

Modelling spatial distribution of Patagonian toothfish through life-stages and sex and its implications for the fishery on the Kerguelen Plateau

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ABSTRACT

Size and sex specific habitat preferences are common in animal populations and can have important implications for sound spatial management of harvested species. Patagonian toothfish (*Dissostichus eleginoides*) is a commercially exploited fish species characterised by its longevity (>50 yo) and its extremely broad distribution in depths ranging from 10 m to 2500 m on most of the Plateaux, banks and seamounts of the Southern Ocean. As many benthopelagic fish species, Patagonian toothfish exhibits sexual dimorphism and ontogenetic habitat shift towards deeper waters as they grow. In this study, we modelled the spatial structure of Patagonian toothfish population (median total length and sex composition) in a data-rich area, the Kerguelen Plateau (Southern Indian Ocean), to better understand the ecological drivers of their distributional patterns and inform current and future fishery management strategies. We applied spatially-explicit statistical models to quantify and predict the effects of the complex topography of the Kerguelen Plateau in structuring the spatial distribution of Patagonian toothfish total length and sex ratio, while controlling for gear selectivity and season. Model predictions showed that juvenile toothfish live in shallow regions (shelf and banks) and move downward progressively up to 600 m while they grow. Between 600 m and 1200 m, the downward movement stops and fish settle at their preferred depths. While in this depth range, fish are ~75 cm long and most vulnerable to fisheries. As they approach maturity large fish move downward to deep-sea habitats (from 1200 m to >2300 m) and head towards the spawning grounds on the western side of the plateau and around Skiff Bank. Importantly, the sex ratio was not evenly distributed across the Plateau; prediction maps revealed a higher proportion of females in the South whereas a strong male-bias sex ratio (70%) occurred in the North-West. Large-scale prediction maps derived from our models assisted in developing hypotheses regarding ecological drivers of Patagonian toothfish habitat-use and movement across different life stages and sex. Such hypotheses are crucial to inform management strategies of this multijurisdictional fishery (France and Australia) at the spatial and temporal scales over which natural processes and fishery extend.

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1. Introduction

Animal populations are not distributed randomly in space and time but exhibit spatial patterns of distribution. Understanding what factors drive these patterns of distribution is both a fundamental ecological question and a requirement for sound management when species are of commercial or conservation interest

(Planque et al., 2011). External controls, such as environmental forcing, are known to affect species distribution; however, internal controls such as population size, age structure, sex, condition and behaviour, can also modulate the spatial distribution of a population, through mechanisms such as density dependence, age- or sex-dependent habitat and food preferences or differential migration capacities (Ward et al., 2006). Ontogenetic habitat shifts and sex-dependent habitat preferences have been observed in many species of marine vertebrates and invertebrates (Ward et al., 2006; Wearmouth and Sims, 2008; Werner and Gilliam, 1984). In fish, the processes that lead to structured populations operate

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throughout the life cycle via egg and larval dispersion, settlement areas, juvenile movements, recruitment, and movements of adults. Ontogenetic shifts in habitat have been reported in many fish species, from coral reef fish (Lirman, 1994) to deep-sea fish species (Dunn et al., 2009; Moteki et al., 2009; Longmore et al., 2011); for example, the roundnose grenadier (*Coryphaenoides rupestris*), found between 600 and 1800 m in the Atlantic Ocean, segregate by depth according to life-stages (Longmore et al., 2011). Sexual habitat segregation occurs where males and females differ in their use of the physical environment (Wearmouth and Sims, 2008). For example, sexual segregation occurs in Atlantic cod (*Gadus morhua*) where males remain on spawning grounds while females move in and out of these male-dominated spawning aggregations when ready to release an egg batch (Robichaud and Rose, 2004).

Harvesting can affect the spatial structure of a population by modifying the density of individuals in a population and selectively targeting certain individuals (Allendorf and Hard, 2009; Kendall and Quinn, 2013) in particular habitats. Despite the broad recognition of significant spatial complexity within fish population, fisheries are commonly managed across large spatial scales that aggregate interacting sub-populations into a single management unit (Benson et al., 2015; Cadrian and Secor, 2009). Modelling spatial structure of fish populations is thus an important step towards the development of spatially-explicit integrated stock assessment models (Goethel et al., 2011).

Patagonian toothfish (*Dissostichus eleginoides*, Smitt, 1898), is a large benthopelagic fish species belonging to the nototheniidae, a family endemic to the southern hemisphere and dominating Antarctic fish assemblages (e.g. Gon and Heemstra, 1990; Kock, 1992). Its geographic distribution encompasses vast areas on the southern Patagonian and Chilean shelves, peri-insular plateaux surrounding subantarctic islands, banks and seamounts in the Southern Ocean (Arkhipkin et al., 2003; Eastman, 1993; Gon and Heemstra, 1990). Its depth range is the widest of any teleost fish, being found from 10 m to 2500 m (Duhamel et al., 2005). As many deep-sea species living in constant and/or predictable environments, Patagonian toothfish exhibits K-selection life-history characteristics such as slow growth, delayed maturity, large body size (up to 2 m and 100 kg) and long lifespan (>50 years). Its large body size coupled with the high quality of its flesh led to the development of highly valuable (legal and illegal) fisheries in the mid 1980s, targeting large adults in deep waters all across its distribution (Collins et al., 2010; Duhamel et al., 2005). As with many new fisheries, the fishery developed ahead of the essential knowledge of the biology and ecology of the target species to promote good management practices (Collins et al., 2010). However, gaining such knowledge is challenging for deep-sea species and many aspects of toothfish ecology such as movements, connectivity, reproductive behaviour and habitat-use remain poorly understood.

Several studies based on fishing data and scientific surveys in the South Atlantic fishing sector (Agnew et al., 1999; Arkhipkin et al., 2003; Arkhipkin and Laptikhovsky, 2010) and Indian Ocean fishing sector (Duhamel, 1987; López Abellán, 2005; Welsford et al., 2011), indicated that body size of Patagonian toothfish increases with depth. This ontogenetic shift in habitat is common in deep-sea fish (Agnew et al., 1999; Longmore et al., 2011) and often associated with predation avoidance and/or a switch from a predatory behaviour to scavenging (Arkhipkin et al., 2003). However, spatial segregation between individuals may also arise from social interactions or reproductive behaviour. Female Patagonian toothfish are larger than males and vertical segregation between sexes has been reported in South Georgia where large mature female were found deeper on the slope compared to males (Agnew et al., 1999). This depth pattern is thought to change seasonally with both sexes converging in intermediate depths to spawn (Agnew et al., 1999; Brown et al., 2013).

Although many of these studies reported on the key role of bottom topography in structuring the population of toothfish, none quantified the effect of bathymetry in structuring the spatial distribution of fish length and sex composition. In this study, we developed a statistical model for the spatial distribution of the length and sex ratio of Patagonian toothfish at a large spatial scale. We used a unique dataset collected in the world's largest fishery for Patagonian toothfish located on the Kerguelen Plateau.

The Kerguelen Plateau is a large submarine Plateau which lies in deep waters of the Indian sector of the Southern Ocean and extends for more than 2200 km in a northwest-southeast direction. Most of the northern part of this Plateau lies within the Exclusive Economic Zones (EEZs) of France and Australia, 200 nautical miles around the Kerguelen Islands and the Heard and McDonald Islands, respectively. After a period of illegal, unregulated and unreported (IUU) fishing in this region, legal and regulated Patagonian toothfish commercial fishing began in 1984/1985 on the Kerguelen Plateau (Duhamel et al., 2011). Since 2000, the French fishery has exclusively used demersal longlines, whereas the Australian fishery began as a trawl fishery before longlines were introduced in 2003 and progressively replaced trawling. Total allowable catches (TAC) have been fluctuating around 5000 tonnes for the French fishery and around 2600 tonnes for the Australian fishery over the last decade (Duhamel and Williams, 2011), and toothfish spawning biomass in 2015 has been estimated to be around 57% of its unfished level in the French EEZ (Sinègre and Duhamel, 2015) and at 64% in the Australian EEZ (Ziegler and Welsford, 2015). Both countries apply principles of ecosystem-based fishery management recommended by the Commission for Conservation of Antarctic Marine Living Resources (CCAMLR, Constable et al., 2000; Croxall and Nicol, 2004), including 100% observer coverage. However, legal geographical boundaries do not reflect natural processes occurring over the Kerguelen Plateau and French and Australian fishery data must be analysed jointly to provide a comprehensive picture of the toothfish population.

Our study is the first to combine 11 years of biological data collected during French and Australian commercial fishing operations and 15 years of research survey data to analyse the large-scale spatial structure of Patagonian toothfish population over the Kerguelen Plateau. It provides a unique biological dataset including fish measurements and sex determination for fish caught over a large spatial and temporal extent and across a wide range of depths (80–2300 m). We modelled the spatial distribution of toothfish median total length and sex ratio to test the null hypothesis that male and female toothfish, of all sizes, were randomly distributed in catches across the Kerguelen Plateau. Large scale prediction maps derived from our models assisted in developing hypotheses regarding ecological drivers of Patagonian toothfish habitat-use and movement across different life stages and sex. Such hypotheses are crucial to inform management strategies of the fishery at the spatial and temporal scales over which natural processes and fishery extend (Berger et al., 2012; Metcalfe, 2006). We also discussed the importance of spatial distribution models for ecosystem-based fisheries management.

2. Methods

2.1. Species biology and study site

The Kerguelen Plateau is the largest submarine plateau in the Southern Ocean; it forms a natural barrier to the deep-reaching Antarctic Circumpolar Current and its iron-rich shelf waters promote recurrent phytoplankton spring blooms (Park et al., 2014; van Wijk et al., 2010). The Kerguelen plateau hosts one of the largest populations of Patagonian toothfish worldwide. Patagonian

toothfish spawn in deep waters (>1000 m) during the austral winter (May–August), producing pelagic eggs and larvae (Collins et al., 2010). At the age of around one, larvae switch to a demersal habitat at around 100 m depth and juveniles inhabit relatively shallow water (in less than 300 m depth) before they begin a gradual migration into deeper water. Growth is relatively quick for the first 10 years, while the fish inhabit relatively shallow water, but following the onset of maturity (70–80 cm total length) growth slows down (Candy et al., 2007; Collins et al., 2007; Duhamel et al., 2005).

2.2. Biological data collection

Biological data including fish length and sex were collected during commercial and research activities conducted by Australian and French vessels operating in their respective EEZs (Fig. 1). The complete dataset totalled over 1.4 million fish measurements of which 80% were sexed (Table 1).

2.2.1. Observer data from commercial fisheries

Since the start of the commercial fisheries, all fishing vessels have carried one or two scientific observers on each French vessel and Australian vessel, respectively. Observers record catch and effort data as well as biological data from a representative sample of the catch. Geographic location of each haul is recorded using a GPS and the mid-haul location is estimated as the mid-point between the start and the end of a haul.

Biological data were collected throughout the year by the French longline fishery which operates all year round except between the 1st of February and the 1st or 15th of March to avoid seabird bycatch. Similarly, the Australian trawl and trap fishery

operates throughout the year, whereas, the Australian longline fishery operates only from April to November to avoid interactions with seabirds. The proportion of fish caught by longlines increased from 2003 to 2013, particularly in the Australian EEZ where longlines progressively replaced trawls (Table 1). Experimental trapping was conducted in the Australian EEZ as an alternative to longlines to prevent toothed whale depredation (whales feeding on fish hooked on a fishing line) occurring on longlines. Despite successful results in preventing whale depredation, catch rates were insufficient and trapping stopped in 2014. The collection of biological data by observers was consistent with the CCAMLR Scheme of International Scientific Observation (SISO). The French data were extracted from the 'Pecheker' database (Martin and Pruvost, 2007), maintained at the Museum d'Histoire Naturelle. The French and Australian fisheries have a contrasting spatial distribution within their respective EEZs. Commercial fishing is prohibited within the 12 nautical mile zone around islands, within Marine Protected Areas (MPAs) and in waters shallower than 500 m in the French EEZ (Fig. 1). Every year since 2003, the French longline fleet have fished consistently on a widespread area encompassing most of the slope areas deeper than 500 m (Fig. 1), whereas the Australian fleet was localised in 3 main fishing grounds from 2003 to 2008 when trawling was dominant. The Australian fishery expanded its fishing grounds only after 2008 when an increasing proportion of the TAC was taken by longlines.

2.2.2. Research survey data

Scientific surveys were conducted across the Plateau in both EEZs to assess the abundance of adult and juvenile toothfish and gain more knowledge on their biology. These surveys focused

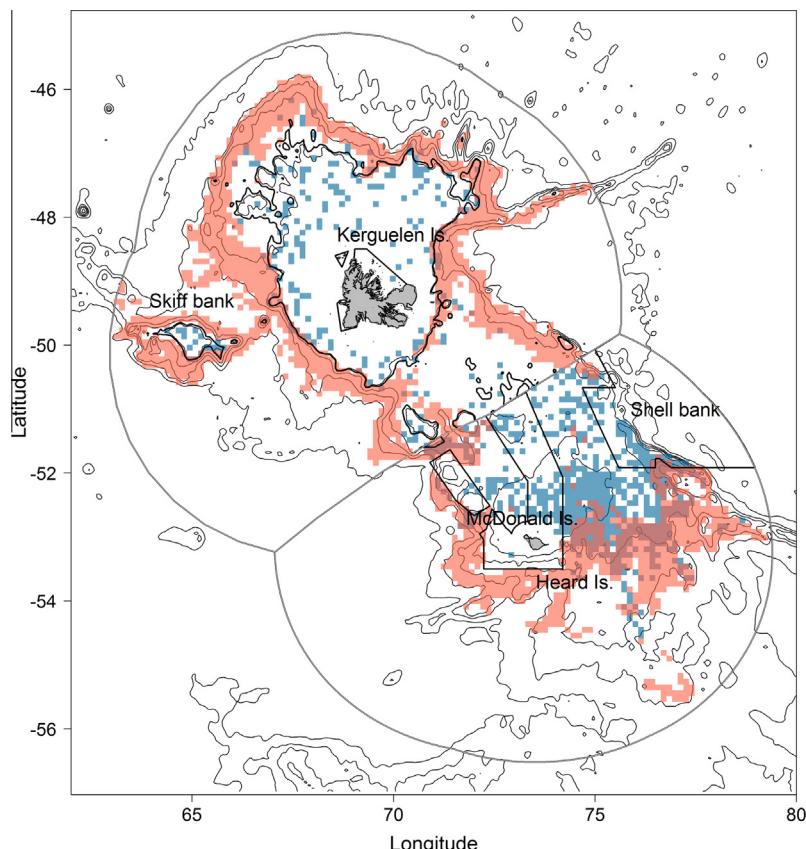


Fig. 1. Map of the Kerguelen Plateau with the distribution of commercial fishing (from 2003 to 2013, in red) and research survey (1998–2013, blue). Areas of overlap between commercial and research surveys are shown by transparency. French and Australian EEZs (to the north and to the south, respectively) are delineated by grey lines and contours of marine reserves are shown in black lines. The 500 m isobath appears in black in the French EEZ to show the area where fishing is prohibited, between 0 and 500 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Numbers of Patagonian toothfish measured on the Kerguelen Plateau during the commercial fishery operations in the Australian and French EEZs and during the scientific Australian RSTS and French POKER research surveys. These data were used in the GAM analyses. (–) indicates that data were available but not included whereas zero means that data were not available (no fishing).

Year	Commercial fishing					Research surveys		
	Australian EEZ			French EEZ		Australia RSTS	French POKER	
	Trawl	Longline	Trap	Longline	Total			
1998	–	0	0	–	–	169	0	169
1999	–	0	0	–	–	2294	0	2294
2000	–	0	0	–	–	2645	0	2645
2001	–	0	0	–	–	2509	0	2509
2002	–	0	0	–	–	2967	0	2967
2003	24,650	2268	0	72,186	99,104	4224	0	4224
2004	17,270	6418	0	70,314	94,002	10,461	0	10,461
2005	16,618	6549	324	71,667	95,158	8051	0	8051
2006	15,119	9059	3995	74,442	102,615	4553	3977	8530
2007	13,972	8780	0	85,473	108,225	2090	0	2090
2008	15,119	16,550	9	77,886	109,564	1280	0	1280
2009	13,282	30,401	773	99,557	144,013	1988	0	1988
2010	11,908	16,881	2654	133,370	164,813	8074	4093	12,167
2011	10,659	22,528	1175	129,042	163,404	2494	0	2494
2012	17,098	20,064	196	128,278	165,636	6063	0	6063
2013	7482	33,270	2418	108,409	151,579	2912	5065	7977
Total	163,177	172,768	11,544	1,050,624	1,398,113	62,774	13,135	75,909
Percentage	12	12	1	75	100	83	17	100

mainly on areas shallower than 500 m (juvenile habitat) and in some areas in waters down to 1000 m. French surveys have been undertaken in 2006, 2010 and 2013, whereas Australian surveys were conducted annually since the start of the fishery in 1998.

2.2.2.1. Australian research survey. Each year since 1998, a research survey (Random Stratified Trawl Survey, RSTS) was conducted around the Heard and McDonald Islands (HIMI) by an Australian commercial trawl vessel, the *FV Southern Champion*. The research surveys typically lasted 20–30 days and were conducted between April and July or occasionally in September–October (1997 and 2010). A 'Champion' 4-panel bottom trawl net with a diamond mesh pattern and a mesh cod end liner of 50 mm mesh size was used for the surveys (Nowara et al., 2006). For each survey, the area of the Australian EEZ down to 1000 m was divided into ten strata, each covering an area of similar depth and/or fish abundance. Typically, 120–160 trawl stations were chosen randomly each year in these strata, including within the HIMI Marine Reserve (Constable and Welsford, 2011; Nowara et al., 2013; Welsford et al., 2006). A station was defined as a trawl event of ~30 min duration on the bottom at a towing speed of 3 knots. Geographic locations of sampling stations were recorded using a GPS and depth recorded from depth sounders (Simrad EK60). Comprehensive data associated to each haul were collected, including the species composition and catch weight per species (in kg). Length measurements were taken from a random sample of toothfish whose number depends on the catch (mean = 20 individuals haul⁻¹, range = 1–420 individual haul⁻¹). Sex was determined on a random subsample of the TL sample; 53% of the fish measured were also sexed.

2.2.2.2. French research survey. Three research surveys ('POissons de KERguelen', POKER) have been undertaken in the French EEZ in September–October 2006, August–October 2010 and September 2013. These scientific surveys lasted 20–30 days and were conducted onboard *FV Austral* using a bottom trawl of 35 m with a mesh size of 40 mm for the 2006 and 2010 surveys and 90 mm for the 2013 survey (Duhamel et al., 2014). About 200 sampling stations were selected randomly over the Plateau for the first survey in 2006 and these locations were revisited (within a radius of

~10 km) during the 2010 and 2013 surveys. Each station corresponded to a trawl event of ~30 min duration on the bottom at a towing speed of 3 knots. Geographic location and depth of each station was recorded using a GPS and a depth sounder (Furuno FCV 1200). Comprehensive data associated to each haul were collected (Duhamel et al., 2014), including the species composition and catch by species (in kg and number when possible). Length measurements were taken from a random sample of toothfish whose number depends on the catch (mean = 23 individuals haul⁻¹, range = 1–249 individuals haul⁻¹). Sex was determined on a random subsample of the TL sample; 25% of the fish measured were also sexed.

2.3. Data checking and topographic data

For both commercial data and scientific surveys, haul locations were checked for errors and corrected when possible. Only high quality locations were kept for the analysis. All analyses and data manipulation were performed using the R software 3.1 (R Development Core Team, 2014). In the Australian EEZ, haul depth was extracted at the mid-coordinates of each haul (middle point between the start and end of a haul) using the high resolution 'Kerguelen Plateau Bathymetric raster Grid' ($0.001^\circ \times 0.001^\circ$) provided by Geosciences Australia (Beaman and O'Brien, 2011). This high-resolution bathymetric grid did not extend into the northern part of the Kerguelen Plateau, and we therefore used the mean depth recorded by fishing vessels for the French haul data. Since the topography of the Kerguelen Plateau is complex, we calculated the steepness of the slope as an additional topographic index. This index was estimated from the GEBCO 2014 topographic dataset (http://www.gebco.net/data_and_products/gridded_bathymetry_data/), at its initial resolution of $0.0083^\circ \times 0.0083^\circ$, using the function *terrain()* from the R package 'raster' (Hijmans, 2014). This function calculated the slope in degrees, using the 8 neighbouring cells. The slope value was then converted into a categorical variable from flat areas ($0\text{--}0.5^\circ$) to very strong slopes ($16\text{--}30^\circ$) as described in Appendix A. The GEBCO 2014 topographic grid was also used for all model predictions at the scale of the Kerguelen Plateau.

2.4. Modelling total length and sex ratio spatial distribution

We modelled the spatial distribution of toothfish total length and sex ratio to test the null hypothesis that male and female toothfish across all sizes and season (i.e. resting or spawning) were randomly distributed in catches across the Kerguelen Plateau.

Median total length (TL, in cm) was calculated for each haul event where at least 5 measurements were taken for each sex category ($n = 50,137$ hauls). The sex ratio was estimated as the number of females versus the total number of fish sexed (males + females) in each haul where at least 10 fish were sexed ($n = 21,997$ hauls). Individuals with unknown sex were excluded for the sex ratio analysis as well as fish smaller than 40 cm because of the difficulty in reliable sexing of juvenile gonad tissues.

Fish total length and sex ratio were modelled using spatially-explicit Generalised Additive Models (GAMs), implemented in R 3.1, using the *gam()* function in the *mgcv* package (Wood, 2006). We tested the effect of depth (continuous variable), slope steepness (four levels, between 1° and 16°), geographic coordinates (i.e. longitude, latitude), fish sex (male, female or unknown) and gear type on toothfish median total length. The 'gear type' included country (Australia, France) and purpose (commercial vs research) to account for selectivity but also for differences in fishing practices. The same variables except for sex were included in the model for sex ratio. Fishing depth was included as it was known to be an important factor structuring the spatial distribution of toothfish across its wide depth range (Duhamel, 1987; López Abellán, 2005; Welsford et al., 2011). Slope steepness was included in the model because it is thought to be an important factor in determining benthic habitat and colonisation in the deep sea (Wilson et al., 2007). Flat areas tend to exhibit different seabed facies and support communities that are different from those on steeply sloping areas (Genin, 2004; Bouchet et al., 2014; Welsford et al., 2014a). Slope may also contribute to current flow amplification, which has consequences for the supply of food to the benthic fauna (Wilson et al., 2007). The intra and inter-annual variations in the distribution of fishing effort prevented exploration of temporal effects at the scale of months and years. However, since we were expecting seasonal differences linked to the spawning behaviour, we split the year by season: 'spawning', from May to August and 'resting' from September to April (Duhamel, 1987; Welsford et al., 2012; Wood, 2006), and included this parameter in the models as a fixed term or in interaction with others parameters such as depth and location.

Length data were modelled assuming a Gamma error distribution and a log link function, whereas models fitted to sex ratio data assumed a binomial error distribution with a logit link function. A comprehensive model was then constructed including all variables in the first instance, with splines fitted to continuous variables (e.g. depth, latitude and longitude). The dimensional basis of the spline (k) was chosen to be large enough to represent the underlying process reasonably well, but small enough to maintain reasonable computational efficiency and avoid over-fitting. We checked the adequacy of k by checking for pattern in the model residuals as recommended in Wood (2006). The most parsimonious model was selected by progressively removing terms to achieve the model with the minimum value of Akaike's Information Criterion (AIC, Akaike, 1974). Interactions among covariates were tested individually. The adjusted- r^2 value and deviance explained for each model was considered as an indication of the quality of fit, as well as scrutiny of the distribution of model residuals using the *gam.check()* function.

Model performance was also quantified using cross-validation: the best GAM model was fitted to a random sample (75%) of the haul data and used to predict the median total length or sex ratio of the haul from the remaining 25% of the data. Pearson correlation

coefficients were calculated to evaluate model performance. This procedure was repeated 100 times (due to computational limitations) to provide an indicative range of the Pearson correlation coefficients.

The contribution of each explanatory variable to the model (effect plot) was plotted with all other variables held fixed at their representative value (mean value for continuous variables or more frequent value for categorical variables). For gear and sex effects, fixed value was set as 'commercial French longline' and 'female', respectively. Depth was set to 1000 m, slope as 1 (gentle) and season as 'resting' for the effect plots.

The best GAM models were then used to predict the distribution of toothfish median total length and sex ratio over the Kerguelen Plateau across the observed depth range (100–2300 m). The generalisation dataset included latitude, longitude, depth, slope steepness (from the 'GEBCO' bathymetric grid, $0.0083^\circ \times 0.0083^\circ$). The effect of sex, gear and season had to be fixed and were set as female, commercial longline (French in the French EEZ and Australian in the Australian EEZ) and resting period for predictions.

3. Results

In total, over 1.4 million Patagonian toothfish were measured between 1998 and 2013; most data came from fish caught on commercial longlines (83%), 11% from commercial trawl, 1% from traps, and 5% during trawl research surveys (Table 1). The French longline catches contributed the most to the TL and sex datasets (Table 1). Commercial and research biological data were mostly collected during the resting season (September–April) except for data collected from longlines in the Australian EEZ, since the fishery operates during the spawning season (May–August, Table 2).

3.1. Total length distribution

The diversity of fishing gears used in the study area enables catching Patagonian toothfish ranging from 8 cm to 210 cm. The smallest length class of fish measuring less than 20 cm (corresponding to 1-*yo* fish), were caught almost exclusively in the French EEZ during the POKER surveys (182 records). These fish were found in shallow waters, between 100 m and 300 m, around Kerguelen Islands and top of Skiff Bank on the north-western part of the Plateau. The smallest length class to be caught abundantly in the Australia EEZ was 30–40 cm (corresponding to 2–3 *yo* fish) in waters <600 m, around Heard Island and on top of Shell Bank and Discovery Bank on the north-eastern side of the Australian EEZ. Conversely, very large fish (>150 cm) were caught in both EEZs, in a large range of depths (from 500 to 2000 m) but mostly in deep slopes located on the western side of the Plateau and Shell Bank.

Model selection by AIC ranking revealed that the best model to explain total length included depth as a continuous smooth term (spline), slope, gear and sex as categorical variables and geographic locations (longitude, latitude) conditioned by season as a smooth term (spline). The ΔAIC between the next competing model was >700, which means we had strong support about our 'best' model and did not require multi-model inference (Burnham et al., 2011). The best model provided a good fit to the data with 73% of the deviance explained and model residuals were randomly distributed in a narrow range around zero. Cross-validation also indicated a good fit to the data with Pearson correlation coefficient ranging from 0.84 to 0.85 ($n = 100$) between observed and fitted median total length data. Model parameters are described in Table 3. The effect of gear by country reflects the expected different selectivity of fishing gears; Australian traps caught significantly larger fish (90 cm in average for females) than the other types of

Table 2

Numbers of Patagonian toothfish measured each season during the commercial and scientific fishery operations in the Australian EEZ and French EEZs.

Season	Commercial fishing			Research surveys		
	Australian EEZ Gear		French EEZ	Australian RSTS	French POKER	
	Trawl	Longline	Trap	Longline	Trawl	Trawl
Resting (September–April)	120,395	32,520	11,409	848,726	22,475	12,370
Spawning (May–August)	42,782	140,248	135	201,898	22,145	765

gear (>80 cm). Australian and French longlines caught fish of similar size in their respective EEZ (~75 cm in average) whereas French research trawls selected smaller fish than the Australian trawl research survey (46 vs 53 cm, Fig. 2b).

As indicated by the spline term, the increase in toothfish total length with depth was non linear (Fig. 2a). Fish total length increased almost linearly from 100 m to 600 m with a 5 cm increase of TL per 100 m depth, then remained stable between 600 m and 1200 m and increased at a lower rate (2.5 cm per 100 m depth) from 1200 to 2300 m (Fig. 2a). Females were on average 5 cm larger than males (Fig. 2d), regardless of depth and larger fish slightly prefer steeper slopes (Fig. 2c). The strong spatial effect indicated that fish were generally larger in deep waters of the North part of the Plateau, particularly during the resting season (Fig. 2e and f).

The prediction map of toothfish median total length across the Kerguelen Plateau illustrates the spatial structure of the toothfish population (Fig. 3). The shelf area around the Kerguelen Island hosts the smallest fish (<50 cm) while juveniles (50–70 cm) were predicted on the continental shelf and banks of both EEZs. Immature and young mature fish of intermediate size (70–100 cm) were predicted to occupy slope areas between 600 m and 1600 m, whereas very large fish (>110 cm) were predicted mostly in waters deeper than 1600 m at the northern and southern ends of the Plateau (Fig. 3). However, in some areas, model predictions extrapolated outside the range of sampled locations, particularly in waters deeper than 1500 m at the northern and southern ends of the Plateau.

3.2. Sex ratio distribution

Model selection by AIC ranking revealed that the best model to explain sex ratio distribution included depth as a continuous

smooth term (spline), slope and gear as categorical variables and geographic locations (longitude, latitude) conditioned by season as a smooth term (spline). Strong support was given to this model because de Δ AIC of the next competing model was >200 and it explained 48% of the deviance (Table 4). Moreover, model residuals were randomly distributed in a narrow range around zero and cross-validation indicated a good predictive ability, with the Pearson correlation coefficient ranging from 0.62 to 0.66 ($n = 100$) between observed and fitted sex ratio values. Table 4 describes the coefficients of the best model. It revealed that traps caught a surprisingly high number of females compared to males (80% of females), whereas the other gear types caught as many females than males in average except a slight female biased sex ratio (55%) for longline in both countries and the French research trawl survey (Fig. 4e).

GAM results also revealed an effect of depth and slope on sex ratio, with more males caught in intermediate depths from 600 to 1600 m and more female caught in shallower (<600 m) and deeper waters (>1600 m, Fig. 4a). The proportion of females also increased linearly by 10% from the flat areas to the steepest slopes (Fig. 4b). Finally, the spatial effect was very important in explaining the distribution of sex ratio; A strong male bias was modelled in the north-west area of the Plateau (20–30% of females), whereas females seem to dominate the catch in the south and north-east part of the Plateau (Figs. 4c, d and 5), during both resting and spawning seasons.

The map of predicted sex ratio highlights the strong pattern of sexual segregation with a majority of females in the Australian EEZ and a majority of males in the north-west of the French EEZ (Fig. 5). Predictions in shallow waters must be considered with caution because they exclude the juvenile fish that are difficult to sex. Similarly to the predictions for total length, model predictions were extrapolated outside of sampled locations in some areas, particularly on the southern and south-western parts of the Plateau (Fig. 5 shows the fishing locations used to fit the model).

4. Discussion

This study is the first to reveal the complex spatial structure of Patagonian toothfish population at a large scale using spatially-explicit statistical models. The size and sex composition of the population appears to be strongly linked with the latitude and topography of the Plateau. These results have important implications for current and future management of Patagonian toothfish and its ecosystem across the Kerguelen Plateau.

4.1. Ontogenetic shift in distribution

The predicted distribution of fish total length distribution indicates a gradual migration from shallow to deep waters as fish grow, except at intermediate depths of around 600–1200 m where fish lengths were consistent (80 cm for females and 75 cm for males). Extended shelves and bank areas in shallow waters of

Table 3

Parameters and fit of the GAM model of median total length for Patagonian toothfish. Note that parametric terms have a *t* statistic and smooth terms have an *F* statistic estimated. The model was run on a sample size of 50,137 hauls.

	df	Estimate	Std. error	<i>t</i> value	<i>Pr(> t)</i>
<i>Parametric terms</i>					
(Intercept)		4.417	0.005	843.34	<0.001
Gear: LL_Com_FR	5	-0.173	0.009	-18.28	<0.001
Gear: Trawl_Com_AUS	5	-0.175	0.003	-51.52	<0.001
Gear: Trap_Com_AUS	5	0.197	0.005	40.34	<0.001
Gear: Trawl_Res_AUS	5	-0.209	0.004	-51.94	<0.001
Gear: Trawl_Res_FR	5	-0.491	0.010	-44.72	<0.001
Sex: Male	2	-0.055	0.001	-53.21	<0.001
Sex: Unknown	2	-0.064	0.001	-42.29	<0.001
Slope 2: very gentle	5	0.003	0.002	1.41	0.159
Slope 3: gentle	5	0.03	0.002	13.43	<0.001
Slope 4: moderate	5	0.051	0.003	17.57	<0.001
Slope 5: strong	5	-0.049	0.004	10.41	<0.001
Slope 6: very strong	5	-0.048	0.006	-7.68	<0.001
<i>Smooth terms</i>					
<i>s</i> (Depth, $k = 7$)	6			1744	<0.001
<i>s</i> (Lon, Lat): resting	29			167	<0.001
<i>s</i> (Lon, Lat): spawning	29			51	<0.001
	edf			<i>F</i>	<i>p</i> -Value

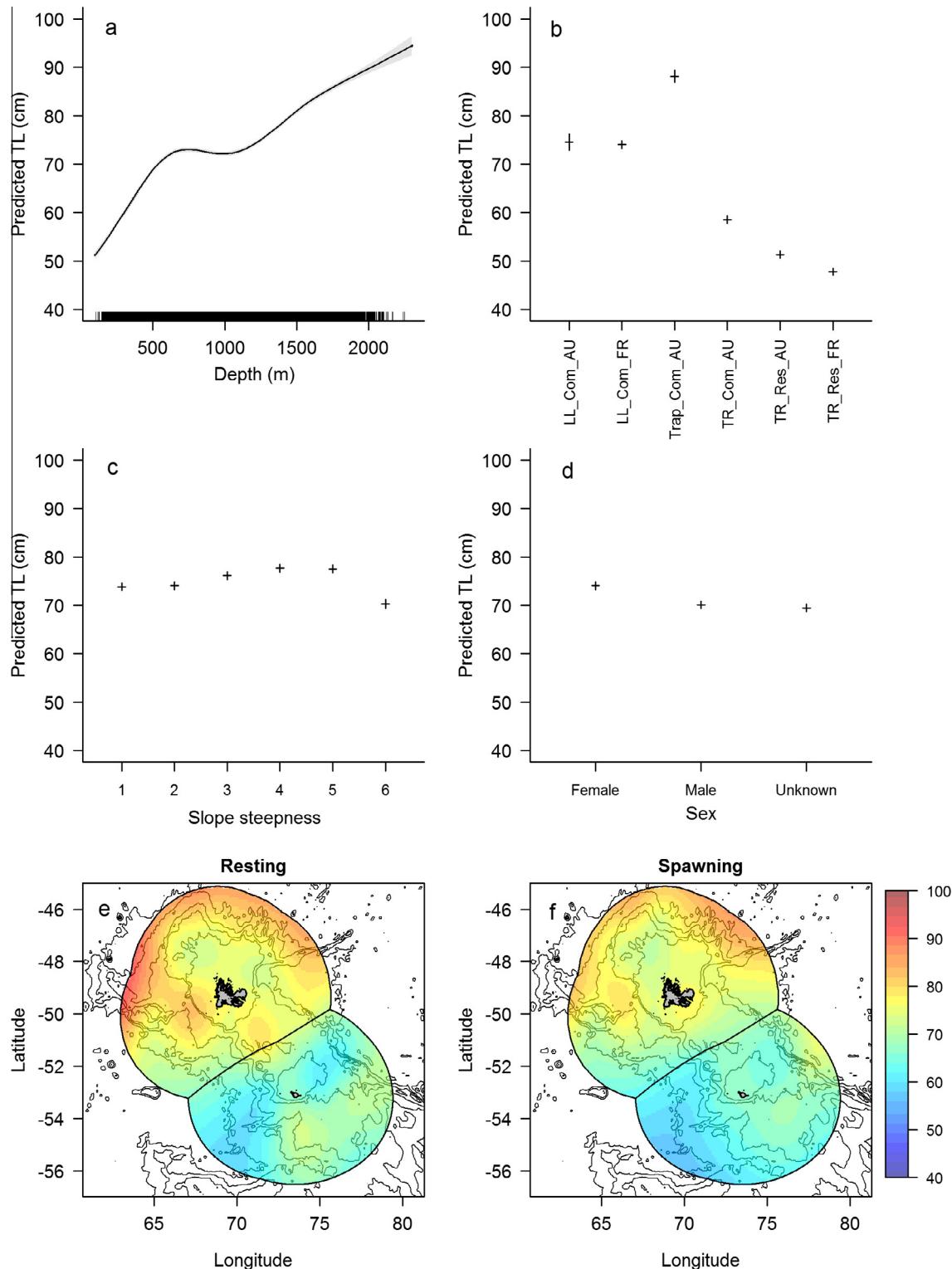


Fig. 2. Predictions of median total length of Patagonian toothfish from the generalised additive model. Plots show the predicted median total length when all other variables were held fixed at their representative values (gear type as 'commercial French longline' and sex as 'Female'). Grey shades and error bars are 95% confidence intervals.

500 m are important habitats for the small fish <60 cm during their first phase of relatively rapid growth (Duhamel, 1987; Ziegler and Welsford, 2015). The lack of interaction between depth and sex

indicated that the shape of this relationship applies to both sexes, except that at similar depths, males are relatively smaller than females. This sexual dimorphism is observed in all Patagonian

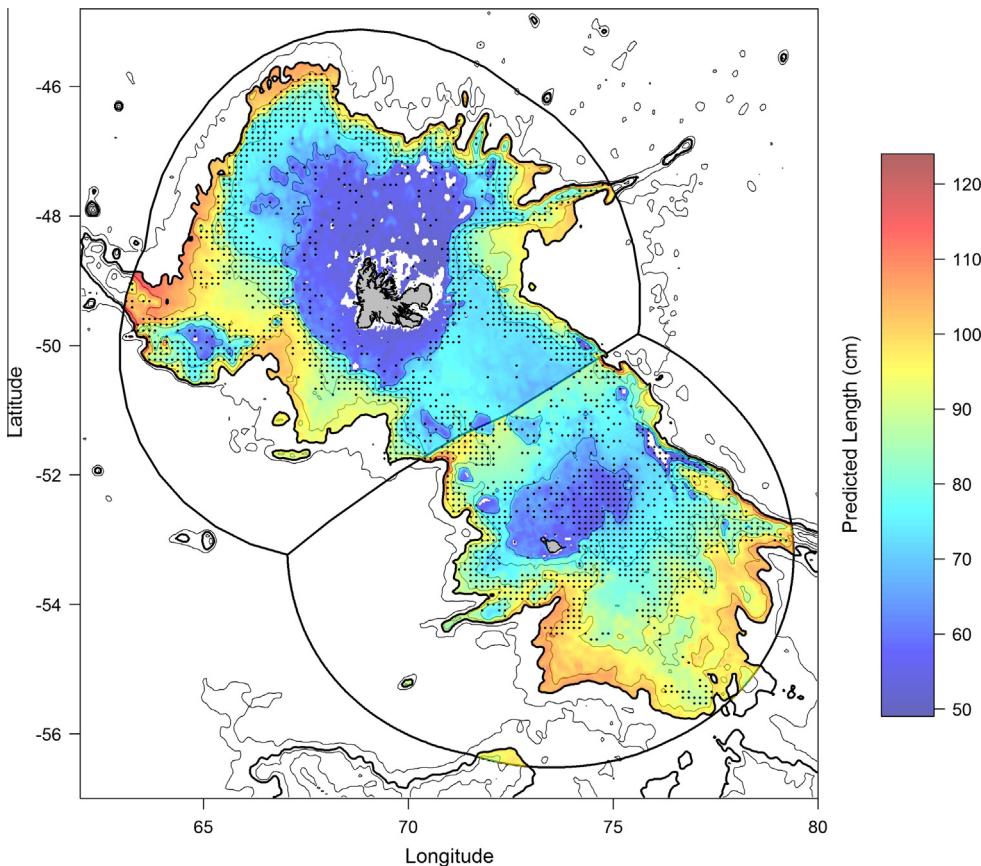


Fig. 3. Prediction map of female Patagonian toothfish median total length when caught with commercial longlines by the French fishery in the French EEZ and Australian fishery in the Australian EEZ. Bathymetry contours (-400 m , -1000 m , -2000 m and -3000 m) are displayed in black. The -2300 m isobath corresponding with the lower limit of the fishing depth is highlighted in bold. Dots correspond to cells where fishing occurred.

Table 4

Parameters and fit of the GAM model of Patagonian toothfish sex ratio. This model was run on a sample size of 21,952 hauls.

	df	Estimate	Std. error	z value	$Pr(> t)$
<i>Parametric terms</i>					
(Intercept)		0.460	0.022	20.67	<0.001
Gear: LL_Com_FR	5	-0.722	0.040	-17.75	<0.001
Gear: Trawl_Com_AUS	5	-0.516	0.017	-29.049	<0.001
Gear: Trap_Com_AUS	5	0.977	0.030	31.835	<0.001
Gear: Trawl_Res_AUS	5	-0.576	0.022	-25.191	<0.001
Gear: Trawl_Res_FR	5	-0.774	0.059	-13.025	<0.001
Slope 2: very gentle	5	0.054	0.008	6.183	<0.001
Slope 3: gentle	5	0.093	0.0009	10.025	<0.001
Slope 4: moderate	5	0.149	0.011	13.166	<0.001
Slope 5: strong	5	0.167	0.019	8.646	<0.001
Slope 6: very strong	5	0.226	0.031	7.225	<0.001
<i>Smooth terms</i>					
$s(\text{Depth}, k = 6)$	edf		Chi. sq.	p-Value	
$s(\text{Lon}, \text{Lat}): \text{resting}$	5		1974	<0.001	
$s(\text{Lon}, \text{Lat}): \text{spawning}$	29		23,121	<0.001	
			9481	<0.001	

(Welsford et al., 2012). The small amount of material that has been collected, primarily around South Georgia, Atlantic Ocean, indicated that the large and yolk eggs of Patagonian toothfish are pelagic, floating up into the top 700 m of the water column after fertilisation, and were mostly encountered over deep (>2200 m) oceanic waters (Evseenko et al., 1995; Kellermann, 1989). Eggs hatch several months after spawning and the pelagic larval phase is thought to be up to 8 months and limited to the upper 200 m of the water column at the early stages while larger larvae tend to be found closer inshore (Evseenko et al., 1995; Koubbi et al., 1990; North, 2002). It is most likely that events and processes that take place during the early life history of fish play a critical role in determining population structure, but tracking movements of these early stages is challenging. Methodologies such as modelling of larval transport by currents (Mori, 2013) or otoliths microchemical analysis may provide further insights. For example, the trace element composition in otoliths cores deposited before and after larval settlement can facilitate geographical discrimination between nursery areas, with the potential to identify natal origin, on a coarse geographical scale (Ashford et al., 2005). This type of analysis may be facilitated by the contrast in water bodies across the latitudes occupied by the Kerguelen Plateau. The lack of vertical segregation by size at intermediate depths from 600 to 1200 m for fish approaching sexual maturity may be indicative of a broader optimal ecological niche and/or abundant profitable food resources with reduced competition at these depths. The size-depth relationship is consistent with preliminary analyses of tagging data that suggests downward movement of small fish but very few

toothfish populations (Collins et al., 2010) where most individuals larger than 120 cm are thought to be females (Gasco, 2013; Welsford et al., 2011).

Our study did not include early life history stages such as eggs and larvae because they were very few samples from the Kerguelen Plateau when early life history stages may be in the water column

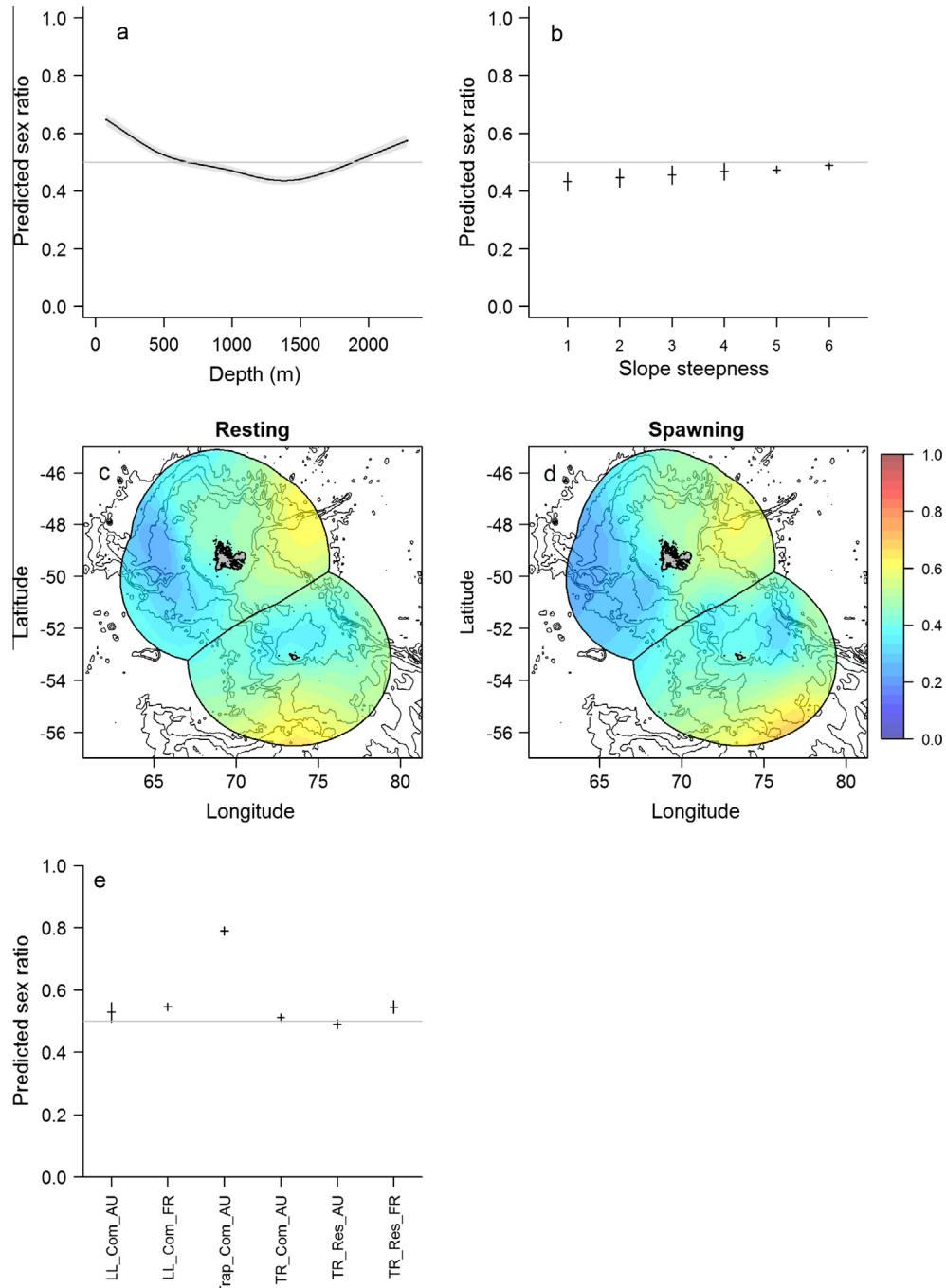


Fig. 4. Predictions of sex ratio (as proportion of females) of Patagonian toothfish from the generalised additive model. Plots show the predicted sex ratio when all other variables were held fixed at their representative value (mean value for continuous variables, gear type ‘commercial French Longline’). Grey shades indicate the 95% confidence intervals. The horizontal grey line in each plot represents a sex ratio of 50% females and 50% males.

vertical and horizontal movements for fish tagged at intermediate depths that settle in their preferred habitat (AAD unpublished data and Welsford et al., 2014b).

In shallow and deep waters, the observed ontogenetic shift in spatial and depth distribution of Patagonian toothfish could have evolved through multiple, non-exclusive, ecological and physiological processes, which usually result in niche expansion and reduction in inter-cohort competition (Polis, 1984). Interestingly, this migratory deep-water life cycle has evolved independently in several fish and squid species inhabiting temperate and sub-polar environments (Arkhipkin and Laptikhovsky, 2010). Changes in physiological abilities between life-stages, particularly, in terms of swimming ability, buoyancy and mouth and jaw size, allow a wider

range of habitats and prey to be exploited as fish grow (Collins et al., 2010; Werner and Gilliam, 1984). As all notothenioids, Patagonian toothfish lacks a swim bladder and acquires near neutral buoyancy through the years by accumulating lipids in their muscles and decreasing the mineral content of their bones (Belchier and Collins, 2008; Collins et al., 2007; Near et al., 2002). These internal ontogenetic changes are likely to explain size-specific segregation in habitat and diet observed for this species. Juveniles are known to be active predators foraging above the seabed and feeding predominantly on euphausiids, amphipods and small fish species (Collins et al., 2007; Duhamel, 1987). With increasing size and down-slope migration, toothfish diet diversifies and includes more squids and fish (Duhamel, 1987; Yau et al., 2002). Large adults are

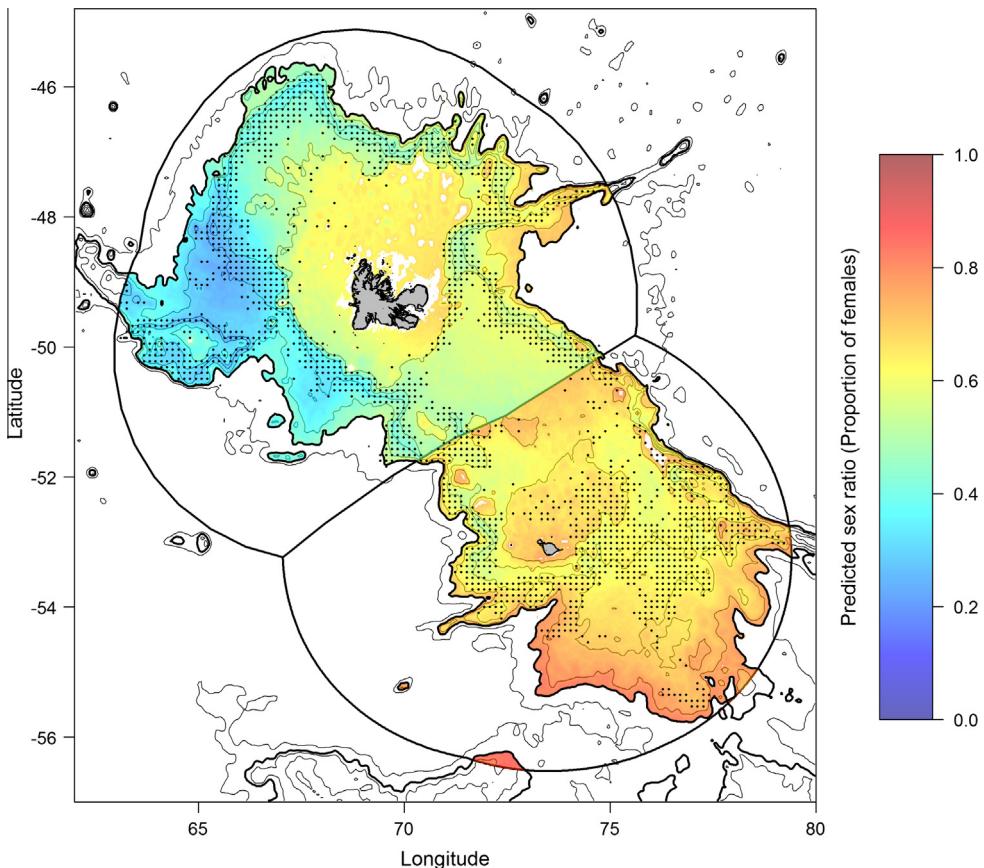


Fig. 5. Prediction map of Patagonian toothfish sex ratio (proportion of females) from the generalised additive model. Bathymetry contours (-400 m , -1000 m , -2000 m and -3000 m) are displayed in black. The -2300 m isobath corresponding with the limit of the fishing depth is highlighted in bold. Dots correspond to cells where fishing occurred.

typical opportunistic predators relying on relatively inactive prey (Arhipkin and Laptikhovsky, 2010). As many deep-water species, toothfish are scavengers (Yau et al., 2002), but their neutral buoyancy also enables exploitation of the pelagic realm (Collins et al., 2010) and thus access to pelagic prey such as squids and mesopelagic fish, especially lantern fish from the genus *Gymnoscopelus* (Duhamel, 1987). The trend of larger fish in deeper habitat is typical of scavenging teleosts fish species relying on sporadic food items (Collins et al., 2005); larger size permits higher swimming speeds and greater endurance as a consequence of larger energy reserves and lower mass specific metabolic rate (Collins et al., 2005).

Habitat partitioning between size classes could also be driven by predation avoidance. Large adult toothfish are cannibalistic and thus smaller cohorts may avoid deep habitats where they are more susceptible to be preyed upon by larger cohorts. Moreover, large fish may select deeper habitats to mitigate predation pressure by others large predators such as sleeper sharks (*Somniosus antarcticus*) and marine mammals (sperm whales *Physeter macrocephalus*, killer whales *Orcinus orca* or elephant seals *Mirounga leonina*) that have considerable diving abilities (Clarke, 1980; Reisinger et al., 2015) and feed naturally on toothfish (Abe and Iwani, 1989; Duhamel et al., 2005; Yuhhov, 1982). Few studies indicate that the richest toothfish fishing grounds are also traditional feeding grounds for sperm whales (Hucke-Gaete et al., 2004; Tixier et al., 2010). Sperm and killer whales are observed more often during the fishing operations in the French EEZ than in the Australian EEZ (Gasco, 2013; Tixier et al., 2010; Welsford and Arangio, 2015) and preliminary analyses showed that the presence of killer whales or sperm whales in the vicinity of fishing vessels could reduce the median total length of fish caught in a haul since whales target

larger fish along the lines (Gasco, 2013). Whether it contributes to the ‘gear type’ effect in our model would need further investigations.

Finally, selection of deep water habitats by large mature fish could also be an adaptation to enhance reproductive success. Recent hydrodynamic modelling studies suggested that spawning at 1500–1900 m depth on the western side of the Kerguelen Plateau could enhance the retention of eggs and larvae over the shallow Plateau (Mori, 2013), where primary productivity is the highest (Park et al., 2014).

4.2. Spatial partitioning by sex

Our sex ratio model revealed strong spatial differences in sex composition over the Kerguelen Plateau. Males were dominant in the catches of the north-western part of the Plateau whereas the sex ratio was balanced or females-biased elsewhere. Coupled with the results of the total length model, this result suggests that the Skiff bank area in the north west of the Plateau hosts a high proportion of the large males of the Kerguelen Plateau whereas large females were found in greater proportions in the south. Skiff Bank is a known spawning location west of Kerguelen Islands (Lord et al., 2006) but the reason for this spatial pattern is unclear. Sexual segregation is common in many fish species on spawning grounds. Typically, males arrive at the spawning grounds before females and remain there for a longer time, which results in a higher proportion of males on spawning grounds (e.g. Atlantic cod, *Gadus morhua*, Robichaud and Rose, 2004, Patagonian hake, *Merluccius hubbsi*, Pájaro et al., 2005, North Sea plaice, *Pleuronectes platessa*, Rijnsdorp, 1989). However, there is no evidence of localised

spawning aggregations for Patagonian toothfish and spawning grounds have also been found recently along the deep slopes on the western side of the Australian EEZ (Welsford et al., 2012). Furthermore, modelled seasonal variations in the length and sex composition on the western slopes were relatively minor.

An alternative hypothesis concerning the observed male-biased sex ratio in the north-west could be a poor longline selectivity of large spawning females which could be distributed deeper than the fishery operates or be less likely to bite on hooks when spawning. This hypothesis could be tested by using traps in this area, since traps caught preferentially (80%) larger females in the Australian EEZ. Analysis of tagging data could shed light on potential short-term seasonal movements of females in this male-dominated area. Sex differences in body size are likely to confer significant sex differences in attributes such as predation risk, nutritional requirements and activity budgets, all of which are likely to influence spatial and temporal habitat use. However, determining the underlying causes of sexual segregation in the marine environment is challenging as fish live in a three-dimensional and relatively inaccessible and concealing environment across large spatial scales.

4.3. Depth as a proxy for other environmental factors

In this study, we used topography (depth and slope steepness) as an environmental predictor of fish total length and sex ratio because we hypothesised that bottom topography was correlated to many others physical and biological variables such as temperature, light intensity, prey distribution or predation risk, for example (Bouchet et al., 2014). Bottom temperature, currents and oxygen concentration could have been relevant predictors of toothfish distribution but these variables are usually derived from hydrodynamic models that are forced by bottom topography and difficult to validate with '*in situ*' data at such a large spatial scale. Moreover, dynamic oceanographic variables such as temperature and currents are less dynamic in deep waters (1000–2000 m) than at the surface and often highly correlated with latitude and depth.

The non-linear relationship between toothfish total length and bottom topography could be investigated at a finer scale using other metrics of terrain complexity such as sea-floor rugosity, curvature or aspect (Bouchet et al., 2014), but the spatial resolution of both the global terrain model (GEBCO 2014) and haul data over the Kerguelen Plateau is insufficient at the moment. Dedicated experiments with depth recorders set along longlines and systematic records of depth and fish total length along the lines could allow a finer quantification of the depth-length relationship. Further investigations will be required to understand the underlying physical and/or biological processes for these spatial patterns and the residual effects present in our models.

4.4. Implications for fishery management

In the context of a multi-jurisdictional fishery, our results have important implications for current and future management of Patagonian toothfish across the Kerguelen Plateau. Large-scale prediction maps describing population structure allowed us to quantify suitable area of different life-stages and sex that contribute differentially to the dynamics of the population. For example, comparison of suitable habitat shows that 67% of the juvenile shallow habitat was located in the French EEZ, whereas suitable adult habitat was comparable between the two countries. The large area suitable to juvenile toothfish ($145,600 \text{ km}^2$) and high level of primary productivity of the Kerguelen Plateau are likely to explain the high productivity of this region that supports the highest biomasses of adult Patagonian toothfish worldwide.

Since the ability for population renewal is directly linked to successful reproduction, survival of juvenile and immature fish is essential. Our spatial models indicate that the habitat of juvenile Patagonian toothfish <60 cm on the Kerguelen Plateau has a high level of protection, thanks to the fishing ban in waters <500 m in the French EEZ and MPAs in the Australian EEZ that cover over 50% of shallow waters (Fig. 1). These management arrangements are in place in addition to decision rules used to set the annual catch limit. These decision rules are consistent with the precautionary CCAMLR harvest strategy specifying a 50% target and 20% escapement level from the pre-exploited spawning stock biomass (Constable and Welsford, 2011; Constable et al., 2000).

The male-biased sex ratio on the north-west and female-biased sex ratio in the Australian EEZ raises questions about toothfish spawning behaviour and underlying causes of sexual segregation Welsford et al. (2012) showed that toothfish spawning activity concentrates between 1700 and 1900 m, where longline fishing effort is low. However, defining the depth range of spawning activity requires further investigation, particularly in the French EEZ. The risk of over-exploitation by fishing in large spawning aggregations seems to be reduced because there is no evidence of spawning aggregation in Patagonian toothfish with spawning occurring over a very large area along the western slopes of the Plateau (Welsford et al., 2012).

Traps strongly selected very large females in the Australian EEZ. The cause of this is unclear, however trap effort was very low and this gear type is no longer in use. Whether fecundity increases with female size in toothfish remains unknown, however, it is the case in most fish species, and reaching old age is usually a sign of overall individual fitness (Froese, 2004). 'Mega-spawners' could be reservoirs and distributors of desirable genes (Froese, 2004), in which case our modelling approach could be used to inform management options in areas where large mature females are predicted to concentrate (very deep areas in the south and on the eastern steep slopes). Hydrodynamic modelling of eggs and larvae transport could also provide key insights on the spatial distribution of the optimal spawning grounds, i.e. locations and depth ensuring transport to suitable juvenile habitat (Mori, 2013).

The prediction maps derived from our GAM models indicates some level of stock connectivity between Patagonian toothfish in the French and Australian EEZs. The lack of juvenile toothfish <20 cm observed in the Australian EEZ (Welsford et al., 2011) suggests that a proportion of the young settlers of the French EEZ move south into the Australian EEZ by the time they are 2–3 years old where they begin to be observed in research trawls. However, spawning grounds have also been found in the western parts of both EEZs (Lord et al., 2006; Welsford et al., 2012) and hydrodynamic modelling predicts that eggs and larvae could be transported and retained in the shelf areas of both EEZs (Mori, 2013). The lack of these small fish in the Australian EEZ could have therefore arisen from sampling artefact, caused by differences in timing and gear selectivity between the French and Australian research surveys.

A dedicated tagging program in deep waters >1600 m could shed light on the behaviour of large and old fish at the deepest range of the fishing area. There is an ongoing debate about movement of large adult toothfish and whether these fish become inaccessible to the fishery by moving deeper than the fishery currently operates. Our model predicted large individuals present in depths from 1600 m to 2300 m, but insufficient data were available for waters deeper than 2300 m to confirm if larger fish continue moving deeper. The use of pop-up archival tags recording depths (Carvalho et al., 2015) and research fishing targeting deeper waters could help answering this question. A concerted effort to survey beyond the range of predictions of our model would be an essential step to better assess the lower limit of toothfish habitat.

Finally, current toothfish stock assessments on the Kerguelen plateau are not sex-based and spatial heterogeneity is approximated by the use of sub-fisheries based on gear selectivity and depth bins. Our results confirmed the need for a sex-specific stock assessment model in both fisheries to assure that neither sex is unduly impacted while the stock remains above the overall conservation target. In a second step, it will be important to account for the spatial structure of the population, ontogenetic movements and migrations to minimise the risk of over-exploitation of the fish stock (Benson et al., 2015; Maunder and Punt, 2013; Punt et al., 2015). Typically, fish populations are modelled using a single region where spatial heterogeneity in populations are approximated by partitioning the data into different fleets or sub-fisheries including gear selectivity and depth range for example (Hurtado-Ferro et al., 2014; Sinègre and Duhamel, 2015; Waterhouse et al., 2014; Ziegler and Welsford, 2015). This approximation is made because data are usually insufficient to quantify the spatial structure of the fish population (Maunder and Punt, 2013). Our results illustrate the complex drivers of fish spatial distribution and the importance of considering ontogenetic habitat change and geographic components. Prediction maps from GAM models can be used to identify spatial boundaries of stock components (Goethel et al., 2011; Hulson et al., 2013) and the TL-depth relationship provides crucial information on the ontogenetic migration rate, particularly for the youngest age classes, that migrate to deep waters at a rate of ~100 m per year, given that they grow about 5 cm per year in the first 5 years of their life (Ziegler and Welsford, 2015). These age-specific and potentially sex-specific movement rates will have to be confirmed and/or refined using tagging data before their incorporation into a spatially-explicit stock assessment (Welsford and Ziegler, 2013; Ziegler, 2013).

4.5. Implication for ecosystem-based management

Ecologically sustainable management of a fishery requires an understanding of the distribution and ecology of the exploited species throughout the life cycle and interactions with other species in the ecosystem. This principle underpins CCAMLR's ecosystem approach to fisheries management (Constable et al., 2000). Being the most abundant fish species in term of biomass and occupying all depths, Patagonian toothfish plays a key ecological role in the Kerguelen Plateau ecosystem. In shallow water, reported predators of toothfish juveniles include penguins, fur seals and elephant seals (references in Collins et al., 2010) but with increased size and habitat depth, the range of potential predators declines (sharks, sperm whales, elephant seals, giant squids, Collins et al., 2010; Duhamel et al., 2005). As predators and scavengers, adult toothfish are also likely to play a key role on benthic communities and mesopelagic organisms in the deep sea (Yau et al., 2002). Spatially-explicit models developed at the scale of the Kerguelen Plateau in this study could thus be used to calibrate ecosystem models (Murphy et al., 2012).

5. Conclusion

Thanks to its primary productivity and extended shelf and banks habitats suitable to juvenile fish, the Kerguelen Plateau supports the largest population of Patagonian toothfish of the Southern Ocean. We contend that a description of the ecology of the early life history stages, up to 2–3 years old, and the dynamics of spawning stand out as the priority for future research into the biology of Patagonian toothfish in this region. Our models revealed strong spatial patterns in the distribution of toothfish by length and sex. Both topographic features and geographic locations were good predictors of the length and sex composition but further investigations are required to understand the underlying physical and/or biological processes for these spatial patterns. It is still

unclear whether seasonal horizontal and/or vertical movements linked to spawning behaviour occur across the Kerguelen Plateau because our models revealed very few seasonal variations in population structure. Combining the tagging datasets of the two EEZs could help understanding movement patterns to quantify the cumulative fishing mortality of cohorts that may be vulnerable to both the French and Australian fisheries during their lifetime. As the Australian longline fishery is expected to expand into previously unfishered areas, the model predictions of suitable habitat will be refined in the future. Research surveys targeting specific size classes, sex, areas or season based on our prediction maps could also improve our models predictions in the future and shed light on mechanisms underlying these segregations. Insights gained from these spatial models are important for defining the suitable habitat of the fish targeted by the fishery and refine spatial management across the Kerguelen Plateau.

Author contributions

CP: did data formatting and spatial analyses, wrote the article.

DW: project leader and manager, Australian database holder, designed the study, and contributed to data analysis and article writing.

PZ: contributed to data formatting, discussions on data analysis, commented on the draft manuscript.

TL, CC and RS: database management and data quality checking.

NG: database management, discussions on data analysis, commented on the draft manuscript.

GD: French database holder, discussions on data analysis, commented on the draft manuscript.

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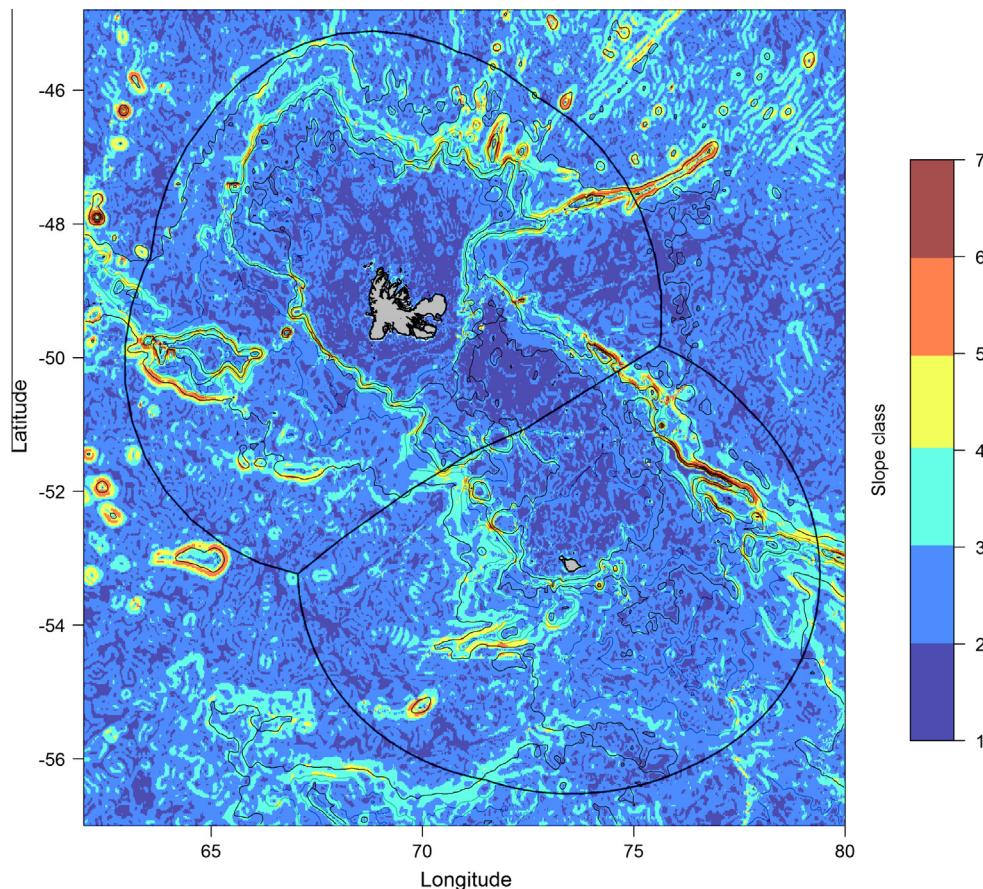
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Appendix A

Categories	Slope range in degrees	Class
1	0–0.5	Flat
2	0.5–2	Very gentle
3	2–5	Gentle
4	5–9	Moderate
5	9–16	Strong
6	>16	Very strong

Map of the slope categories described in the table.



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