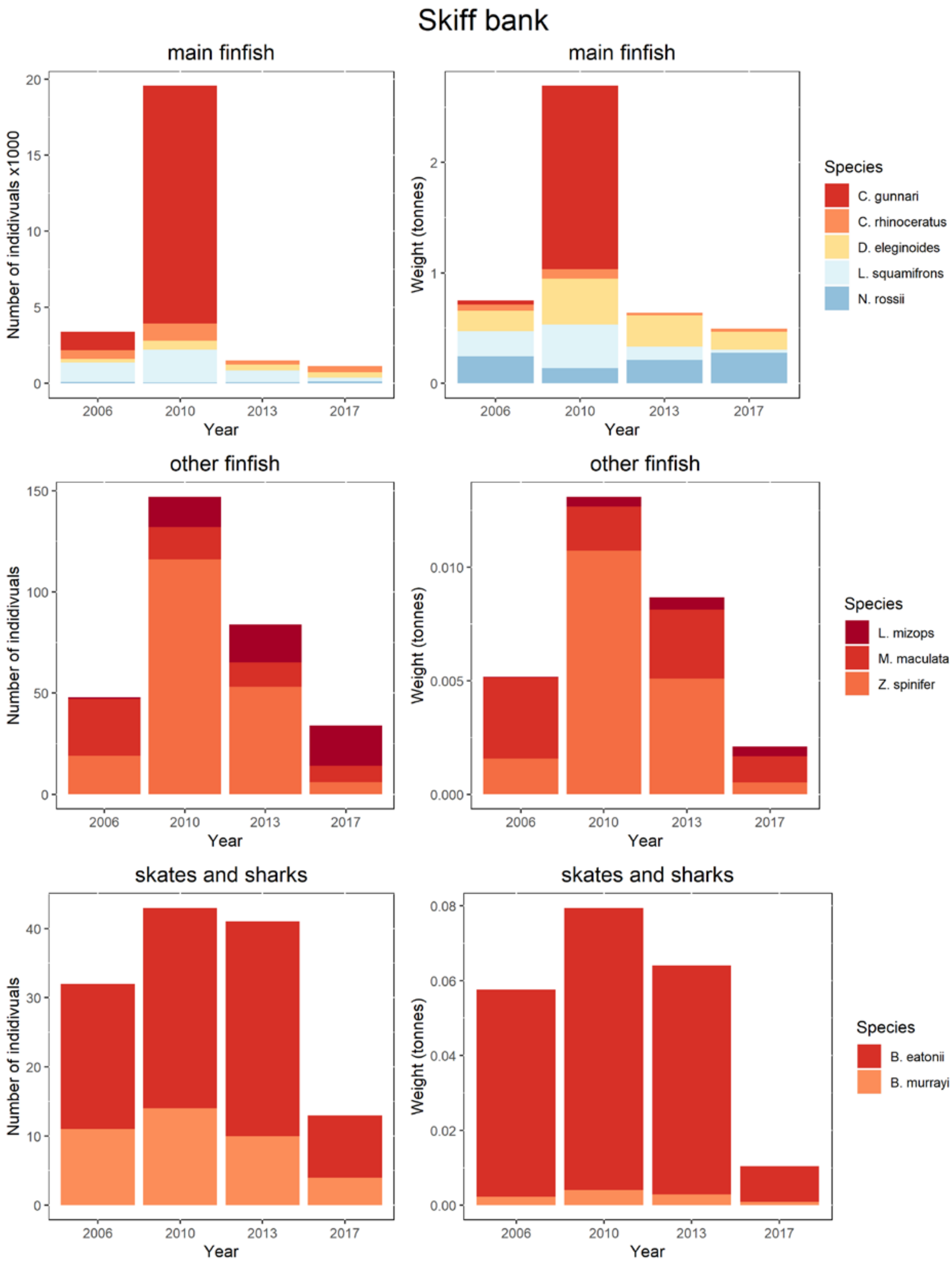

Figure 3: Fish species composition in number and weight at the POKER stations located on Skiff Bank (southwest of the Kerguelen Islands EEZ).

and *L. squamifrons* were low both in numbers and weights compared to previous years. A gradual increase of *N. rossii* and *C. gunnari* between surveys was noticeable among the dominant species whereas the contribution of *D. eleginoides* was relatively stable.

For other less abundant finfish species, species composition was relatively stable over years with bigeye grenadier (*Macrourus carinatus*) and Antipodean slickhead (*Alepocephalus antipodianus*) being dominant in this group. Interestingly, triangular notothen (*Gobionotothen acuta*) were more abundant in the species composition in the first two years (2006 and 2010) whereas they were almost absent in 2013 and 2017 (Figure 2). The relative proportion of the three species of skates caught (Eaton's skate (Bathyraja eatonii), Kerguelen sandpaper skate (*Bathyraja irrasa*), and Murray's skate (*Bathyraja murrayi*)) was remarkably stable over time, compared to sharks which were only caught occasionally in varying proportions.

Skiff Bank

Species composition of Skiff Bank (<500 m) was similar to the Kerguelen Plateau (in the same depth range) but with the absence of velifer icefish (*Channichtys velifer*). Only 10 species were common, with the same six dominant species as on the Kerguelen Plateau but only two species of skates (*B. eatonii* and *B. murrayi*) and two finfish species (spotted flounder (*Mancopsetta maculata*) and toad notothen (*Lepidonotothen mizops*)) (Figure 3). Except for a large dominance of *C. gunnari* in 2010 (POKER 2), the species composition of Skiff Bank was relatively stable over the years. The other important finfish species seem to be *L. squamifrons*, *D. eleginoides* and *N. rossii*.

Spatial and temporal variations in fish densities within strata

Comparison of fish density estimated per haul showed that densities were higher in average in the shelf strata of the Kerguelen Plateau (median = 131 kg km^{-2}) compared to deep waters (median = 93 kg km^{-2}) and Skiff Bank (median = 80 kg km^{-2}). Densities were slightly higher in the northern part of the Kerguelen shelf than on the south shelf, a spatial pattern also observed in deep waters (Figure 5). Extremely high densities resulting for occasional hauls within dense fish aggregations (up to 36 000 kg km^{-2}) occurred mostly on the shelf of the Kerguelen Plateau, particularly on the southern part of the shelf (Figures 4 and 5).

Comparing the four surveys by strata showed remarkable stability in density estimations through time, except for a slight increase on the south shelf of the Kerguelen Plateau and decreasing trends in the south deep strata of the Kerguelen Plateau and Skiff Bank (Figures 4 and 5).

Trends in fish biomass 2006–2017

The fish biomass estimations for the entire shelf and deep area of the Kerguelen Plateau tended to increase from ~250 000 tonnes in 2006 to >400 000 tonnes in 2017 (Figure 6). The contribution of *N. rossii* and *C. gunnari* to the total biomass increased in 2017 while the contribution of *D. eleginoides* seemed more constant through time (see also Appendix 2). The proportion of *C. rhinoceratus*, *Z. spinifer* and *L. squamifrons* in contrast was lower in 2017 than in previous years.

Skiff Bank biomass (Figure 6) was much smaller with estimated biomass ranging from 1 200 to 2 300 tonnes on average, except in 2010 (7 000 tonnes) due to high catches of *C. gunnari*. It is to note that this species was not caught during the 2013 and 2017 surveys. In most years, *D. eleginoides* and *N. rossii* were dominant on Skiff Bank, along with *L. squamifrons* whose contribution to the biomass seemed to decrease in 2013 and 2017 (see also Appendix 2). Skates contributed less to the total biomass estimation than on the Kerguelen Plateau and sharks were never caught on Skiff Bank.

Pattern of species distribution

The analysis of species distribution for each cruise revealed three categories of species: (i) species with wide depth and/or geographical distributions, (ii) species with patchy distributions and (iii) species at the margin of their distribution range (deep-sea living species, shallow species).

Ten species had widespread spatial distribution across the study area (category 1). *Channichthys rhinoceratus* (Figure 7) had a typical widespread shelf distribution with the most number of high-density stations on the northern shelf. Marbled moray cod (*Muraenolepis marmorata*) (see

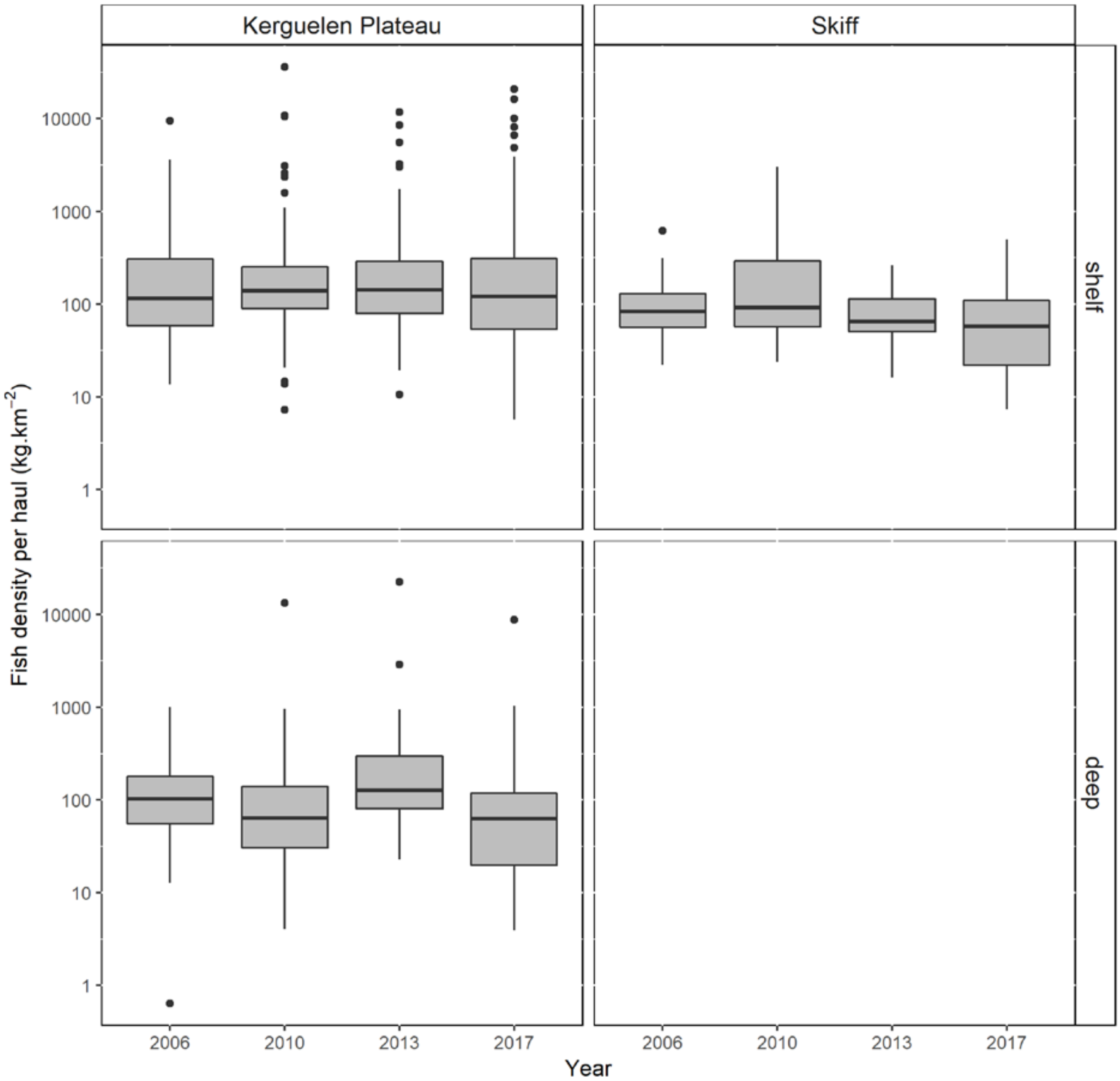

Figure 4: Comparison of the mean fish density per haul (all species included) during the four POKER surveys over the shelf and deep waters of the Kerguelen Islands EEZ (northern Kerguelen Plateau and Skiff Bank). Note the log-scale of the y-axis (density) to allow for outlier hauls of extremely high catches.

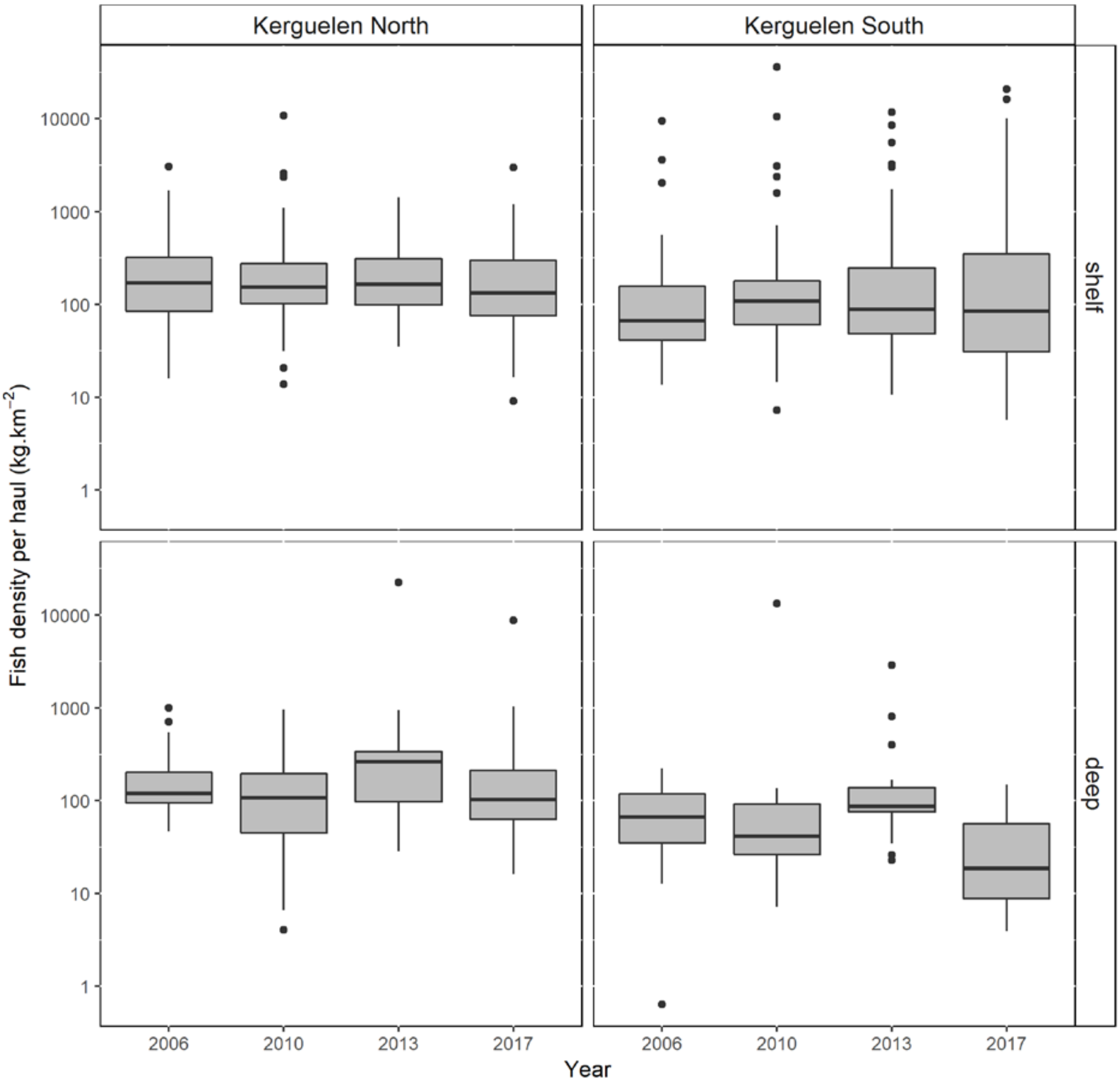

Figure 5: Comparison of the mean fish density per haul (all species included) during the four POKER surveys in the shelf and deep waters of the northern and southern parts of the Kerguelen Islands EEZ. Note the log-scale of the y-axis (density) to allow for outlier hauls of extremely high catches.

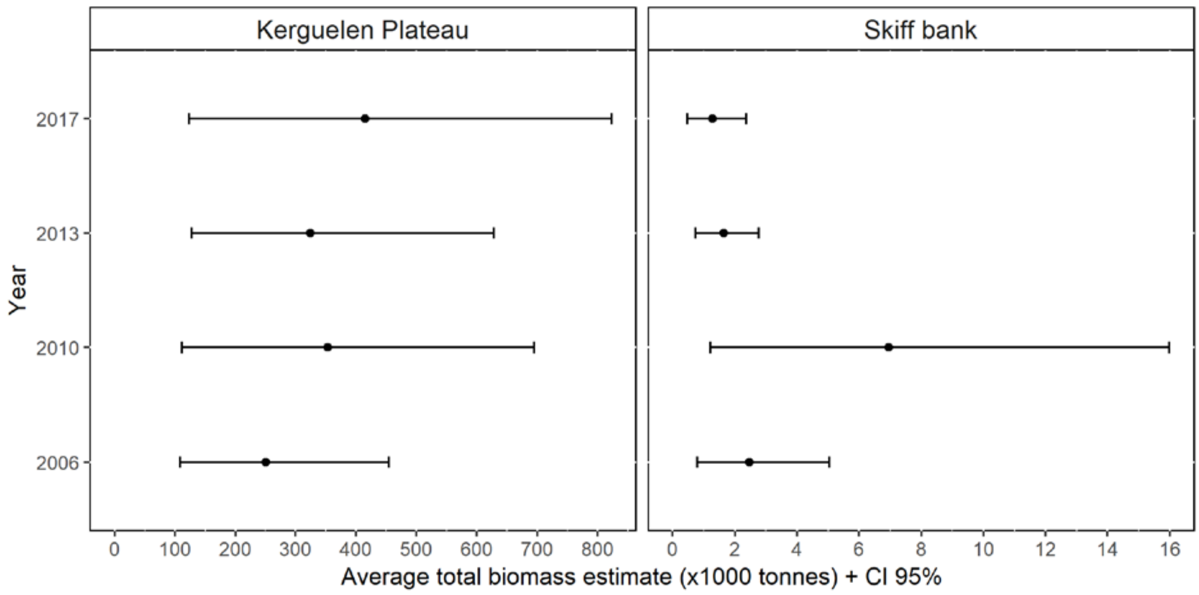

Figure 6: Mean fish biomass of the northern Kerguelen Plateau (left) and Skiff Bank (right) estimated using a non-parametric bootstrap procedure accounting for the survey stratification during the four POKER surveys (2006–2017) (Kerguelen Islands EEZ). Note the difference in scale.

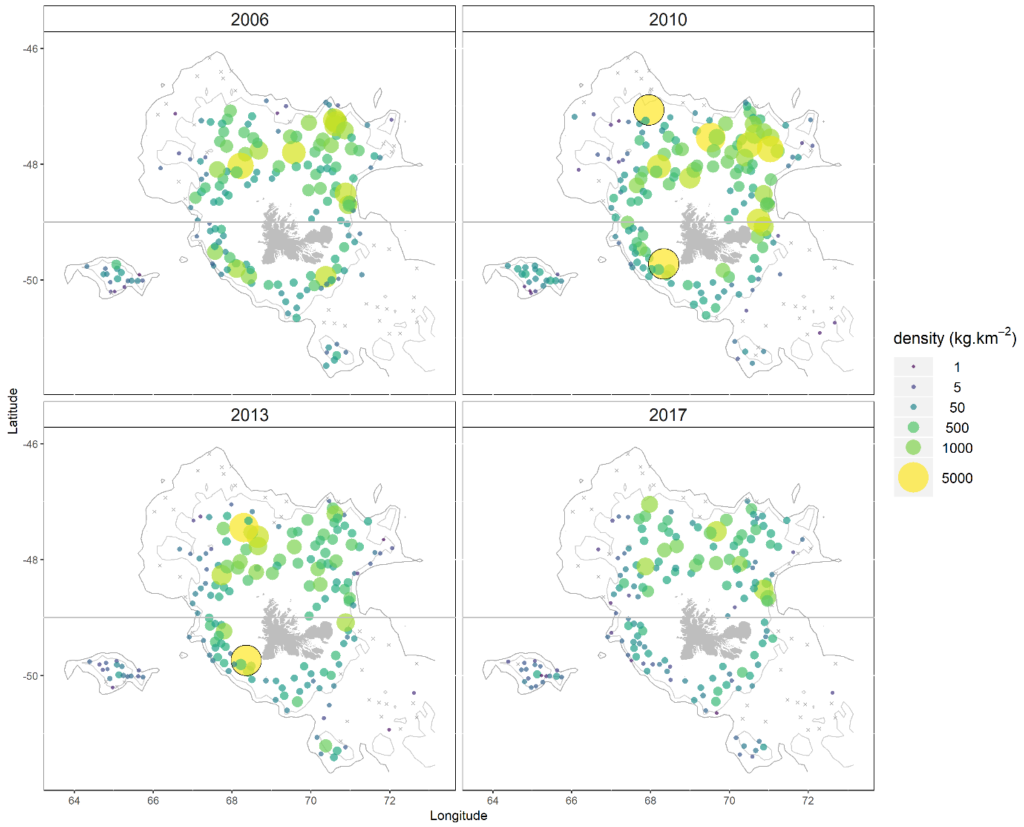

Figure 7: Distribution of *Channichthys rhinoceratus* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 49 000 kg km^{-2}).

Appendix 1l), had both shelf and deep-sea distribution. In contrast, *D. eleginoides* (Figure 8), *L. squamifrons* (Figure 9), *B. eatonii* (see Appendix 1b) and *M. maculata* (see Appendix 1j) belong to the same category but showed highest densities along the shelf break. *Bathyraja murrayi* (see Appendix 1d) also showed an intermediate distribution both on the shelf and upper slope. *Channichthys velifer* (see Appendix 1e) and *G. acuta* (see Appendix 1g) had a widespread but exclusively shallow shelf distribution as *C. rhinoceratus*, in contrast to snake mackerel (*Paradiplospinus gracilis*) found in the deepest range of the POKER survey (see Appendix 1m). *Lepidonotothen mizops* had a shelf and upper banks distribution (see Appendix 1h).

Five species had patchy distributions (category 2), including two of the predominant species: *N. rossii* (Figure 12) and *C. gunnari* (Figure 13). *Notothenia rossii* occurred mostly on the southern shelf, but extended southwest in the more recent cruises. In contrast, the distribution of *C. gunnari* was stable in the northeastern shelf of the Kerguelen Plateau throughout the surveys. The species occurred on Skiff Bank only during the first two surveys (2006 and 2010). *Zanclorhynchus spinifer* (Figure 10) and *A. antipodianus* (Figure 11) had typical patchy distributions in localised areas located on the northwest shelf and in northwest deep waters respectively.

Finally, five species were at the margin of their suitable habitat (category 3), either in the medium slope areas (800–1 000 m) or in coastal waters (100 m). Four species (*M. carinatus*, *B. irrasa*, blue antimore (*Antimora rostrata*) and southern lantern shark (*Etmopterus viator*)) occurred in the deepest waters of our surveys, in the north and northeastern sectors and one species (limp eelpout (*Melanostigma gelatinosum*)) in the northwestern sector (see Appendices 1i, 1c, 1a, 1f, 1k). Three coastal species: orange throat notothen (*Notothenia magellanica*), bluegill notothen (*Notothenia cyanobrancha*), deep-water spiny plunderfish (*Harpagifer spinosus*) were recorded occasionally at shallow depths (<110 m) at the margin of their maximum bathymetric distribution.

Spatial variations in diet of *N. rossii* and *C. gunnari*

Champsocephalus gunnari were observed in higher densities in the northeastern sector (Figure 13) where Euphausiid (*Euphausia vallentini*) was the only component in their stomach contents (Figure 14). Elsewhere, hyperiid amphipods (*Themisto gaudichaudii*) dominated in their diet. In contrast, higher densities of *N. rossii* in the south (Figure 12) coincided with a diet dominated by gelatinous organisms (salpa, medusa) (Figure 15).

Juvenile monitoring of *N. rossii* in coastal waters

The *N. rossii* juvenile population index (CPUE) showed a sharp drop at the beginning of the period (1982–1984), followed by a regular increase (Figure 16) from 1984 (CPUE = 0.89) until 1989 (CPUE = 12.64). The values of the last two years (1990, 1991) were similar to those of 1989 showing a stabilisation of part of the population.

Commercial fishing catches during the POKER period (2006–2017)

Dissostichus eleginoides is caught in depths ranging from 500 m to 2 300 m, overlapping partially with the depth range of the POKER surveys. Over the POKER studied period, the annual catch did not fluctuate (~5 000 tonnes, Figure 17). By-catch in this longline fishery consisted mostly of grenadiers (*M. carinatus*), skates (both *B. eatonii* and *B. irrasa*), *A. rostrata* and more occasionally deep-sea sharks (*E. viator*, Antarctic sleeper shark (*Somniosus antarcticus*) and Portuguese dogfish (*Centroscymnus coelolepis*)). By-catch did not fluctuate much during the period except from 2014 for skates when the cut-off method was applied following CCAMLR recommendations. Average annual catches reached 760 tonnes for grenadiers, <500 tonnes for skates and 55 tonnes for blue antimore. During the study period (2006–2017) only one commercial pelagic trawl targeted *C. gunnari* occurred (in 2015/16, with a landing of less than 200 tonnes). In total, the longline and trawl commercial catches reached 75 500 tonnes (including 61 500 tonnes of *D. eleginoides*) over the studied period which is to add to the previous historical catches (see Duhamel et al., 2011).

Marine environmental data.

The Kerguelen EEZ is situated in the permanent meander of the PF. Its time-mean average signature extends from south to north along the eastern escarpment of the shelf along the 500 m isobaths before bending southeastward (Figure 18). The

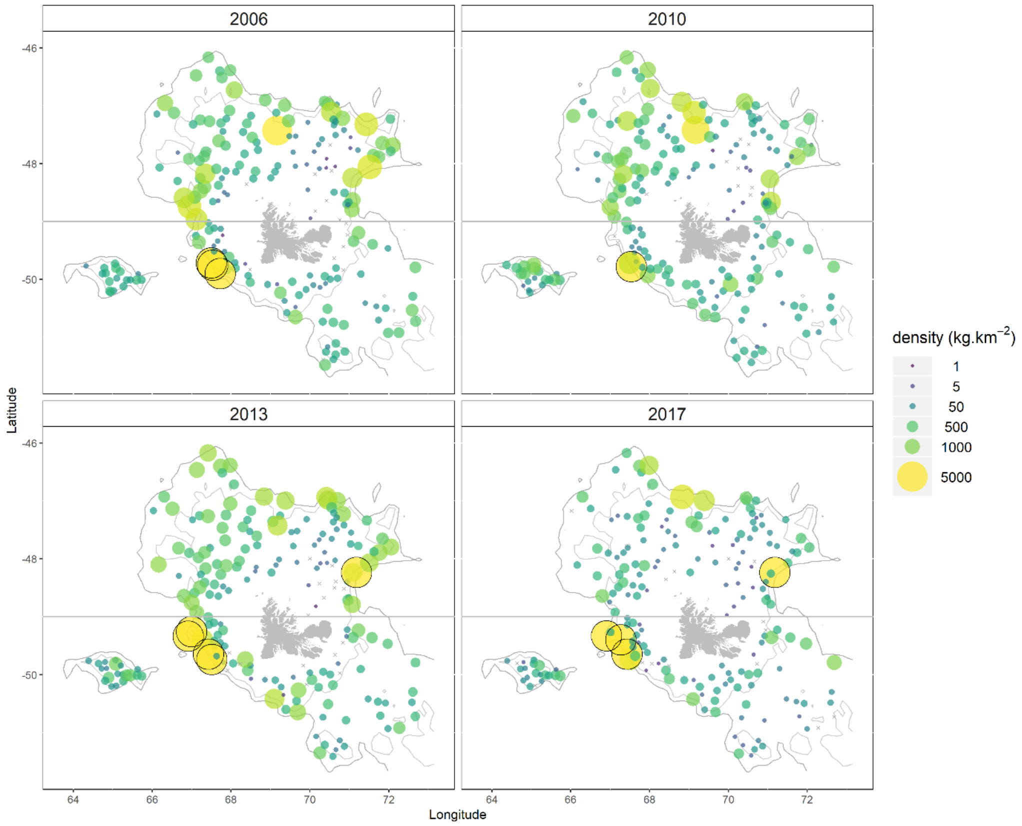

Figure 8: Distribution of *Dissostichus eleginoides* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 90 000 kg km^{-2}).

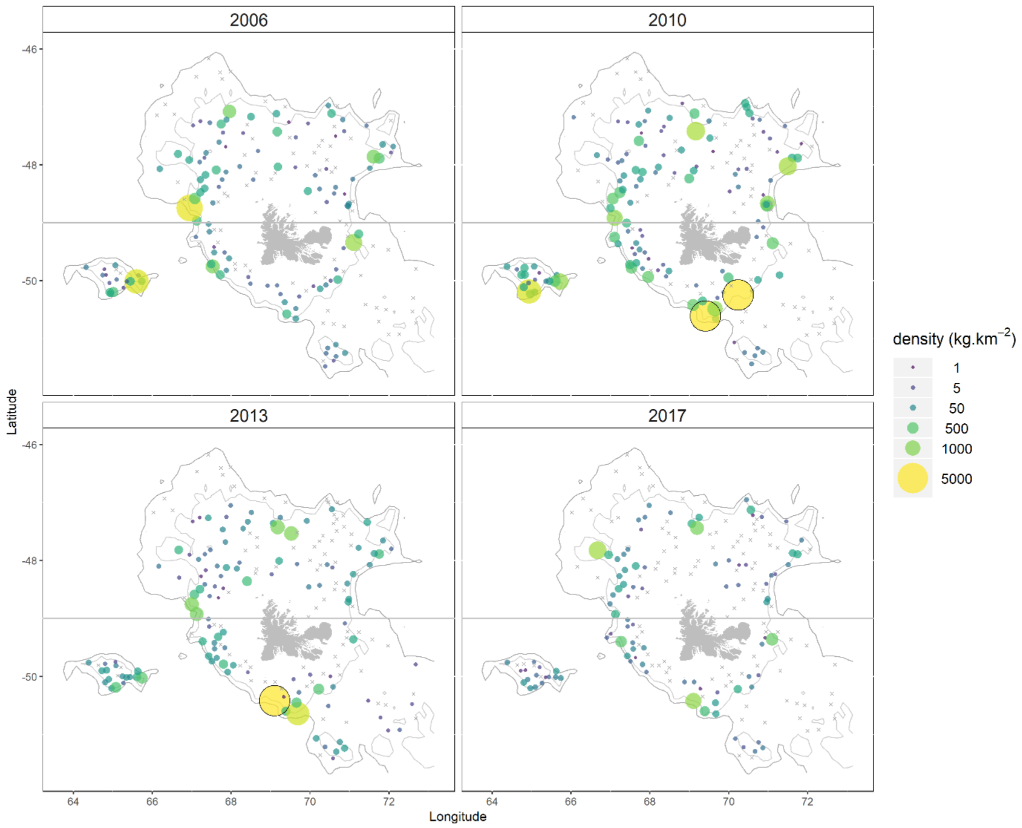

Figure 9: Distribution of *Lepidonotothen squamifrons* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 66 000 kg km^{-2}) (see remarks in the text for caution in the species results due to surveys in spring time).

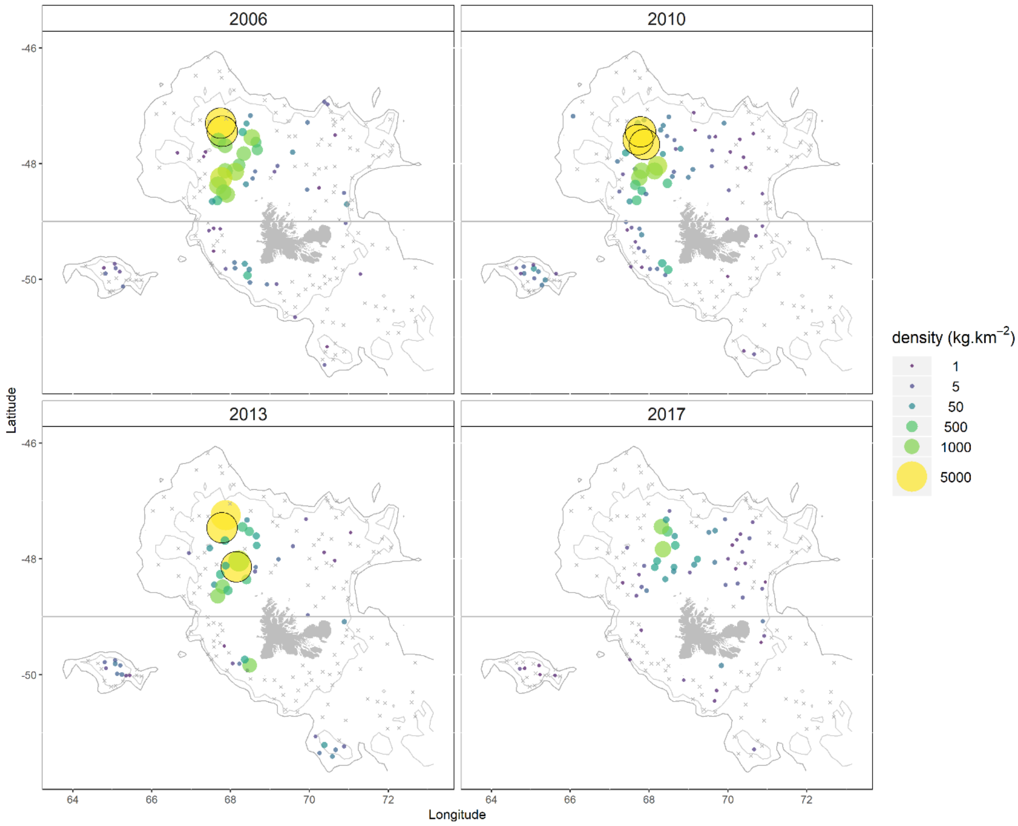

Figure 10: Distribution of *Zanclorhynchus spinifer* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 75 000 kg km^{-2}).

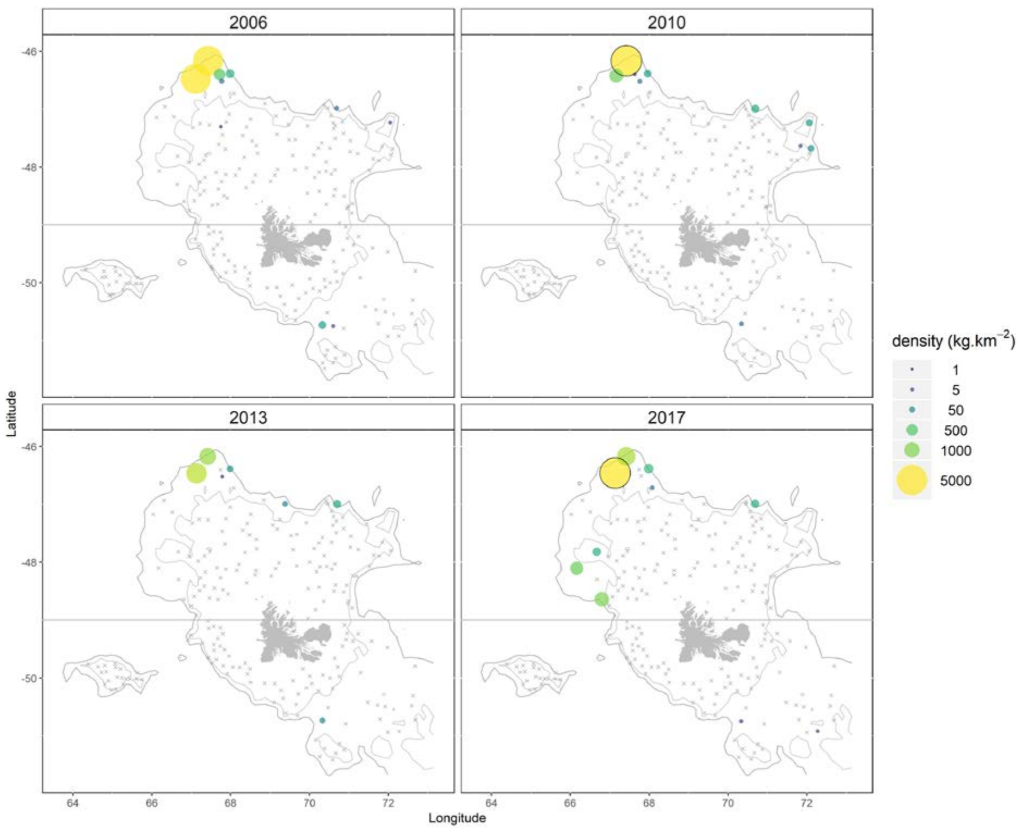

Figure 11: Distribution of *Alepocephalus antipodianus* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 6 000 kg km^{-2}).

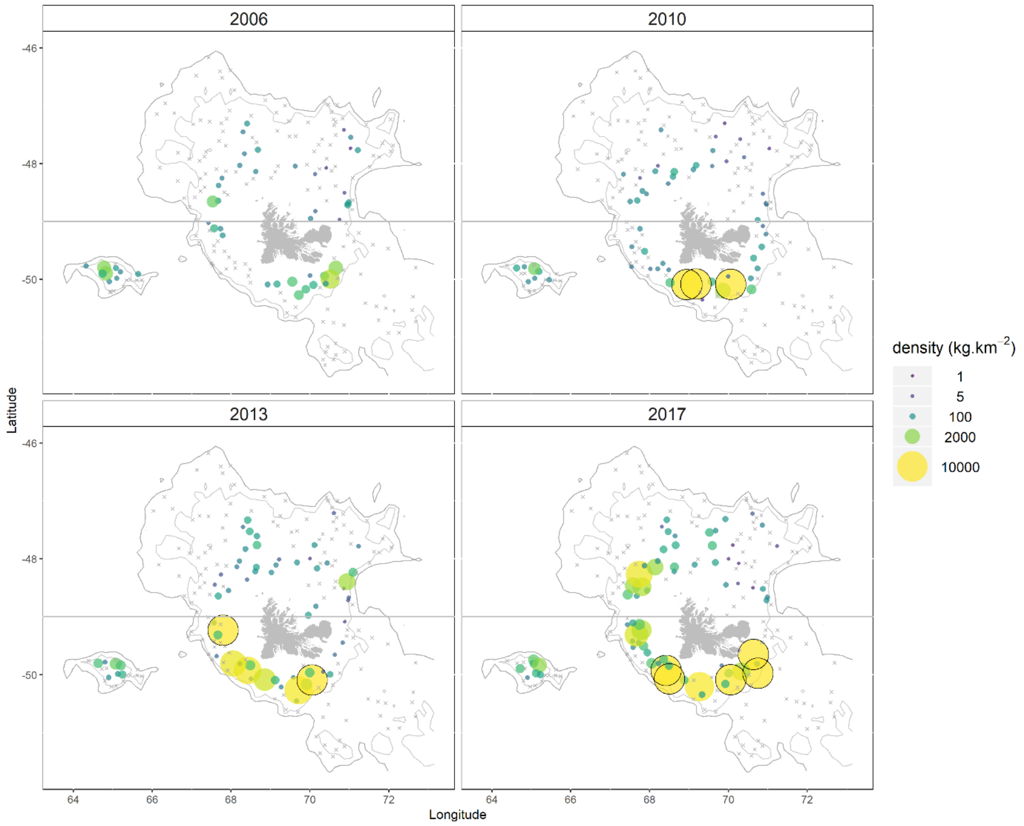

Figure 12: Distribution of *Notothenia rossii* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >10 000 kg km^{-2} (up to 180 000 kg km^{-2}).

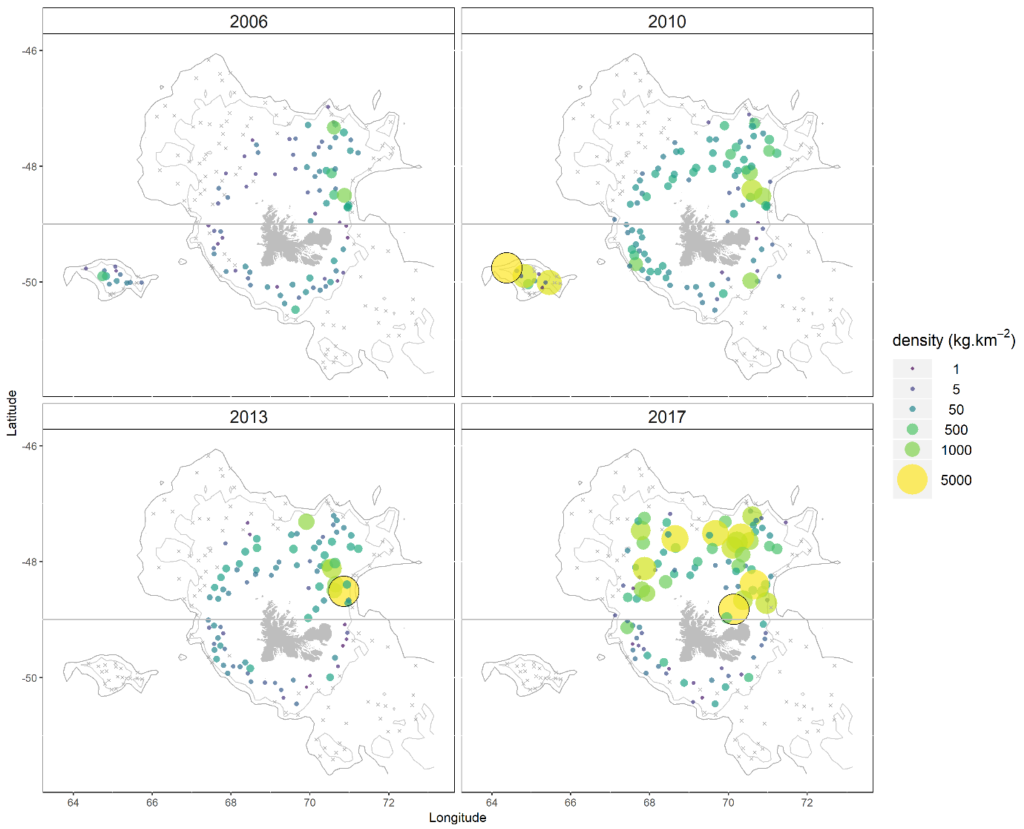

Figure 13: Distribution of *Champsocephalus gunnari* densities during the POKER cruises (Kerguelen Islands EEZ). Circles with black contours indicate densities >5 000 kg km^{-2} (up to 21 000 kg km^{-2}).

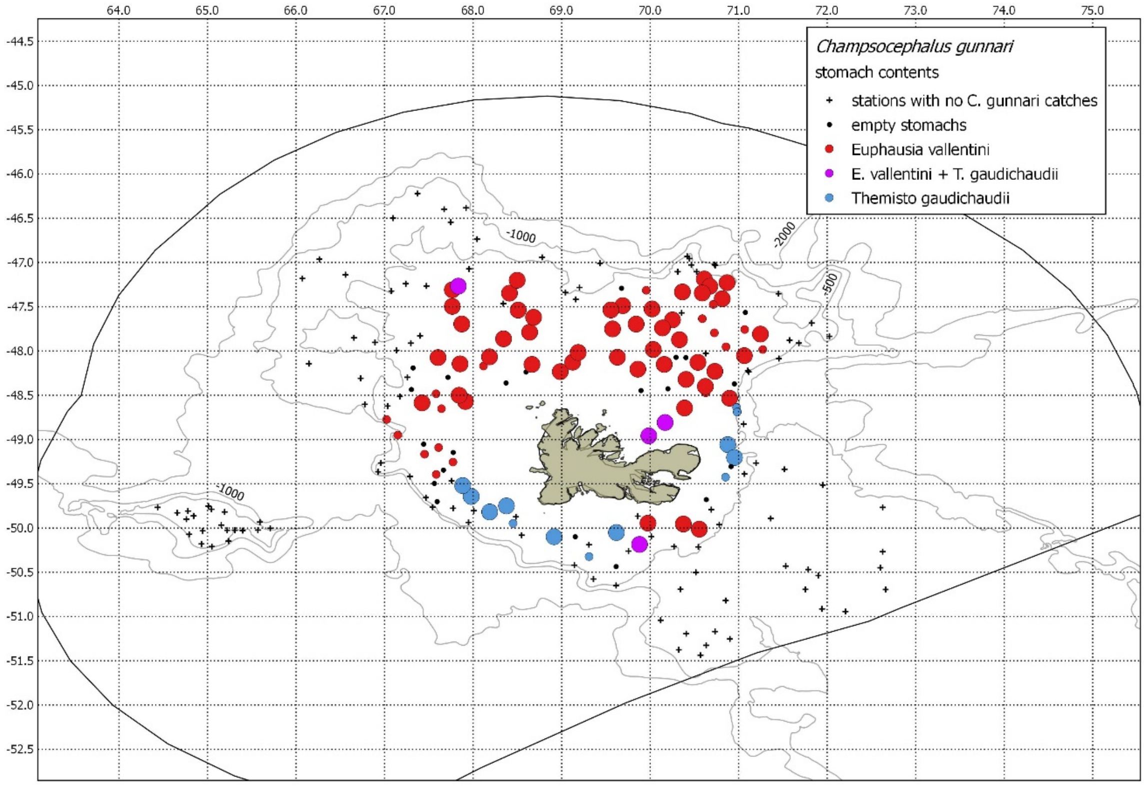

Figure 14: Diet composition (from stomach contents prey dominance) of (age 2+) *Champsocephalus gunnari* during the POKER 4 (2017) survey (Kerguelen Islands EEZ).

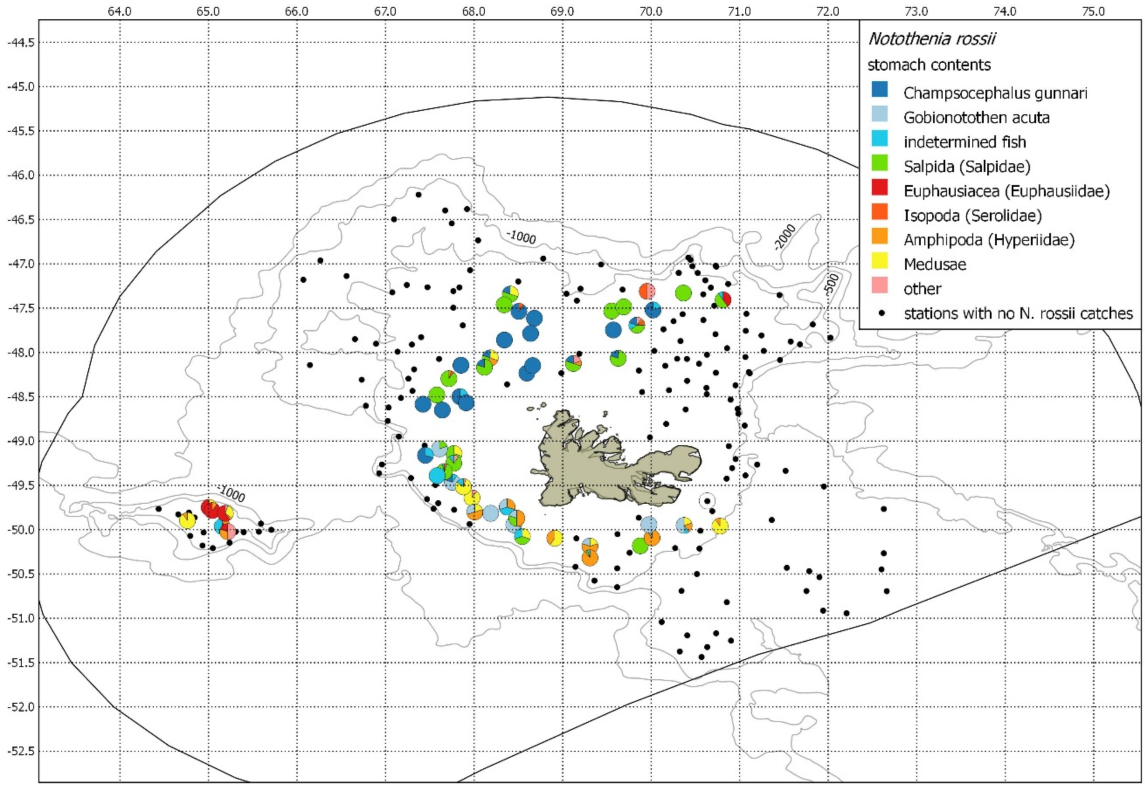

Figure 15: Diet composition (from stomach contents prey dominance) of *Notothenia rossii* adult fish during the POKER 4 (2017) survey (Kerguelen Islands EEZ).

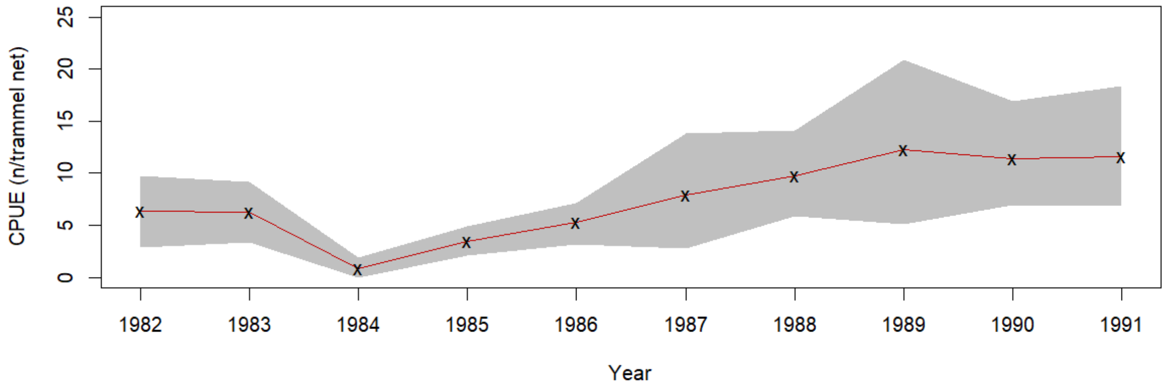

Figure 16: Abundance index of juveniles *Notothenia rossii* from catch per unit effort (annual mean CPUE, in number of fish caught by trammel net with standard error in grey) in coastal Kerguelen Islands area (Morbihan Bay) monitored from 1982 to 1991.

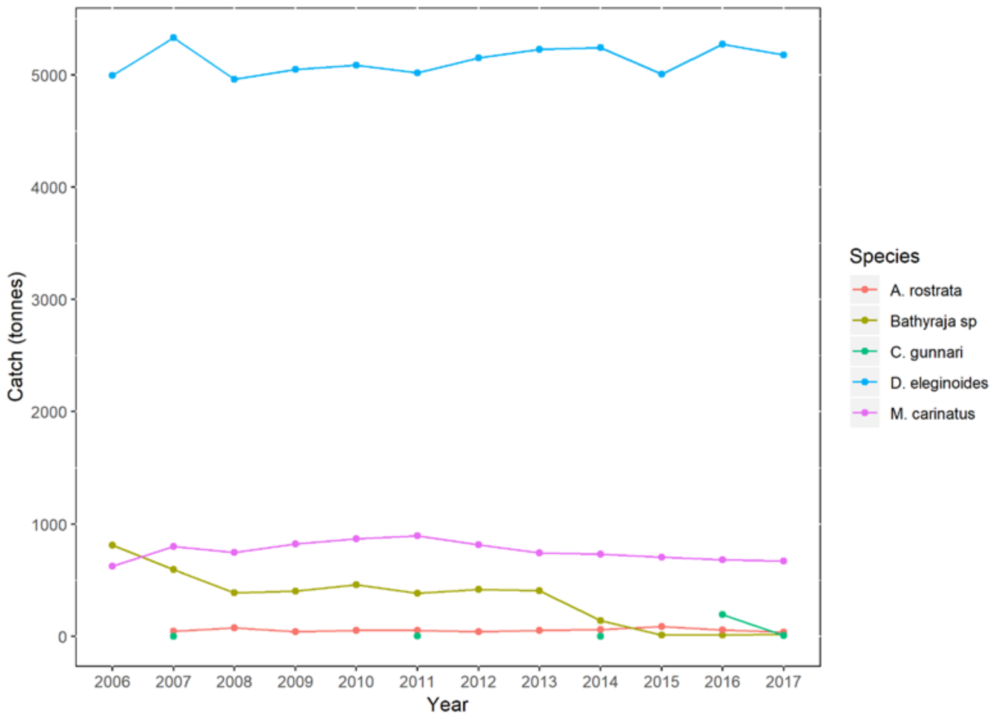

Figure 17: Catches of the main species caught in the *D. eleginoides* and *C. gunnari* commercial fisheries during the studied period (2006–2017). Non-targeted species were mostly discarded except for *Bathyraja* spp. and *M. carinatus* for which a proportion was landed. *Bathyraja* spp.: *Bathyraja eatonii* and *B. irrasa*. By-catch of *Bathyraja* spp. were reduced from 2014 onwards by the application of the cut-off CCAMLR conservation measure.

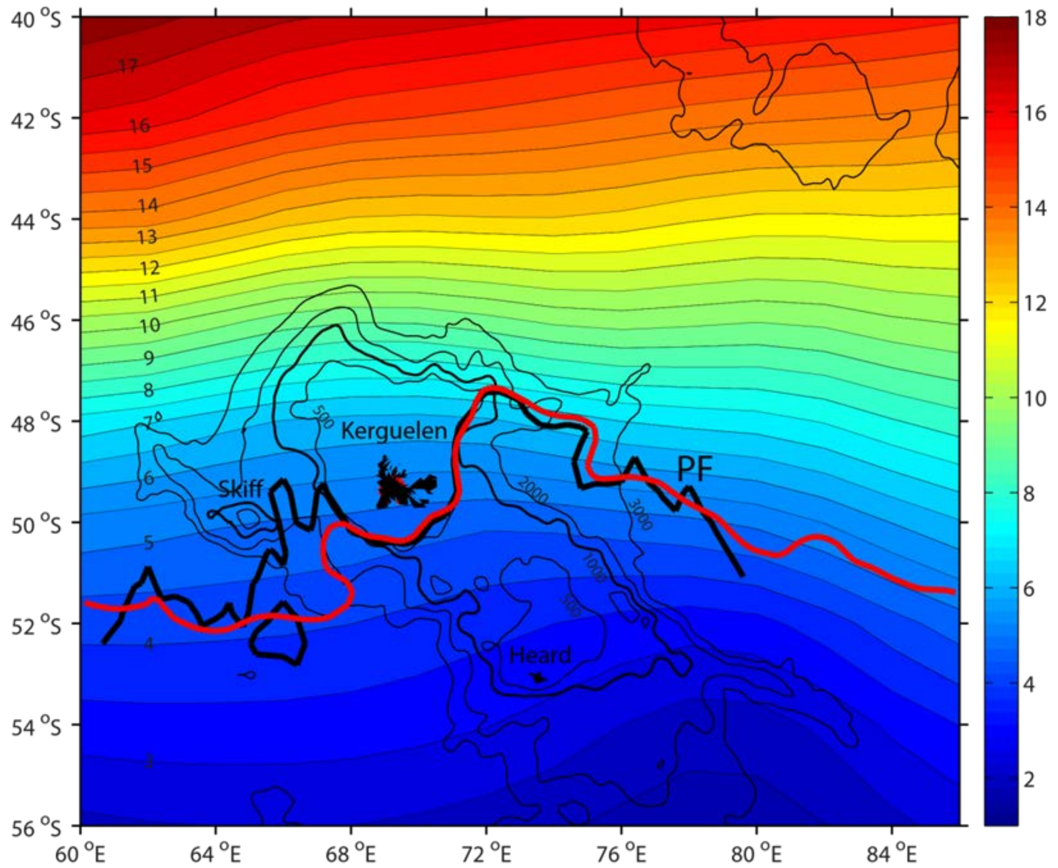

Figure 18: Time-mean austral summer (January through March) sea-surface temperature (SST) (colour in °C, with solid lines every 0.5°C) in the Kerguelen region for the period 1981–2017 from the 2° × 2° resolution ERSST dataset. The superimposed Polar Front (PF) position (black thick line) is the updated version of the front determined by Park et al. (2014) as the northernmost location of the subsurface temperature minimum of 2°C from all available historical hydrographic data in the region. The thick red line corresponds to the closest mean dynamic topography (–0.625 m) from the satellite altimetric product MDT CNES-CLS13.

satellite-derived SST data for 1981–2017 showed that the mean summer temperature ranged from 8–9°C (north) to 3–4°C (south) in this northern part of the Kerguelen Plateau.

EOF analysis of the summertime SST (Figure 19) showed the predominant leading mode (EOF1 explaining 66.5% of the total variance) with a positive mono pole (>0.35°C) north of the Kerguelen Plateau at 41°S 69°E, gradually decreasing to zero in the Fawn Trough region near 56°S. The observed root mean square SST variations in the POKER survey area ranged from 0.25 (near 47°S) to 0.1°C (near 52°S).

The correlation between the Kerguelen region SST EOF1 and El Niño Southern Oscillation (ENSO, a dominant tropical mode of climate variability active at interannual time scales) and the Southern Annular Mode (SAM, a dominant mode of Antarctic variability active interannual to decadal time scales), was weak (r = –0.24 for ENSO and r = 0.2 for SAM), both insignificant at the 90% confidence level (Figure 20).

Discussion

Noticeably, the mesh size used in the POKER 3 cruise (90 mm versus 40 mm during the other cruises) introduced a small bias (mainly in the abundance) for the very small species (underrepresentation of small size in the LFD) but we consider that it had a minor impact in the biomass estimations (due to a low weight of these species: 0.05% to 0.55% of the total in the other cruises).

Dominant species biomass and distribution

Results from the four POKER surveys showed that the four historically commercially targeted species (*N. rossii*, *D. eleginoides*, *C. gunnari* and *L. squamifrons*) represented the bulk of the biomass

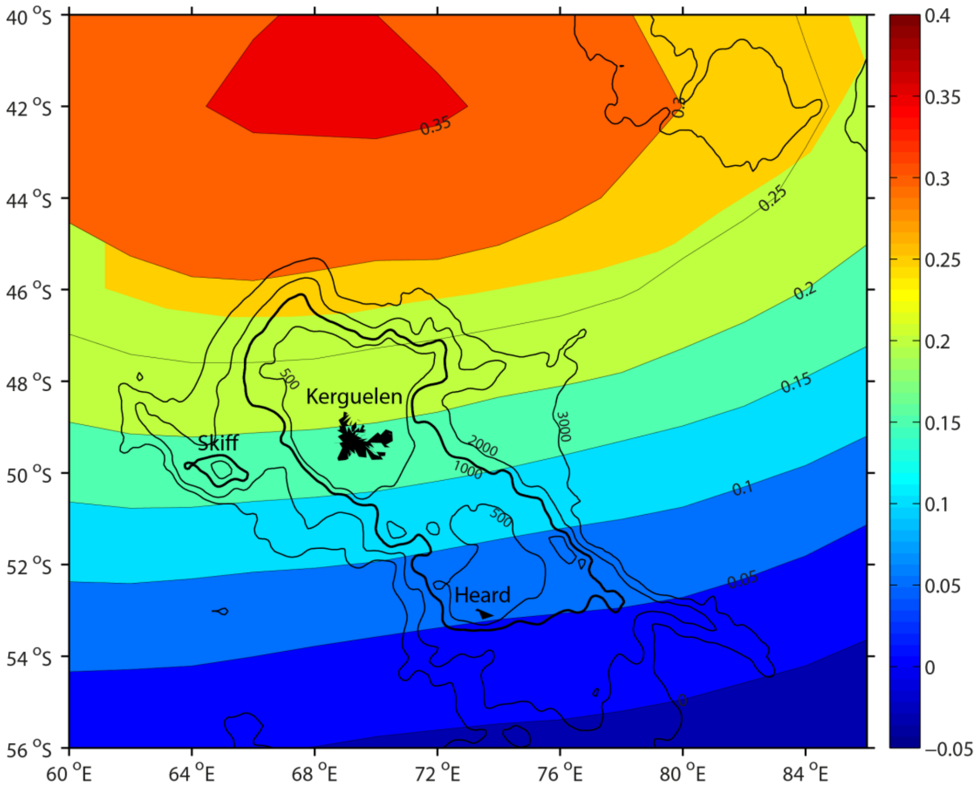

Figure 19: Leading Empirical Orthogonal Function mode (EOF1 – 66.5%) of the austral summer SST variations for the period 1981–2017 from the 2° × 2° resolution ERSST data set. Colour scale is every 0.05°C.

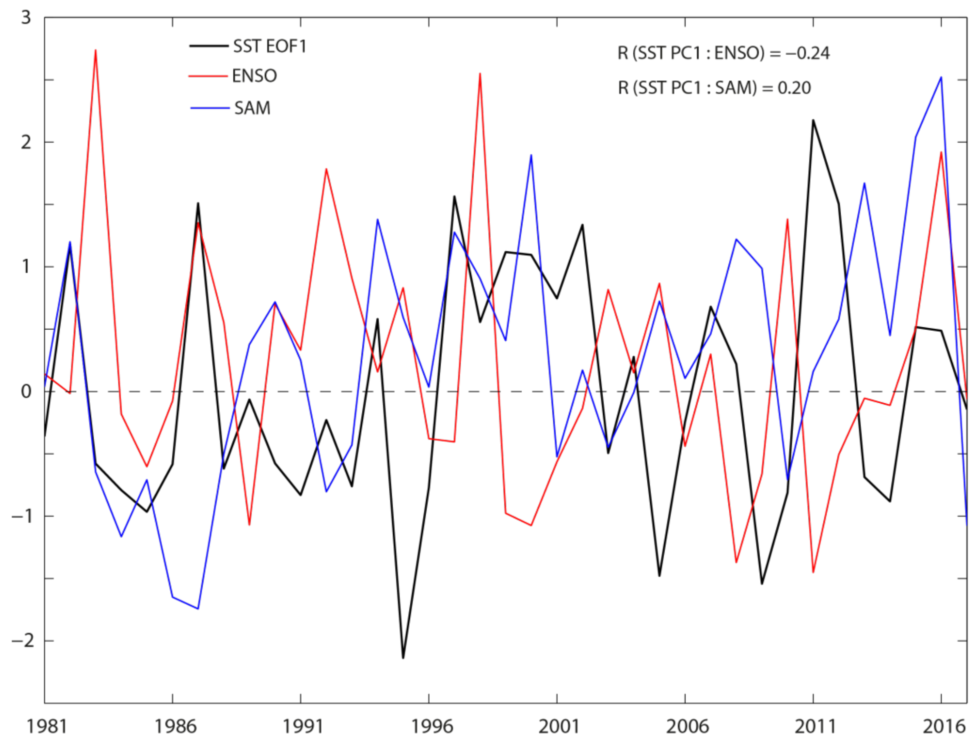

Figure 20: Principal component (PC1) time series (black) of austral summer SST corresponding to Figure 19. Also inserted are the time series of El Niño Southern Oscillation ENSO (red) and the Southern Annular Mode SAM (blue) indices. Correlation coefficients between SST PC1 and both the ENSO and SAM indices are indicated. All the time series are standardised relative to their respective standard deviations.

and abundance at each survey, along with two other species never exploited commercially (the large head/tiny body *C. rhinoceratus* and the all spikes *Z. spinifer*). Distributions of these major fish species were studied prior to the groundfish POKER biomass surveys (Slosarczyk and Wysokinski, 1980; Sosinski, 1981; Duhamel, 1981, 1982, 1987). The SKALP surveys in 1987 and 1988 on the shelf of the Kerguelen Plateau (Duhamel, 1993) showed the same area of high densities for both target species (*N. rossii*, *L. squamifrons*, *C. gunnari*, *D. eleginoides*) and by-catch (*Z. spinifer* or *C. rhinoceratus*) species. However, the sampling strategy and season (summer/ autumn) of these surveys differed to the POKER cruises and were thus not fully comparable. The POKER cruises offered information on a larger range of species but also extended the knowledge on deep-sea species (down to 1 000 m) compared to the SKALP data, which was limited to a depth of 500 m. Interestingly, fish distribution did not change much (i.e. *Z. spinifer*) during the 20 year period separating SKALP and POKER surveys, indicating both little seasonal and interannual variations. Apart from the main species, POKER surveys provided information on abundance, biomass and distribution of 14 species (see Appendices 1 and 2) never studied previously in the Kerguelen EEZ such as *A. antipodianus*, which displayed a very patchy and restricted distribution in the deep northwest. Some species were limited to the shelf (and bank) strata (i.e. all Channichthyidae, Nototheniidae, *Z. spinifer* and *B. murrayi*), others to the deep-sea ones (i.e. *A. antipodianus*, *A. rostrata*, *B. irrasa*, *E. viator*, *M. carinatus* and *P. gracilis*). These results are essential for conservation matters in the Marine Reserve and our understanding of the ecosystem, notably trophic relationships.

Biomass estimation and limitations

The POKER biomass estimates, ranging from 250 000 to 400 000 tonnes, represent conservative values for the Kerguelen EEZ since they only included the 100–1 000 m bathymetric range, while the deeper area (1 000–2 500 m) and shallow area (<100 m) were not accounted for. The large confidence intervals around the mean groundfish biomass estimated through a bootstrap procedure is likely to be a consequence of: (i) the patchy distribution of some of the most abundant species which can form very large schools, and (ii) the strata used for the total biomass extrapolation. For example, the strata 'Kerguelen south deep' includes both flat areas and areas of steep slopes, which constitute different fish habitats and could be considered as different strata according to the results of the POKER surveys. Moreover, future research efforts will need to include the shallow grounds (0–100 m), inhabited by other coastal species (mainly Notothenioids like *Harpagifer* spp., *N. cyanobrancha* and *P. magellanica*) or juveniles of many species encountered on the shelf and deep-sea species (1 000–2 000 m).

Deep-sea species inhabiting the lower part of the slope were not, or partially, sampled by POKER (i.e. *D. eleginoides* and species caught as by-catch in the toothfish fishery). The true deep-sea species (e.g. *A. antipodianus*, *E. viator* and *P. gracilis*) and *M. marmorata* (Duhamel et al., 2005; Duhamel et al., 2017) were also partially sampled during POKER which means that biomass estimations for these species were incomplete. Consequently, the POKER biomass represents the minimum values for the Kerguelen EEZ.

Temporal trends in biomass showed stability for some species (*D. eleginoides*), whilst others increased (*C. gunnari* and *N. rossii*) or decreased (*C. rhinoceratus* and *Z. spinifer*) during the 2006–2017 period. The past or current fisheries seem to be a potential driver. Large commercial catches of some species (*N. rossii*, *L. squamifrons*, *D. eleginoides* and *C. gunnari*) were recorded in the area (Duhamel and Williams, 2011), by both legal and illegal vessels, leading to overexploitation for three species (*N. rossii*, *L. squamifrons* and *C. gunnari*) (Duhamel, 1987) until the closure of the bottom trawl fishery in 1995. Ten years later, in 2006, the first POKER survey gave biomass estimates and began to monitor the recovery rate of these species. The biomass of some species caught as by-catch in the current longline fishery such as deep-sea skates (*B. irrasa* and, to a lesser extent, *B. eatonii*) and grenadier (*M. carinatus*) fluctuated in other respects in the same range than other unexploited species (i.e. *B. murrayi* for the skates) during the study period. *Bathyraja eatonii* always showed the highest biomass among skates. Recent analysis of skates taken in the toothfish fishery on the whole Kerguelen Plateau up to 2014 (Nowara et al., 2017) found little temporal changes in their abundance.

Prior to the surveys it was expected that the timing of the cruise was inadequate for the biomass estimation of one species (*L. squamifrons*) due to overlapping with the short spawning period where large adults annually aggregate in a very localised area (Duhamel and Ozouf-Costaz, 1985; Duhamel, 1987). The LFD analysis (Appendix 2) showed that specimens larger than 35 cm (known size of maturity; Duhamel and Ozouf-Costaz, 1985) were absent in POKER 1 (Duhamel and Hautecoeur, 2009) and 4 samples validating such assumption for these years. The biomass of *L. squamifrons* was underestimated because the absence of a part of the population and needs to be considered with caution.

These results concern the Kerguelen EEZ (northern Kerguelen Plateau) but not the whole Kerguelen Plateau. It would be also beneficial to incorporate the Australian assessment of the southern part of the plateau (Heard Island and McDonald Islands – HIMI) to complete the picture, and inform conservation management.

Species-specific biomass temporal trends

We discuss in further detail the biomass trends of the dominant species in the ecosystem, particularly the three species historically over-exploited by the trawl fisheries and the species which are currently caught by long-line.

Marbled notothen (*N. rossii*)

Notothenia rossii is a case of overexploitation followed by slow recovery over the past 45 years. Overexploitation by 30 large-capacity trawlers of the overall stock in the 1970s (Pshenichnov, 2011), followed by a second phase of overfishing in the 1980s of the remaining localised and unique spawning grounds where adults concentrate in winter (southeast slope, 1981–1983, see Duhamel, 1987) prompted the total closure of the fishery in 1986. The steep decline and low coastal recruitment of *N. rossii* in 1984 and 1985 is consistent with the collapse of the adult spawning stock in the early 1980s when biomass declined again from 20 000 to less than 4 000 tonnes (Duhamel, 1987; Duhamel et al., 2011). Closure of the *N. rossii* fishery in 1986 on the southeast spawning grounds was followed by a slow but regular increase in recruitment of the juveniles in the nursery area (to the end of coastal fish monitoring in 1992) suggesting supply of new recruits after fishery closure of spawning fish. Such a profile suggested recovering after a severe depletion. This increase in juveniles was not reflected in the shelf sub-adult/adult part of population, which seem to take longer to recover according to the low biomass estimate at the beginning of the POKER survey (7 500 tonnes in 2006). This slow recovery is typical of such species which exhibit late maturity (first maturity at 6 to 7 years for females; Duhamel, 1982, 1987) and a complex life cycle (Burchett, 1983) with ontogenetic migration and changes in the diet habits. The POKER decadal trends revealed the strong recovery of the *N. rossii* adult biomass, culminating in 193 000 tonnes in the last survey (2017). Moreover, the expansion of its spatial distribution fits well with distributions observed in the past, corresponding to areas of concentration of their main pelagic prey (gelatinous plankton (*Salpa thompsoni*), Medusae and crustacean (*T. gaudichaudii*)) (Hunt et al., 2011), and now extending to the spatial distribution of another prey species: *C. gunnari*, suggesting a progressive recolonisation of its profitable feeding grounds.

A similar pattern was observed in South Georgia (Atlantic Ocean sector of the Southern Ocean, the other main area where the species occurs) where recovery from overexploitation (in the 1980s) occurred in the last decade. Similarly, recent estimations (71 500 and 59 100 tonnes in 2015 and 2016 respectively) were considerably above the long-term average observed in the mid-1980s (Belchier et al., 2017) when the trawl fishery depleted the stock.

These results indicated that both Kerguelen and South Georgia stocks of *N. rossii* are recovering towards the pre-exploitation levels of the 1970s when *N. rossii* was the dominant species in the commercial catches (see CCAMLR, *Statistical Bulletins*).

Mackerel icefish (*C. gunnari*)

Champsocephalus gunnari was also over-exploited in the 1980s by a fleet of up to eight trawlers fishing simultaneously. The stock was considered as overfished with a considerably reduced stock in the late 1990s (Duhamel and Agnew, 1990) and fishing stopped in 1995. We expected a faster recovery rate for this species compared to *N. rossii* because of the strong cohorts of this short-living species which complete its life cycle in three years (see Duhamel et al., 2011). However, 10 years later, in 2006 (POKER 1), its biomass was still low (<3 500 tonnes) with a reduced geographical distribution over the shelf. It is only in spring 2017 (POKER 4) that the population showed evidences of recovery with a global geographical distribution of the main cohort (see LFD in Sinègre and Duhamel, 2017) similar to the one observed in the 1988 summer SKALP survey (Duhamel, 1993). This result shows the considerable time needed to recover a significant biomass (2017: 72 000 tonnes), even for a short-lived species (maximum 5 to 6 years old at Kerguelen). The dynamic of zooplankton abundance, especially *E. vallentini*, its major prey from previous and present studies, may have been a strong driver of the biomass recovery for this species. Diet analysis of *C. gunnari* during 2017 showed apparent favourable trophic conditions, the same as those observed during the summer of 1988 when Pakhomov (1993) stated 'the juxtaposition of the density fields of euphausiids and hyperiids with the distribution pattern of *C. gunnari* aggregations showed good spatial coincidence of both'. The POKER surveys show a regular increase in *C. gunnari* density in the northeast shelf sector, the recognised more stable area in productivity from the time series, but trends need to be confirmed in future surveys because *C. gunnari* populations show large fluctuations elsewhere due to the environmental effects. The presence of *C. gunnari* in two years (2006, 2010) of the four surveys on the Skiff Bank remains unexplained but such fluctuation in presence has been observed in historical commercial fishery data (Duhamel et al., 2011). A possible explanation could be the interannual variation in the location of the PF (north or south of Skiff Bank) which probably influences the composition and abundance of the main zooplanktonic prey of *C. gunnari* (Hunt et al., 2011).

It is useful to compare the *C. gunnari* situation at the Kerguelen Islands with that of HIMI in the southern part of the Kerguelen Plateau where there is no history of overfishing and limited current fishing (one or two trawlers, maximum catch in 2003 of 2 345 tonnes) since 1996/97. Results from annual biomass surveys in this region showed that, in 2017, *C. gunnari* LFDs were dominated (96%) by an age 3+ cohort (observed at age 2+ one year before) but the total biomass did not exceed, in any one main shelf sector, 7 000 tonnes (Maschette et al., 2017). Overall fish density was estimated to be the lowest over the two previous years. In the same year, the LFDs in the Kerguelen Islands area included mostly (98%) an abundant 2+ age cohort reaching more than 35 000 tonnes in the northeast shelf (Sinègre and Duhamel, 2017). It means that there was no synchrony between the northern and southern LFDs from one year to another. Hence the Kerguelen Plateau stocks (Kerguelen shelf northeast, Skiff Bank at Kerguelen Islands; Gunnari Ridge, Shell Bank at HIMI) appear to be separate stocks with different population dynamics. The observed differences between north and south *C. gunnari* stocks could be also linked to the smaller habitat available on the HIMI shelf and its southern position from the PF zooplankton productivity area (see Figure 19). It would be furthermore interesting to study genetic connectivity on the entire Kerguelen Plateau and relationships with other known populations (Bouvet, South Georgia and islands of the Scotia Sea to the west).

Grey-rockcod (*L. squamifrons*)

The stock of *L. squamifrons* was depleted in the 1990s after a biomass drop from 30 000 tonnes (1980) to 3 500 tonnes (1987) according to virtual population analysis (Duhamel, 1987). The fishery was renounced in 1991. Unfortunately, the timing of the POKER surveys in 2006 and 2017 was not adequate to assess the biomass of the adult population because it fell during the annual spawning season when adults were in a restricted slope area of the southern shelf (Duhamel and Ozouf-Costaz, 1985) and were absent from some surveys as observed in the LFDs (Duhamel and Hautecoeur 2009 and see Appendix 3). Consequently, decadal trend interpretation was not fully possible for this species. However, the biomass observed in 2013 (36 000 tonnes), when adults were recorded in the LFD, showed some recovery since the 1970–1990s directed fishery. The late maturity of this species (9–10 years; Duhamel, 1987) could explain the delay in recovery. The favourite gelatinous diet of *L. squamifrons*, abundant over the deep waters south of 49°S (Hunt et al., 2011), seems not to be a limiting factor for a proper recovery.

Patagonian toothfish (*D. eleginoides*)

The biomass estimate (fluctuating around 100 000 tonnes) and spatial distribution were relatively stable during the POKER survey periods. This suggests adequate management of the adult targeted stock under the CCAMLR objectives (Sinègre et al., 2017). The sustainable annual catch (~5 000 tonnes) for the regulated deep-sea fishery seems to not contribute to further depletion of the stock biomass as observed after the period of IUU fishing (1997–2004; see Duhamel et al., 2011). The low level of exchange between stocks through the Kerguelen Plateau (Kerguelen and HIMI) from the results of the current large-scale CCAMLR tagging experiment underlines the limited population connectivity between the two exploited stocks, treated as separate stocks. The meta-population concept, via interbreeding (Toomey et al., 2016), is, however, genetically proven for the whole Indian Ocean sector (Kerguelen, Heard, Crozet) of the Southern Ocean. *Dissostichus eleginoides* diet gradually shifts from pelagic crustaceans to fish and cephalopods as they grow (Duhamel, 1987). This ontogenic diet change is associated with changes in habitat: adults move towards deeper habitats as they grow (Péron et al., 2016) occupy the largest geographical and bathymetrical range among all the groundfish species caught during the POKER surveys and *D. eleginoides* is probably the most robust species in the area.

Unicorn icefish (*C. rhinoceratus*) and spiny horsefish (*Z. spinifer*)

These two species exhibited both an increase and then a decrease in their trends during the POKER surveys. A direct fishery effect cannot be invoked to explain the trends because these species have never been exploited. Their geographic distributions were stable, both during (Figures 8 and 11) and before the POKER surveys, when compared to the results of the 1987–1988 SKALP surveys (Duhamel, 1993). A plausible explanation can be put forward: the inter-specific trophic competition with the other recovering species balancing their respective biomasses. The two channichthyidae *C. rhinoceratus* and *C. gunnari*, were both found in high densities in the northeast shelf, where they could compete for pelagic crustaceans (see Figures 8 and 14) since *C. rhinoceratus* is larger and more of a generalist than *C. gunnari* in its diet requirement (Duhamel and Hureau, 1985). *Channichthys rhinoceratus* could temporarily replace *C. gunnari* when its biomass is weak, typically after overexploitation. Further studies would be needed to test this inter-species competition hypothesis. Interesting is the contrast in the values of biomass for the two species in the icefish genus *Channichthys*: *C. velifer* never exceeded a biomass of 1 000 tonnes compared to *C. rhinoceratus* reaching >10 000 tonnes during some surveys.

The declining trend in biomass of the benthic feeder *Z. spinifer* since the second survey (2010) was more difficult to explain because nothing is known about the abundance of its known, mostly benthic, prey (Mysidacea, Cumacea, Ophiurids) (Duhamel, 1987) and its life cycle. Increasing predation is very unlikely given the strong spiny body of this species – named 'spiny horsefish' (the species has never been recorded in the stomach contents of any other species). Inter-specific competition for food resources also seems unlikely given: (i) the small overlap in benthos-feeder distributions (see Duhamel, 1987), and (ii) their relative low biomass. Changes in the recent benthic environment from human pressure (trawling for example) cannot be responsible for this decline because no fishing has occurred in the main geographic distribution of the species for decades. A potential driver could be a change in the inshore shelf benthic marine environment due to the recent melting of the Cook Ice Cap of the Kerguelen Islands (Verfaillie et al., 2015), especially on the northern shelf in the plume of the islands where the species occurs, inducing temperature/salinity changes and potential communities alterations. This hypothesis could be explored through benthic and oceanographic monitoring.

Other indicators and potential drivers of fish biomass changes

General oceanographic conditions available for the area show little change in positions of the fronts, and effect of global warming, even temporal effects such as ENSO, seem not to be strong drivers in the observed trends for fish species encountered at the depths of POKER surveys.

Trophic relationships of groundfish on the Kerguelen Plateau were comprehensively investigated in 2017 to confirm or complete knowledge from previous surveys (Chechun, 1984; Duhamel, 1987; Duhamel et al., 2005, 2011). We found three main diet categories:

(i) the benthos feeders (molluscs, benthic amphipods, isopods, annelids, ophiurids): *Z. spinifer*, *L. mizops*, *G. acuta*, *B. eatonii* (in part), *B. murrayi*, *M. marmorata* and *M. maculata*.

(ii) the plankton feeders specialised either on:

   (a) gelatinous organisms (salps, ctenophors, cnidaria): *N. rossii* (adults), *L. squamifrons* and *A. antipodianus* or

(b) crustaceans (euphausiids, hyperiid amphipods): *C. gunnari*, *D. eleginoides* (juveniles) and *C. rhinoceratus* (juveniles),

(iii) the top predators (fish, squids): *D. eleginoides* (adult), *C. rhinoceratus* (adult), *C. velifer*, *B. irrasa*, *B. eatonii* (in part) and *P. gracilis*.

Most of the dominant species in the POKER biomass survey (5 out of 6) belong to the second category (plankton feeders) and are consequently dependent on the pelagic productivity and its specific geographical position. Time series of survey data for the zooplankton in the area are, however, scarce compared to currently available satellite-derived phytoplankton data. According to satellite imagery, the spring/summer blooms of chlorophyll *a* on the Kerguelen Plateau is highest over the eastern shelf (Mongin, 2011) due to a relatively shallow depth, supply of iron and major nutrients to surface waters from iron-rich deep water below (Blain et al., 2007) and strong vertical mixing (Dragon et al., 2011). This primary production is transferred to higher-trophic levels via macrozooplankton (copepods, euphausiids, hyperiid amphipods, gelatinous organisms) with a maximum seston biomass in late summer to early autumn (April–May) (Hunt et al., 2011).

The distribution of all plankton feeders caught during the POKER surveys corresponded to the known specific zooplankton distribution described in the past (1987–1988) where *E. vallentini* concentrated in the northeastern shelf and salps and medusa in south/southeastern deeper slope (see Hunt et al., 2011). Interseasonal and annual variability in macrozooplankton was, however, strong but some concentrations (swarms) can persist within the quasi-stationary meandering frontal features. It could explain the stability of geographic/bathymetric fish concentrations as currently observed (outside the unrelated annual spawning migration period). Lack of more recent monitoring of seston (both inshore and offshore) limits our understanding of regional seasonal/annual productivity cycles. However, macrozooplankton seems to be the key to sustaining major fish populations on the Kerguelen Plateau. PF Zone meandering close to the shelf creates a favorable situation in cold waters. Nevertheless, dynamics of pelagic prey species such as the formation of swarms at the micro-scale (10 km) need to be investigated at the scale of the Kerguelen Plateau.

Benthos feeders are recognised as important for the marine ecosystem because the majority of these species are endemic, do not sustain large biomass populations (except localised *Z. spinifer*) but dynamics of their habitats and that of their potential prey are poorly known (Améziane et al., 2011).

Conclusion

Biomass trends during the recent decade (the POKER surveys) show stability for some species (*D. eleginoides*), whilst others increase (*C. gunnari* and *N. rossii*) or decrease (*C. rhinoceratus* and *Z. spinifer*). Historical and current fisheries are probably the main drivers of groundfish biomass fluctuations in the last 50 years. POKER surveys revealed that the groundfish community is still readjusting from historical overexploitation and that recovery takes a long time, even for short-lived species.

Depletion of stocks by the fishery has probably changed the relationships between species in the area, with unexploited species fluctuating as well (*C. rhinoceratus* and *Z. spinifer*) which suggests important readjustments in the Kerguelen Plateau marine ecosystem. Five out of the six dominant species of the Kerguelen Plateau and Skiff Bank are zooplankton feeders which means that they rely on marine primary/secondary productivity. The PF crossing the Kerguelen Plateau seems crucial for maintaining a high zooplankton biomass. The regional dynamic of Southern Ocean ecosystems influences the Kerguelen Plateau fish biomass at different timescales which warrant further investigation. Most of the endemic and sub-Antarctic groundfish species living on the northern part of the Kerguelen Plateau are also found in the southern part of the plateau with the same assemblages (Hill et al., 2017) which means that they can tolerate a large range of environmental conditions. This suggests that these species could be able to respond to changes in their environment due to climate change. Currently, such changes seem limited in the marine environment (SST variation less than 0.2°C in three decades) compared to warming trends recorded on land (Favier et al., 2016), but many unknowns can hide or postpone the effects on the fish populations. Further analyses would be needed to understand the causes of the local SST variability on interannual to decadal scales.

The next three major challenges to improve biomass analysis will be to better: (i) follow the inter-annual zooplankton productivity on the Kerguelen Plateau, (ii) correlate it with dynamics of the major fish-dependent species, and (iii) characterise the benthic habitats and understand their role in the fish distribution. The POKER surveys are crucial to monitor future readjustments of the marine ecosystem of the Kerguelen Plateau. A change in the design of the survey could be considered in the future to better track the recovery of the main fish species in term of biomass and distribution.

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Appendix 1

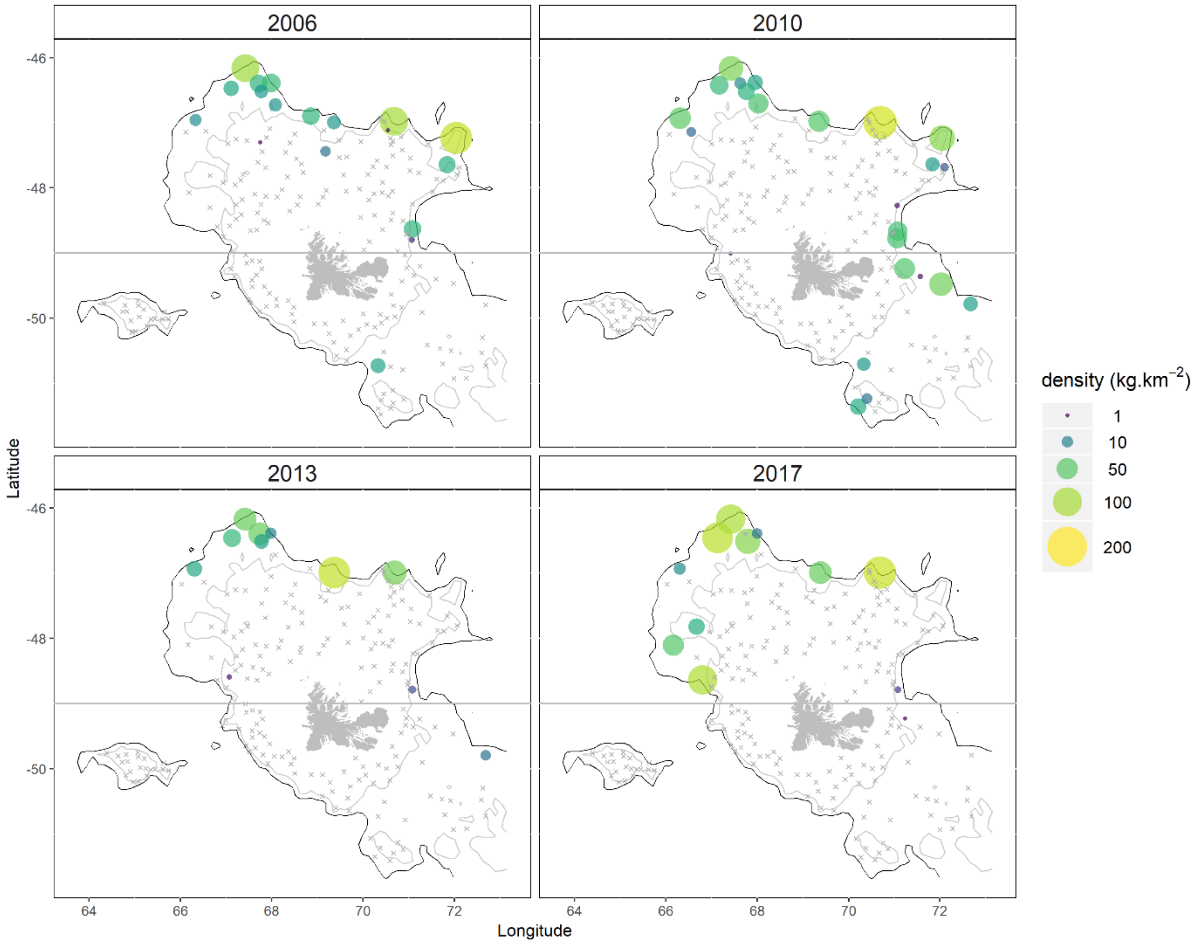
Geographical distribution of densities (in kg km^{-2}) of

(a) *Antimora rostrata*, (b) *Bathyraja eatonii*, (c) *Bathyraja irrasa*, (d) *Bathyraja murrayi*, (e) *Channichthys velifer*, (f) *Etmopterus viator*, (g) *Gobionotothen acuta*, (h) *Lepidonotothen mizops*, (i) *Macrourus carinatus*, (j) *Mancopsetta maculata*, (k) *Melanostigma gelatinosum*, (l) *Muraenolepis marmorata*, (m) *Paradiplospinus gracilis*

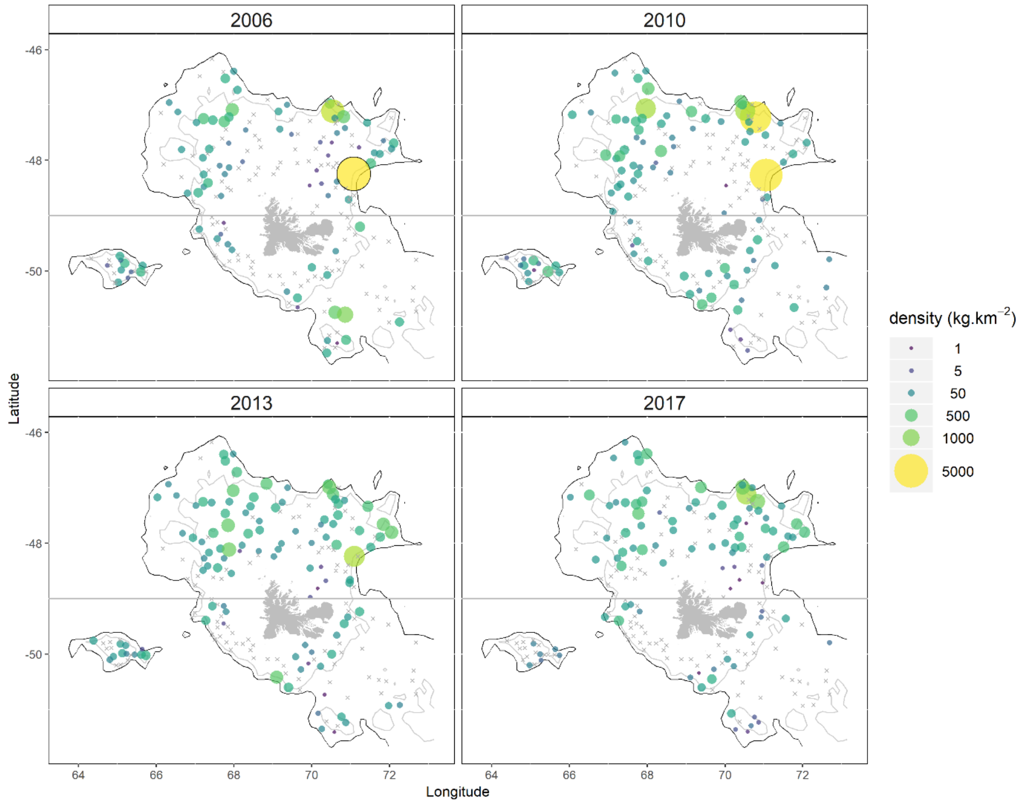
during the POKER cruises. Top left POKER 1 (2006), top right POKER 2 (2010), bottom left POKER 3 (2013), bottom right POKER 4 (2017).

Circles with black contours indicate densities > highest kg km^{-2} value in the scale.

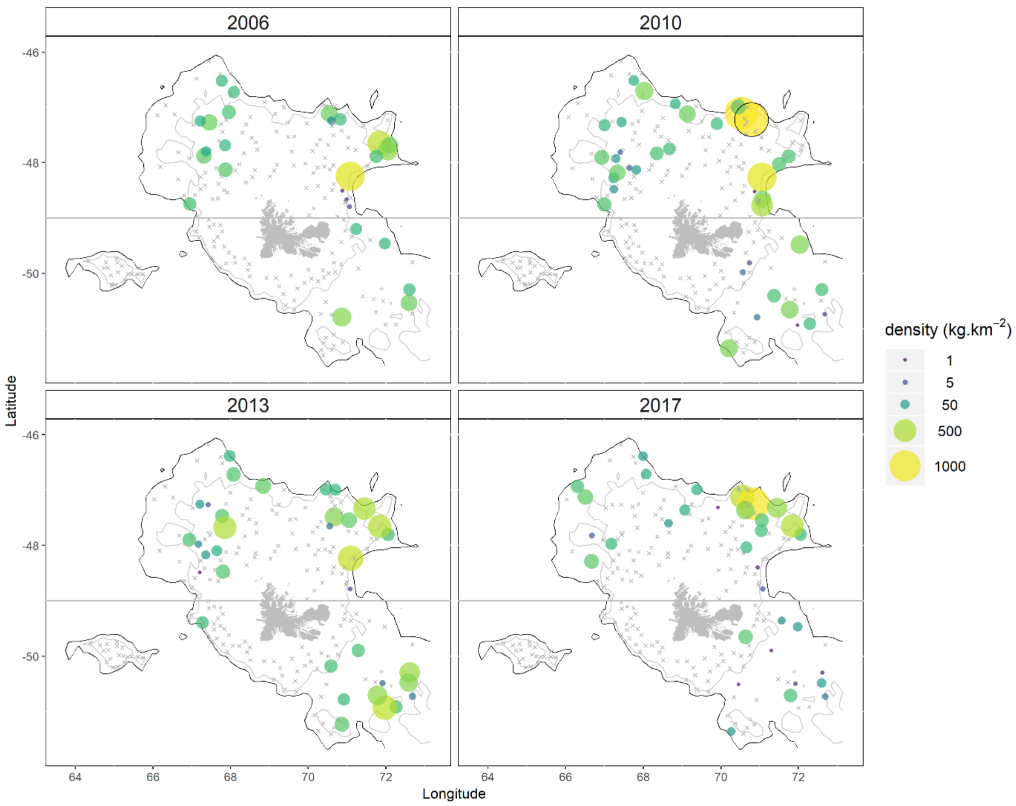
(a) *Antimora rostrata*



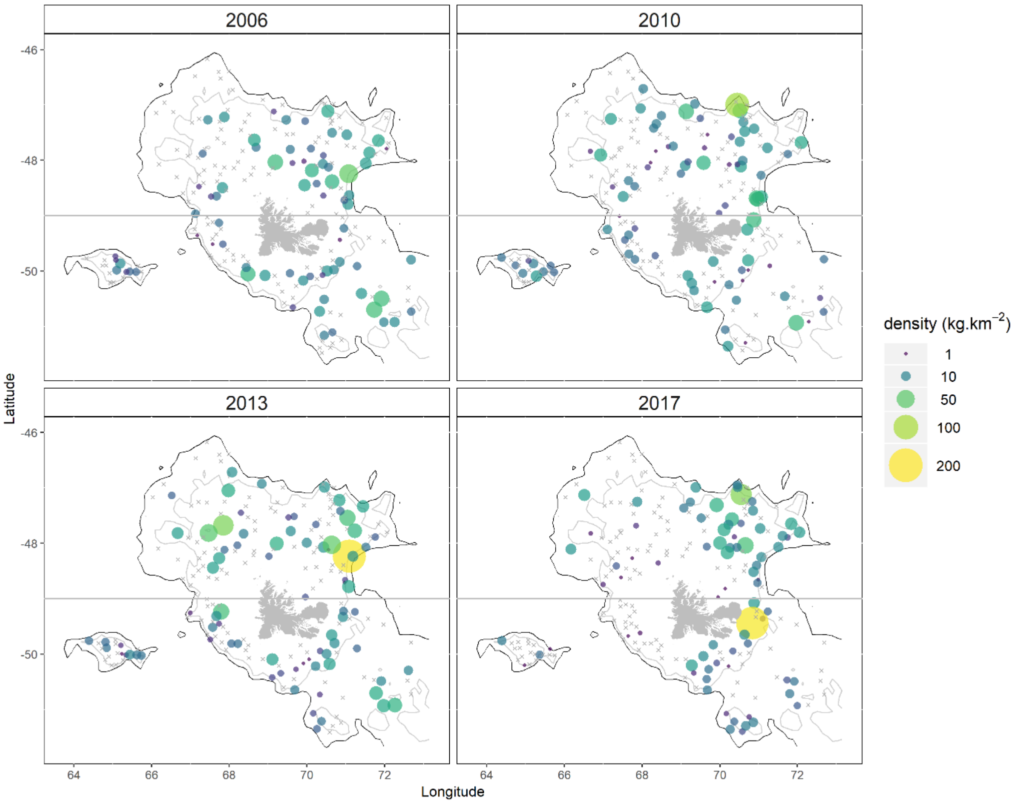
(b) *Bathyraja eatonii*



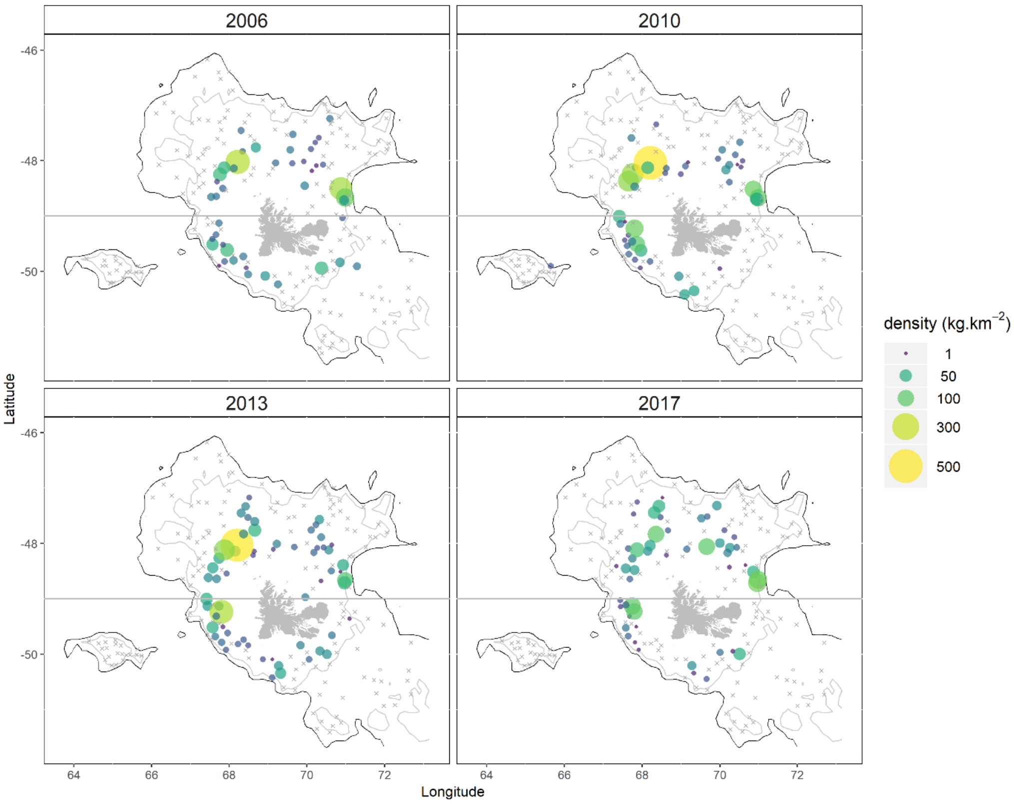
(c) *Bathyraja irrasa*



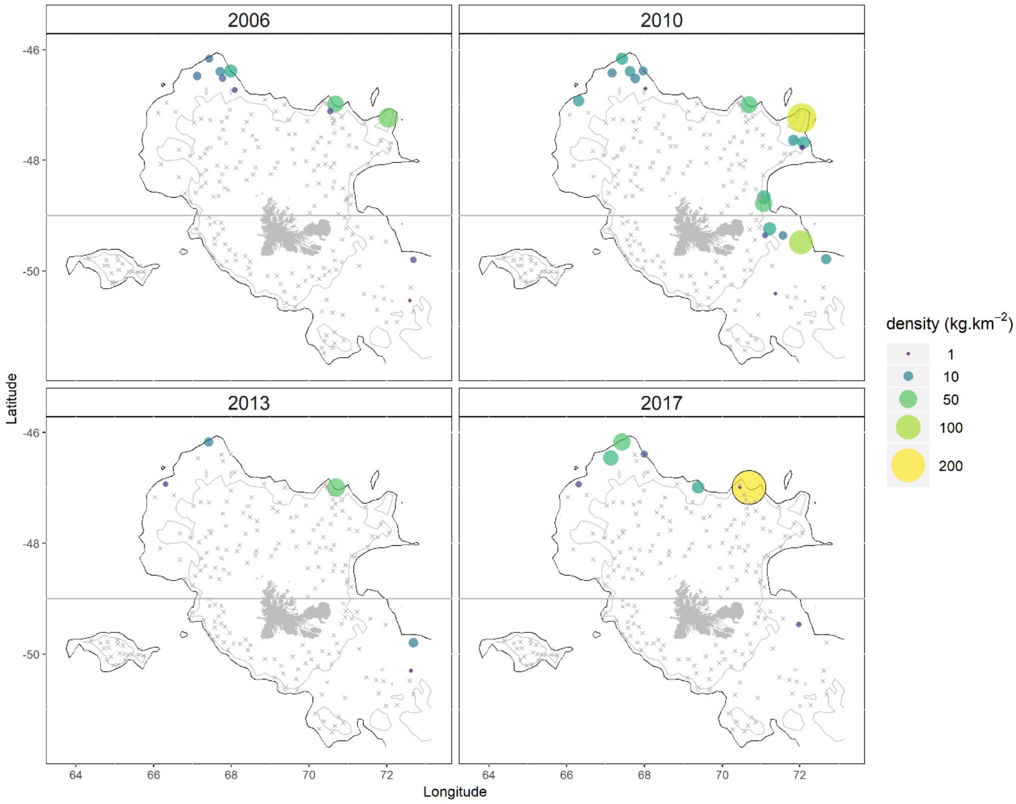
(d) *Bathyraja murrayi*



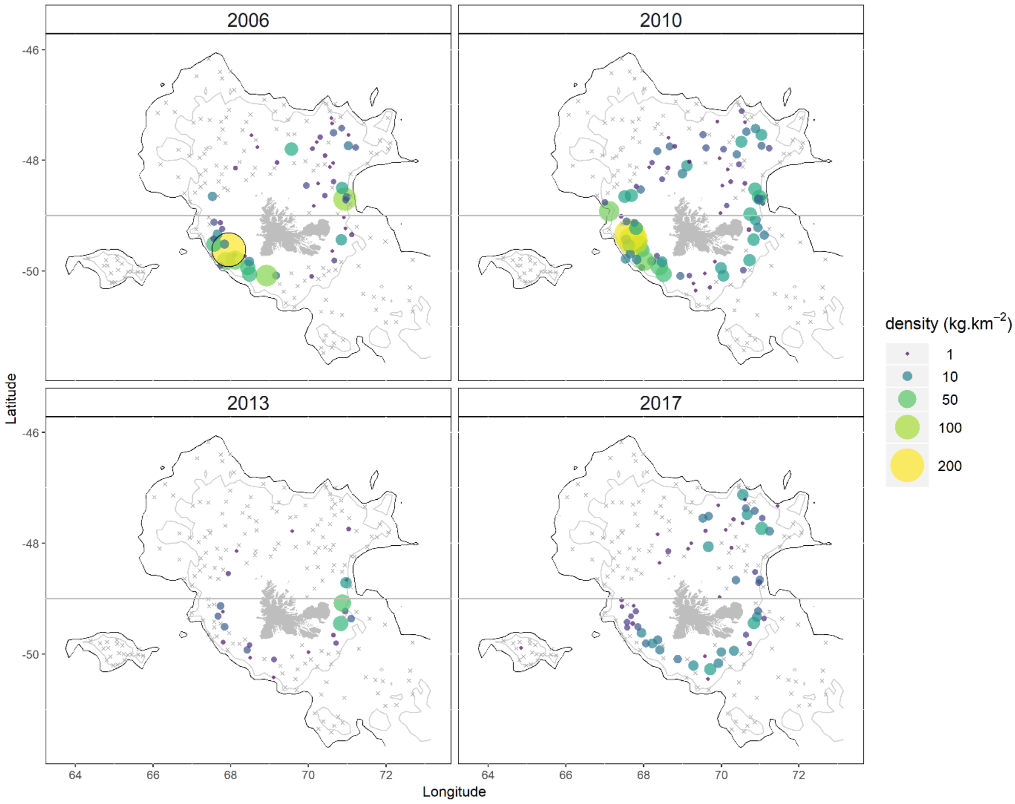
(e) *Channichthys velifer*



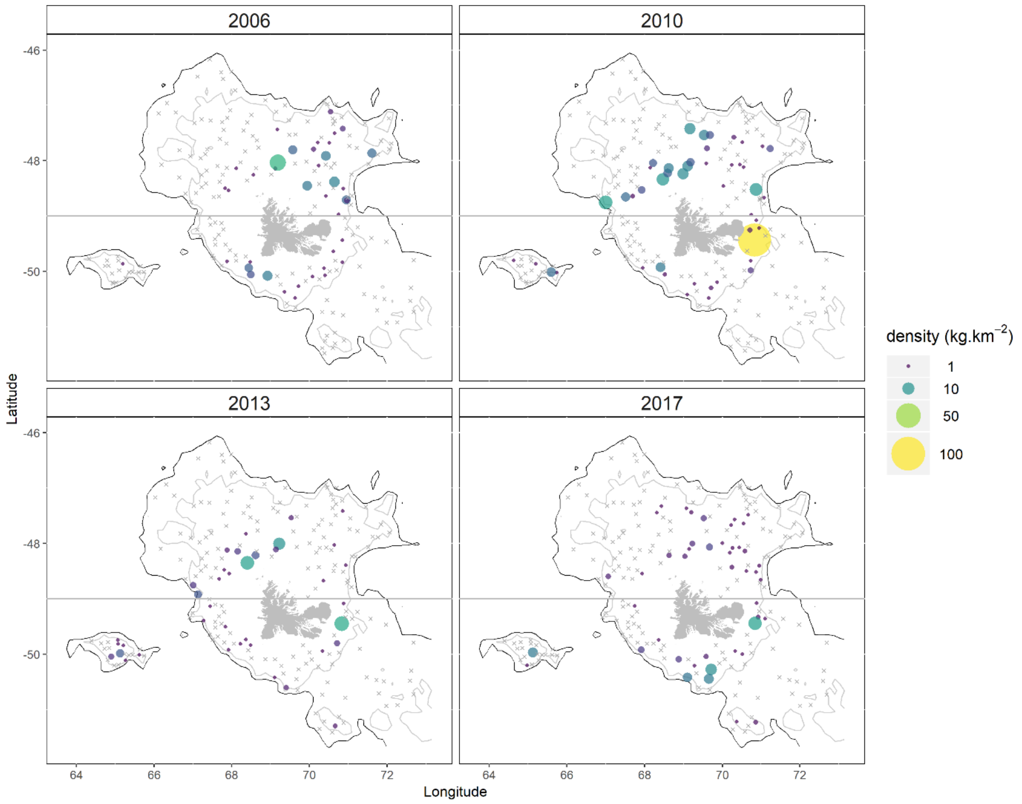
(f) *Etmopterus viator*



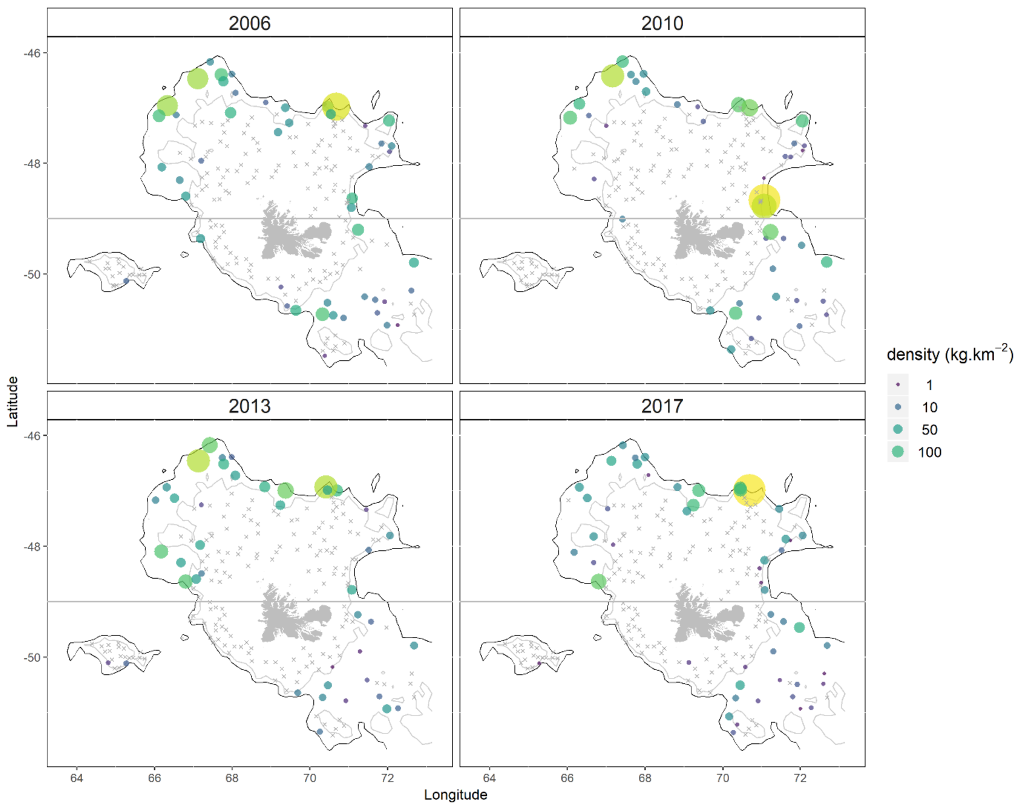
(g) *Gobionotothen acuta*



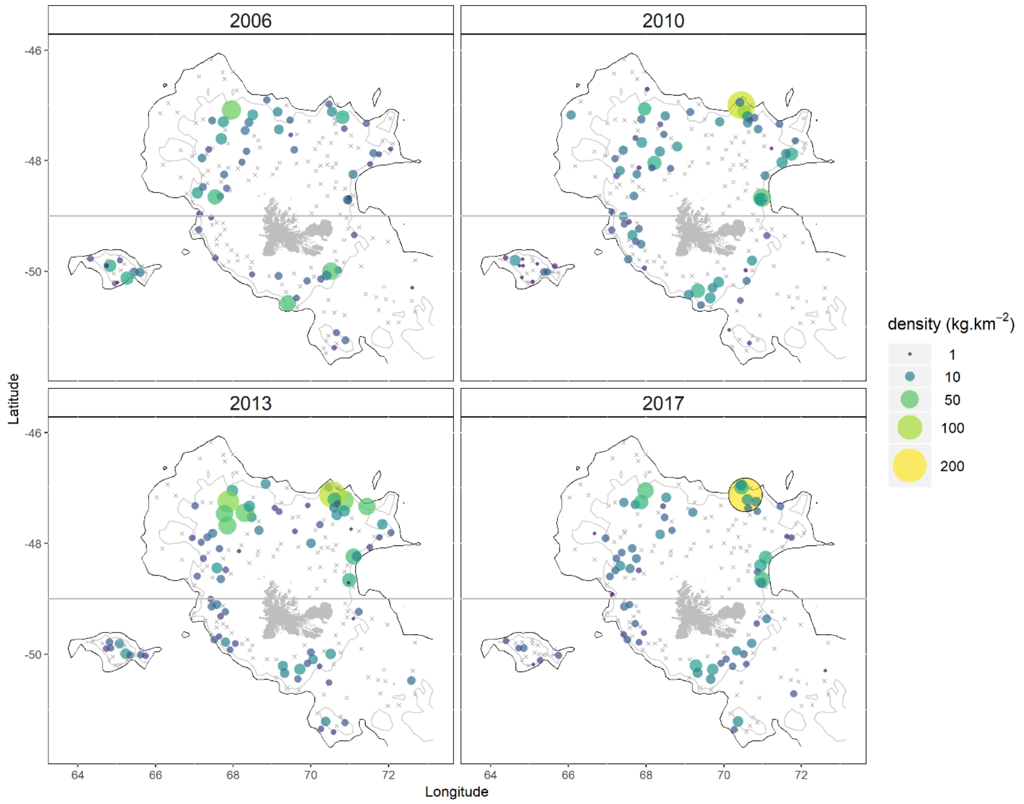
(h) *Lepidonotothen mizops*



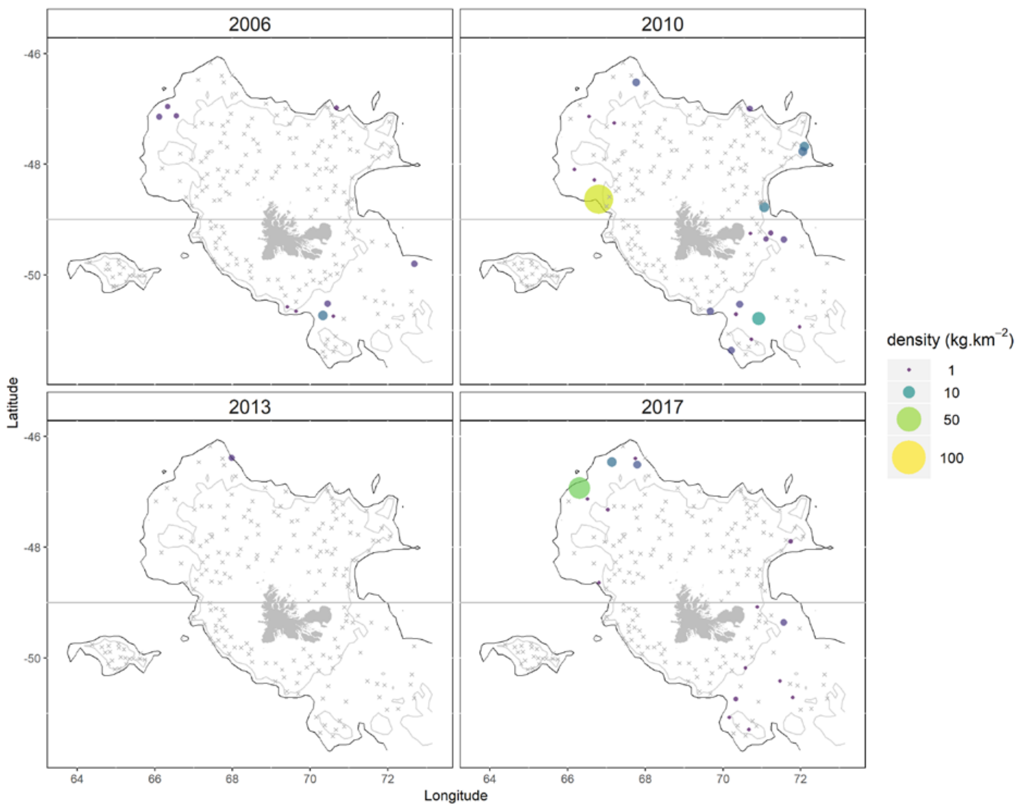
(i) *Macrourus carinatus*



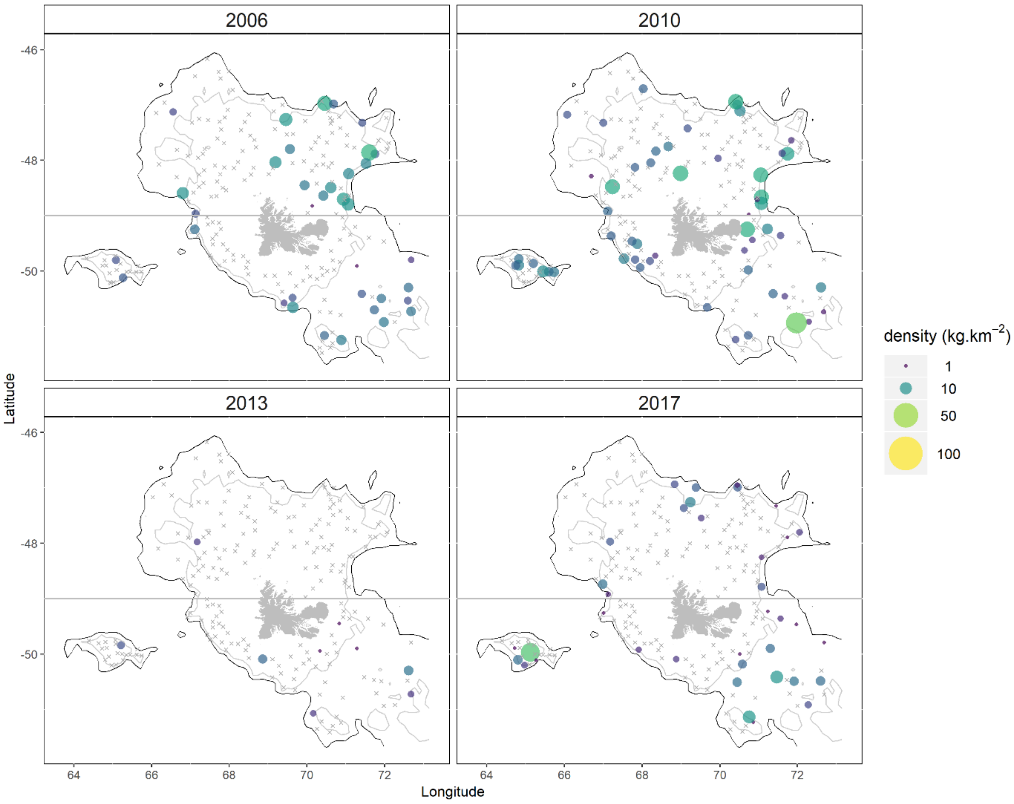
(j) *Mancopsetta maculata*



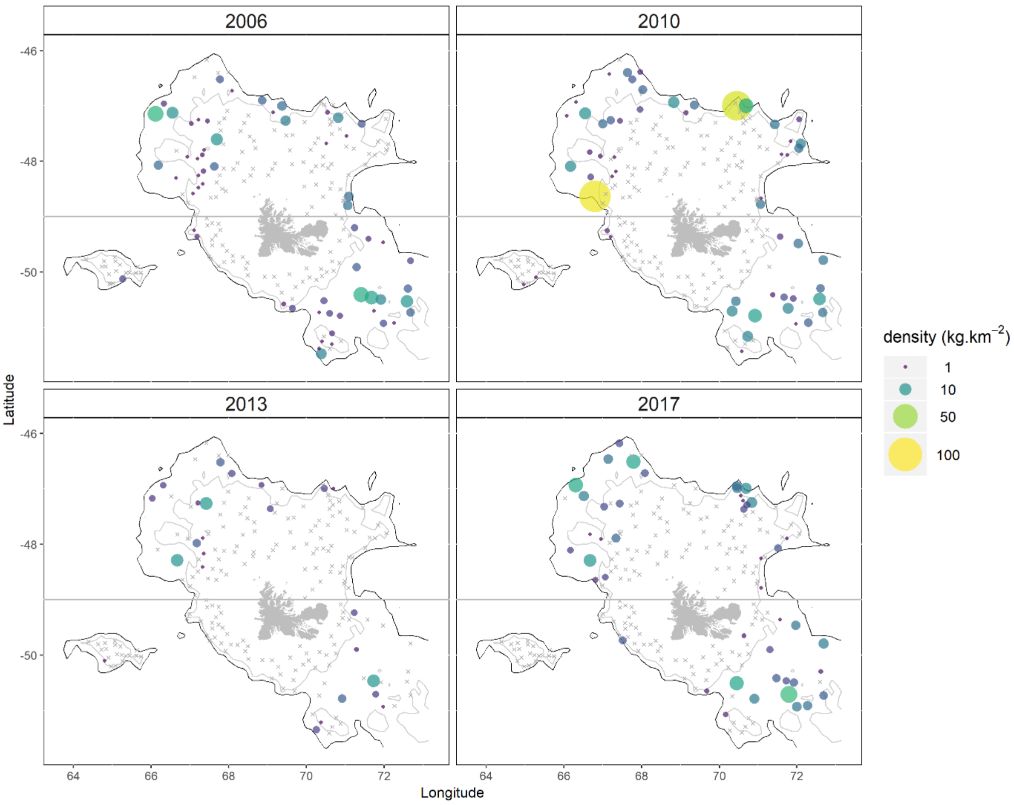
(k) *Melanostigma gelatinosum*



(l) *Muraenolepis marmorata*



(m) *Paradiplospinus gracilis*



Appendix 2

Strata biomass (in tonnes) of fish species estimated by bootstrapping hauls from the four POKER surveys. SD = standard error; Lower and Upper CL = lower and upper confidence intervals; OneSide95 = lower one-sided 95% confidence limit.

(a) *Alepocephalus antipodianus*, (b) *Antimora rostrata*, (c) *Bathyraja eatonii*, (d) *Bathyraja irrasa*, (e) *Bathyraja murrayi*, (f) *Champsocephalus gunnari*, (g) *Channichthys rhinoceratus*, (h) *Channichtys velifer*, (i) *Dissostichus eleginoides*, (j) *Etmopterus viator*, (k) *Gobionotothen acuta*, (l) *Lepidonotothen mizops*, (m) *Lepidonotothen squamifrons*, (n) *Macrourus carinatus*, (o) *Mancopsetta maculata*, (p) *Melanostigma gelatinosum*, (q) *Muraenolepis marmorata*, (r) *Notothenia rossii*, (s) *Paradiplospinus gracilis*, (t) *Zanclorhynchus spinifer*.

(a) *Alepocephalus antipodianus*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	2	2	0	5	0
2006	Kerguelen south shelf	0	0	0	0	0
2006	Kerguelen north deep	14 117	8 789	414	33 673	975
2006	Kerguelen south deep	282	263	0	832	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	14 401				
2010	Kerguelen north shelf	6	6	0	18	0
2010	Kerguelen south shelf	0	0	0	0	0
2010	Kerguelen north deep	9 504	7 624	444	26 068	630
2010	Kerguelen south deep	33	32	0	99	0
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	9 543				
2013	Kerguelen north shelf	0	0	0	0	0
2013	Kerguelen south shelf	0	0	0	0	0
2013	Kerguelen north deep	5 241	3 349	176	12 780	345
2013	Kerguelen south deep	108	106	0	328	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	5 349				
2017	Kerguelen north shelf	169	167	0	503	0
2017	Kerguelen south shelf	0	0	0	0	0
2017	Kerguelen north deep	14 307	8 859	1 829	34 797	2 722
2017	Kerguelen south deep	19	13	0	47	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	14 326				

(b) *Antimora rostrata*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	28	23	0	79	1
2006	Kerguelen south shelf	0	0	0	0	0
2006	Kerguelen north deep	708	232	297	1 204	355
2006	Kerguelen south deep	42	41	0	126	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	778				
2010	Kerguelen north shelf	14	14	0	43	0
2010	Kerguelen south shelf	4	4	0	13	0
2010	Kerguelen north deep	853	237	439	1 354	489
2010	Kerguelen south deep	369	168	90	744	122
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	1 240				
2013	Kerguelen north shelf	1	1	0	3	0
2013	Kerguelen south shelf	0	0	0	0	0
2013	Kerguelen north deep	563	214	197	1 018	240
2013	Kerguelen south deep	14	14	0	43	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	578				
2017	Kerguelen north shelf	21	21	0	63	0
2017	Kerguelen south shelf	0	0	0	0	0
2017	Kerguelen north deep	932	311	379	1 576	452
2017	Kerguelen south deep	2	2	0	5	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	955				

(c) *Bathyraja eatonii*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	8 518	4 298	2 187	18 540	2 612
2006	Kerguelen south shelf	551	192	220	968	257
2006	Kerguelen north deep	2 517	655	1 362	3 872	1 516
2006	Kerguelen south deep	4 297	2 093	886	8 901	1 213
2006	Skiff shelf	160	57	59	280	71
	Total POKER 1	16 043				
2010	Kerguelen north shelf	11 692	4 851	3 756	22 421	4 591
2010	Kerguelen south shelf	1 129	303	592	1 763	660
2010	Kerguelen north deep	4 274	1 151	2 220	6 695	2 504
2010	Kerguelen south deep	1 573	711	341	3 081	503
2010	Skiff shelf	180	65	68	318	80
	Total POKER 2	18 848				
2013	Kerguelen north shelf	7 499	1 654	4 664	11 132	5 059
2013	Kerguelen south shelf	976	338	422	1 735	487
2013	Kerguelen north deep	5 244	1 237	2 985	7 791	3 305
2013	Kerguelen south deep	1 047	420	322	1 937	408
2013	Skiff shelf	145	41	72	230	82
	Total POKER 3	14 911				
2017	Kerguelen north shelf	6 521	1 489	3 920	9 674	4 280
2017	Kerguelen south shelf	576	196	247	1 006	284
2017	Kerguelen north deep	4 558	983	2 751	6 594	3 014
2017	Kerguelen south deep	620	331	72	1 354	119
2017	Skiff shelf	23	8	8	41	10
	Total POKER 4	12 298				

(d) *Bathyraja irrasa*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	2 202	844	801	4 056	972
2006	Kerguelen south shelf	0	0	0	0	0
2006	Kerguelen north deep	1 397	589	389	2 659	499
2006	Kerguelen south deep	1 716	798	396	3 459	589
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	5 315				
2010	Kerguelen north shelf	3 575	1 559	928	6 980	1 289
2010	Kerguelen south shelf	79	70	0	225	2
2010	Kerguelen north deep	2 817	870	1 263	4 633	1 474
2010	Kerguelen south deep	2 443	1 006	641	4 604	902
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	8 914				
2013	Kerguelen north shelf	2 167	806	779	3 913	947
2013	Kerguelen south shelf	168	119	0	436	0
2013	Kerguelen north deep	2 058	827	696	3 891	856
2013	Kerguelen south deep	4 326	1 516	1 646	7 570	1 997
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	8 719				
2017	Kerguelen north shelf	2 420	1 058	697	4 776	896
2017	Kerguelen south shelf	90	90	0	269	0
2017	Kerguelen north deep	1 765	649	638	3 149	782
2017	Kerguelen south deep	656	313	160	1 360	209
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	4 931				

(e) *Bathyraja murrayi*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	295	64	181	432	196
2006	Kerguelen south shelf	78	23	39	127	44
2006	Kerguelen north deep	75	35	16	150	23
2006	Kerguelen south deep	322	98	149	530	169
2006	Skiff shelf	6	2	2	11	3
	Total POKER 1	776				
2010	Kerguelen north shelf	330	81	194	505	209
2010	Kerguelen south shelf	90	25	47	144	53
2010	Kerguelen north deep	199	67	78	339	96
2010	Kerguelen south deep	240	81	100	412	118
2010	Skiff shelf	10	3	4	16	5
	Total POKER 2	869				
2013	Kerguelen north shelf	528	170	254	912	285
2013	Kerguelen south shelf	92	26	47	146	52
2013	Kerguelen north deep	108	41	35	196	45
2013	Kerguelen south deep	304	83	152	475	175
2013	Skiff shelf	7	2	3	12	4
	Total POKER 3	1 039				
2017	Kerguelen north shelf	318	75	187	477	205
2017	Kerguelen south shelf	160	96	42	369	47
2017	Kerguelen north deep	151	46	65	245	77
2017	Kerguelen south deep	93	27	42	148	49
2017	Skiff shelf	2	1	0	6	0
	Total POKER 4	724				

(f) *Champsocephalus gunnari*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	2 932	1 014	1 231	5 162	1 422
2006	Kerguelen south shelf	552	138	317	849	347
2006	Kerguelen north deep	0	0	0	0	0
2006	Kerguelen south deep	0	0	0	0	0
2006	Skiff shelf	121	64	25	266	31
	Total POKER 1	3 605				
2010	Kerguelen north shelf	8 550	2 099	4 998	13 126	5 429
2010	Kerguelen south shelf	2 246	769	1 005	3 934	1 114
2010	Kerguelen north deep	5	5	0	16	0
2010	Kerguelen south deep	36	35	0	107	0
2010	Skiff shelf	4 239	3 148	125	11 246	482
	Total POKER 2	15 076				
2013	Kerguelen north shelf	11 969	4 540	5 015	22 342	5 661
2013	Kerguelen south shelf	505	120	295	762	321
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	2	2	0	5	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	12 476				
2017	Kerguelen north shelf	47 397	13 124	26 021	77 156	28 648
2017	Kerguelen south shelf	1 121	431	431	2 081	502
2017	Kerguelen north deep	59	53	0	171	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	48 577				

(g) *Channichthys rhinoceratus*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	35 283	4 868	26 398	45 182	27 636
2006	Kerguelen south shelf	6 863	1 713	3 929	10 551	4 304
2006	Kerguelen north deep	309	84	153	485	177
2006	Kerguelen south deep	600	337	91	1 374	132
2006	Skiff shelf	148	57	62	277	69
	Total POKER 1	43 203				
2010	Kerguelen north shelf	44 855	6 917	32 287	59 675	34 117
2010	Kerguelen south shelf	14 271	7 223	5 318	30 064	5 742
2010	Kerguelen north deep	527	168	230	883	269
2010	Kerguelen south deep	288	139	82	602	99
2010	Skiff shelf	197	36	131	269	140
	Total POKER 2	60 138				
2013	Kerguelen north shelf	28 449	4 570	20 489	38 310	21 624
2013	Kerguelen south shelf	8 336	2 649	4 401	14 499	4 748
2013	Kerguelen north deep	167	76	47	336	58
2013	Kerguelen south deep	316	136	90	611	116
2013	Skiff shelf	52	15	27	86	30
	Total POKER 3	37 320				
2017	Kerguelen north shelf	20 092	2 895	14 806	26 095	15 562
2017	Kerguelen south shelf	2 282	338	1 669	2 979	1 751
2017	Kerguelen north deep	207	151	7	548	15
2017	Kerguelen south deep	276	126	61	549	85
2017	Skiff shelf	71	26	30	128	33
	Total POKER 4	22 928				

(h) *Channichtys velifer*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	677	260	234	1 243	293
2006	Kerguelen south shelf	169	56	73	291	85
2006	Kerguelen north deep	0	0	0	0	0
2006	Kerguelen south deep	21	21	0	64	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	867				
2010	Kerguelen north shelf	1 016	418	350	1 953	414
2010	Kerguelen south shelf	244	89	90	436	109
2010	Kerguelen north deep	0	0	0	0	0
2010	Kerguelen south deep	0	0	0	0	0
2010	Skiff shelf	1	1	0	2	0
	Total POKER 2	1 261				
2013	Kerguelen north shelf	970	406	375	1 900	425
2013	Kerguelen south shelf	302	128	119	598	132
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	0	0	0	0	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	1 272				
2017	Kerguelen north shelf	734	188	397	1 128	444
2017	Kerguelen south shelf	169	78	39	346	52
2017	Kerguelen north deep	0	0	0	0	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	903				

(i) *Dissostichus eleginoides*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	24 177	5 084	15 229	34 958	16 476
2006	Kerguelen south shelf	31 124	17 775	3 426	71 207	6 935
2006	Kerguelen north deep	30 591	5 278	21 101	41 572	22 416
2006	Kerguelen south deep	16 383	2 466	11 720	21 311	12 395
2006	Skiff shelf	549	63	429	674	447
	Total POKER 1	102 824				
2010	Kerguelen north shelf	19 215	3 806	12 567	27 460	13 448
2010	Kerguelen south shelf	9 166	2 941	4 581	15 822	5 037
2010	Kerguelen north deep	25 893	5 389	15 962	37 082	17 371
2010	Kerguelen south deep	7 966	1 477	5 365	11 126	5 700
2010	Skiff shelf	981	196	617	1 385	670
	Total POKER 2	63 221				
2013	Kerguelen north shelf	19 296	2 859	14 106	25 244	14 871
2013	Kerguelen south shelf	32 541	16 195	6 651	68 743	8 345
2013	Kerguelen north deep	65 919	31 811	27 660	134 592	29 162
2013	Kerguelen south deep	25 840	10 674	11 469	49 455	12 322
2013	Skiff shelf	666	154	391	989	426
	Total POKER 3	144 262				
2017	Kerguelen north shelf	6 710	999	4 842	8 761	5 120
2017	Kerguelen south shelf	42 885	23 778	4 526	96 270	10 996
2017	Kerguelen north deep	43 626	24 144	12 163	97 668	13 860
2017	Kerguelen south deep	7 847	2 363	3 787	12 985	4 282
2017	Skiff shelf	411	98	231	614	259
	Total POKER 4	101 479				

(j) *Etmopterus viator*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	2	2	0	5	0
2006	Kerguelen south shelf	0	0	0	0	0
2006	Kerguelen north deep	199	96	40	413	57
2006	Kerguelen south deep	7	6	0	19	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	208				
2010	Kerguelen north shelf	10	10	0	31	0
2010	Kerguelen south shelf	1	1	0	4	0
2010	Kerguelen north deep	486	207	165	943	194
2010	Kerguelen south deep	289	199	17	724	30
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	786				
2013	Kerguelen north shelf	0	0	0	0	0
2013	Kerguelen south shelf	0	0	0	0	0
2013	Kerguelen north deep	90	74	0	252	3
2013	Kerguelen south deep	19	16	0	54	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	109				
2017	Kerguelen north shelf	1	1	0	2	0
2017	Kerguelen south shelf	0	0	0	0	0
2017	Kerguelen north deep	455	305	45	1143	68
2017	Kerguelen south deep	4	4	0	12	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	460				

(k) *Gobionotothen acuta*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	140	69	40	296	48
2006	Kerguelen south shelf	793	588	113	2043	134
2006	Kerguelen north deep	0	0	0	0	0
2006	Kerguelen south deep	0	0	0	0	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	933				
2010	Kerguelen north shelf	252	64	142	389	157
2010	Kerguelen south shelf	413	123	208	678	230
2010	Kerguelen north deep	4	3	0	10	0
2010	Kerguelen south deep	0	0	0	0	0
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	669				
2013	Kerguelen north shelf	16	13	1	44	2
2013	Kerguelen south shelf	60	29	15	125	18
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	0	0	0	0	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	76				
2017	Kerguelen north shelf	99	28	50	158	57
2017	Kerguelen south shelf	88	18	54	125	59
2017	Kerguelen north deep	1	1	0	3	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	188				

(l) *Lepidonotothen mizops*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	48	16	21	84	24
2006	Kerguelen south shelf	9	4	2	18	3
2006	Kerguelen north deep	0	0	0	0	0
2006	Kerguelen south deep	0	0	0	0	0
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	57				
2010	Kerguelen north shelf	75	19	42	114	46
2010	Kerguelen south shelf	59	51	3	166	4
2010	Kerguelen north deep	0	0	0	1	0
2010	Kerguelen south deep	0	0	0	0	0
2010	Skiff shelf	1	1	0	3	0
	Total POKER 2	135				
2013	Kerguelen north shelf	32	13	11	62	13
2013	Kerguelen south shelf	13	8	3	31	3
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	0	0	0	0	0
2013	Skiff shelf	1	1	0	2	0
	Total POKER 3	46				
2017	Kerguelen north shelf	18	3	11	25	12
2017	Kerguelen south shelf	23	9	8	43	10
2017	Kerguelen north deep	0	0	0	0	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	1	1	0	3	0
	Total POKER 4	42				

(m) *Lepidonotothen squamifrons*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	6 698	2 865	2 578	13 316	2 879
2006	Kerguelen south shelf	2 067	876	685	4 049	810
2006	Kerguelen north deep	1 148	611	232	2 516	310
2006	Kerguelen south deep	758	511	46	1 903	98
2006	Skiff shelf	733	515	110	1 857	133
	Total POKER 1	11 404				
2010	Kerguelen north shelf	6 249	1 768	3 225	10 046	3 604
2010	Kerguelen south shelf	8 559	5 566	1 815	20 650	2 115
2010	Kerguelen north deep	3 302	2 130	347	8 097	565
2010	Kerguelen south deep	23 418	22 319	255	69 316	304
2010	Skiff shelf	949	469	256	2 011	301
	Total POKER 2	42 477				
2013	Kerguelen north shelf	4 708	1 352	2 369	7 636	2 660
2013	Kerguelen south shelf	23 831	22 152	811	68 897	922
2013	Kerguelen north deep	789	437	162	1 762	211
2013	Kerguelen south deep	6 620	5 198	267	18 073	386
2013	Skiff shelf	302	94	141	504	160
	Total POKER 3	36 250				
2017	Kerguelen north shelf	3 058	1 293	1 051	5 955	1 223
2017	Kerguelen south shelf	1 654	735	449	3 276	567
2017	Kerguelen north deep	784	371	123	1 574	244
2017	Kerguelen south deep	678	391	61	1 540	101
2017	Skiff shelf	66	16	36	100	41
	Total POKER 4	6 240				

(n) *Macrourus carinatus*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	215	105	36	445	61
2006	Kerguelen south shelf	5	4	0	14	0
2006	Kerguelen north deep	3 296	1 230	1 249	5 972	1 469
2006	Kerguelen south deep	1 090	361	456	1 850	537
2006	Skiff shelf	1	1	0	4	0
	Total POKER 1	4 607				
2010	Kerguelen north shelf	9	6	0	24	1
2010	Kerguelen south shelf	12	8	0	31	2
2010	Kerguelen north deep	4 524	1 720	1 579	8 207	1 955
2010	Kerguelen south deep	1 279	524	406	2 400	505
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	5 824				
2013	Kerguelen north shelf	133	69	11	283	36
2013	Kerguelen south shelf	0	0	0	0	0
2013	Kerguelen north deep	3 475	1 024	1 725	5 693	1 958
2013	Kerguelen south deep	364	103	176	576	202
2013	Skiff shelf	1	1	0	4	0
	Total POKER 3	3 973				
2017	Kerguelen north shelf	175	105	25	417	29
2017	Kerguelen south shelf	2	1	0	5	0
2017	Kerguelen north deep	3 001	1 557	941	6 483	1 059
2017	Kerguelen south deep	515	186	205	926	243
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	3 693				

(o) *Mancopsetta maculata*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	225	57	127	349	139
2006	Kerguelen south shelf	74	33	21	146	25
2006	Kerguelen north deep	35	14	11	66	14
2006	Kerguelen south deep	15	10	0	37	1
2006	Skiff shelf	12	5	3	23	4
	Total POKER 1	361				
2010	Kerguelen north shelf	354	107	182	595	202
2010	Kerguelen south shelf	80	20	43	122	48
2010	Kerguelen north deep	86	40	20	175	27
2010	Kerguelen south deep	19	13	0	48	1
2010	Skiff shelf	5	2	2	10	2
	Total POKER 2	544				
2013	Kerguelen north shelf	559	138	315	856	347
2013	Kerguelen south shelf	72	15	44	104	48
2013	Kerguelen north deep	73	28	25	133	31
2013	Kerguelen south deep	37	17	9	73	11
2013	Skiff shelf	7	2	3	12	3
	Total POKER 3	748				
2017	Kerguelen north shelf	419	179	172	828	191
2017	Kerguelen south shelf	72	18	41	109	45
2017	Kerguelen north deep	70	38	10	157	15
2017	Kerguelen south deep	31	14	7	60	8
2017	Skiff shelf	3	1	1	5	1
	Total POKER 4	595				

(p) *Melanostigma gelatinosum*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	0	0	0	0	0
2006	Kerguelen south shelf	0	0	0	0	0
2006	Kerguelen north deep	7	3	2	15	2
2006	Kerguelen south deep	18	10	2	40	4
2006	Skiff shelf	0	0	0	0	0
	Total POKER 1	25				
2010	Kerguelen north shelf	0	0	0	0	0
2010	Kerguelen south shelf	1	1	0	3	0
2010	Kerguelen north deep	130	98	14	341	18
2010	Kerguelen south deep	51	25	14	107	17
2010	Skiff shelf	0	0	0	0	0
	Total POKER 2	182				
2013	Kerguelen north shelf	0	0	0	0	0
2013	Kerguelen south shelf	0	0	0	0	0
2013	Kerguelen north deep	2	2	0	7	0
2013	Kerguelen south deep	0	0	0	0	0
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	2				
2017	Kerguelen north shelf	0	0	0	0	0
2017	Kerguelen south shelf	0	0	0	0	0
2017	Kerguelen north deep	70	51	7	184	10
2017	Kerguelen south deep	8	5	1	19	2
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	78				

(q) *Muraenolepis marmorata*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	71	24	29	123	35
2006	Kerguelen south shelf	9	5	1	19	2
2006	Kerguelen north deep	70	25	26	123	31
2006	Kerguelen south deep	94	25	49	144	55
2006	Skiff shelf	1	1	0	3	0
	Total POKER 1	245				
2010	Kerguelen north shelf	73	23	33	122	38
2010	Kerguelen south shelf	36	11	17	61	19
2010	Kerguelen north deep	97	38	31	177	39
2010	Kerguelen south deep	132	72	32	291	39
2010	Skiff shelf	6	2	3	10	3
	Total POKER 2	344				
2013	Kerguelen north shelf	2	2	0	5	0
2013	Kerguelen south shelf	3	2	0	9	0
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	20	11	2	46	4
2013	Skiff shelf	0	0	0	1	0
	Total POKER 3	25				
2017	Kerguelen north shelf	14	6	4	27	5
2017	Kerguelen south shelf	3	1	0	5	0
2017	Kerguelen north deep	32	12	12	57	14
2017	Kerguelen south deep	106	33	46	175	55
2017	Skiff shelf	6	4	0	14	0
	Total POKER 4	161				

(r) *Notothenia rossii*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	1 798	885	592	3 810	676
2006	Kerguelen south shelf	5 001	2 241	1 425	9 954	1 776
2006	Kerguelen north deep	0	0	0	0	0
2006	Kerguelen south deep	0	0	0	0	0
2006	Skiff shelf	739	398	94	1 622	128
	Total POKER 1	7 538				
2010	Kerguelen north shelf	1 075	290	553	1 679	629
2010	Kerguelen south shelf	90 686	54 203	2 217	207 574	11 963
2010	Kerguelen north deep	0	0	0	0	0
2010	Kerguelen south deep	1 471	1 447	0	4 409	0
2010	Skiff shelf	302	193	47	730	60
	Total POKER 2	93 534				
2013	Kerguelen north shelf	4 599	2 217	1 565	9 549	1 783
2013	Kerguelen south shelf	33 671	13 374	10 909	63 220	13 711
2013	Kerguelen north deep	0	0	0	0	0
2013	Kerguelen south deep	0	0	0	0	0
2013	Skiff shelf	451	206	99	895	140
	Total POKER 3	38 721				
2017	Kerguelen north shelf	15 671	6 921	4 757	31 374	5 740
2017	Kerguelen south shelf	176 611	85 734	35 768	367 144	50 784
2017	Kerguelen north deep	0	0	0	0	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	689	334	151	1 446	203
	Total POKER 4	192 971				

(s) *Paradiplospinus gracilis*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	22	9	7	43	8
2006	Kerguelen south shelf	1	1	0	2	0
2006	Kerguelen north deep	93	28	45	154	51
2006	Kerguelen south deep	173	40	102	256	112
2006	Skiff shelf	0	0	0	1	0
	Total POKER 1	289				
2010	Kerguelen north shelf	65	55	4	181	5
2010	Kerguelen south shelf	7	4	0	17	1
2010	Kerguelen north deep	248	117	94	503	102
2010	Kerguelen south deep	156	38	86	236	97
2010	Skiff shelf	0	0	0	1	0
	Total POKER 2	476				
2013	Kerguelen north shelf	16	9	2	37	3
2013	Kerguelen south shelf	0	0	0	1	0
2013	Kerguelen north deep	34	15	10	68	12
2013	Kerguelen south deep	44	22	10	93	13
2013	Skiff shelf	0	0	0	0	0
	Total POKER 3	94				
2017	Kerguelen north shelf	22	8	8	40	10
2017	Kerguelen south shelf	2	2	0	6	0
2017	Kerguelen north deep	118	32	61	186	68
2017	Kerguelen south deep	174	50	88	283	99
2017	Skiff shelf	0	0	0	0	0
	Total POKER 4	316				

(t) *Zanclorhynchus spinifer*

Year	Strata	Estimate	SD	Lower CL	Upper CL	OneSide95
2006	Kerguelen north shelf	33 278	18 101	9 094	74 700	10 460
2006	Kerguelen south shelf	210	123	41	496	51
2006	Kerguelen north deep	8	7	0	22	0
2006	Kerguelen south deep	17	10	0	38	4
2006	Skiff shelf	5	2	1	9	2
	Total POKER 1	33 518				
2010	Kerguelen north shelf	34 378	16 460	5 301	71 240	10 199
2010	Kerguelen south shelf	270	151	42	610	52
2010	Kerguelen north deep	21	17	0	58	1
2010	Kerguelen south deep	0	0	0	0	0
2010	Skiff shelf	24	9	9	45	10
	Total POKER 2	34 693				
2013	Kerguelen north shelf	18 976	8 229	5 094	37 115	6 965
2013	Kerguelen south shelf	662	505	51	1 781	71
2013	Kerguelen north deep	6	6	0	18	0
2013	Kerguelen south deep	30	22	0	81	0
2013	Skiff shelf	12	4	5	20	6
	Total POKER 3	19 686				
2017	Kerguelen north shelf	2 889	1 267	821	5 729	1 005
2017	Kerguelen south shelf	28	14	7	59	9
2017	Kerguelen north deep	0	0	0	0	0
2017	Kerguelen south deep	0	0	0	0	0
2017	Skiff shelf	1	1	0	2	1
	Total POKER 4	2 918				

Appendix 3

Length-frequency distribution (total length in cm) of *Lepidonotothen squamifrons* caught during the four POKER groundfish surveys. Note that the 35 cm length (blue arrow) at sexual maturity (both sexes) indicates that surveys inadequately sample the adult part of the population (due to the annual southeast slope spring spawning migration), especially during 2006 and 2017.