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Distribution and abundance of skates (*Bathyraja* spp.) on the Kerguelen Plateau through the lens of the toothfish fisheries

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ABSTRACT

Three species of skate, *Bathyraja eatonii*, *B. irrasa* and *B. murrayi*, are commonly taken as incidental by-catch in Patagonian toothfish (*Dissostichus eleginoides*) longline and trawl fisheries, and the mackerel icefish (*Champsocephalus gunnari*) trawl fishery on the Kerguelen Plateau (KP) in the southern Indian Ocean. Data from fishery observations for 1997–2014 shows that the three skates were widely distributed across the Kerguelen Plateau, showing different spatial distributions, linked mainly with depth. Off Heard Island and McDonald Islands (HIMI), in the southern part of the KP, *B. eatonii* and *B. irrasa* were most abundant to the north and northwest of Heard Island, out to the edge of the Australian Exclusive Economic Zone (EEZ), and were caught down to depths of 1790 m and 2059 m respectively. The smallest species, *B. murrayi*, occurred mainly in the shallower waters down to 550 m, and was most abundant to the north and northeast, close to Heard Island. Around Kerguelen Islands, in the northern part of the KP, skates were most abundant between the 500 m and 1000 m contours circling and extending from the islands.

Catch rates were modelled using zero-inflated GAMs and GLMs. The catch rates of skates from the trawl fisheries in the Australian EEZ surrounding Heard Island and McDonald Islands have shown little evidence of depletion on the main trawl fishing grounds, although there is evidence of a decrease in the average total length of *B. eatonii*. The marine reserves and the conservation measures employed by the Commission for the Conservation of Antarctic Marine Living Resources in the HIMI fisheries, appear to provide effective protection for the skates, at least in the shallower waters where the trawl fisheries operate. *B. irrasa* taken in the deeper waters where longline fishing occurs have shown a slight decline in catch rate over the years of the HIMI fishery. Although all skates are returned to the water from this fishery, survival rates are unknown and careful monitoring should continue to assess the status of these stocks. There appears to be little change in the abundance of the skate species at Kerguelen in the time period.

This study provides the first review of skate by-catch across both the HIMI and Kerguelen fisheries. Ongoing monitoring of species specific by-catch levels and further research to determine the important life history parameters of these species are required, particularly for *B. irrasa* which is taken in both trawl and longline fisheries.

1. Introduction

The Kerguelen Plateau (KP) is the largest peri-insular plateau in the Southern Ocean and is located in the Indian Ocean Sector. A longline fishery for Patagonian toothfish, *Dissostichus eleginoides*, operates in the northern part of the Kerguelen Plateau, in the French Exclusive Economic Zone (EEZ) around Kerguelen Island. In the southern part, trawl fisheries target both toothfish and mackerel icefish, *Champsocephalus gunnari*, and a longline fishery targets toothfish, operating in the Australian EEZ surrounding Heard Island and McDonald Islands (HIMI). In addition to the target species, incidental by-catch of skates, sharks, other finfish and invertebrates are taken. Skates (Rajiformes) are the most abundant by-catch in these fisheries at HIMI and second most abundant at Kerguelen

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(grenadiers, *Macrourus* spp., are first), and are caught across the KP area. Three species of skates are caught, *Bathyraja eatonii*, *B. irrasa* and *B. murrayi,* which are distributed mostly on the KP, but with occasional reported occurrences in other areas of the Southern Ocean.

A demersal gear fishery has occurred on the KP since the 1970's targeting four main species, endemic to the Southern Ocean: mackerel icefish, Patagonian toothfish, marbled notothen (*Notothenia rossii*) and grey notothen (*Lepidonotothen squamifrons)* (Duhamel and Williams, 2011). The fishery for Patagonian toothfish in the high seas off the Kerguelen Islands began in 1984/85 when it was exploited by former USSR trawlers (Lord et al., 2006). Longlining commenced in 1990/91, and by 2001/02 became the only fishing method, with annual catches of about 5000 t of toothfish since 1993/94 (Lord et al., 2006; Duhamel et al., 2011). Soon after the declaration of the French EEZ in 1979, an observer program was established to record biological measurements of the target and by-catch species in this fishery, with 100% observer coverage (Duhamel et al., 2011; Gasco, 2011). As of 2014, there were seven vessels fishing in the EEZ. The fishery is managed by Terres Australes et Antarctiques Françaises. Fishing is prohibited in waters shallower than 500 m and generally occurs at depths between 500 and 2000 m (Gasco, 2011).

The Australian offshore fishery around HIMI began as a trawl fishery with one vessel in 1997. It was joined by a longlining vessel in 2003, and a second longliner entered the fishery in 2008. In 2013 and 2014 the number of vessels in the longline fishery had risen to three. There has been 100% observer coverage with two observers on all trips since the commencement of the fishery, enabling the collection of a comprehensive time series of data on the catch and biological observations. The fishery is managed by the Australian Fisheries Management Authority (AFMA) under the precautionary principles of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). This includes measures to ensure that the spawning stock of fished species are maintained at a level which ensures stable recruitment, and that the size of the stocks do not fall to levels which compromise the ecological relationships in the food web. This is achieved through conservation measures and an annual catch quota on toothfish and by-catch species, based on stock assessments.

Of the three species of skate most commonly taken as by-catch in these fisheries, the most frequently caught species in the trawl fisheries at HIMI is *B. eatonii,* which can grow to over 120 cm total length (TL) and inhabit depths to 1100 m (Duhamel et al., 2005). *B. irrasa* can grow to 139 cm TL and is found at depths of 300–1700 m (Duhamel et al., 2005). *B. irrasa* is the most commonly caught species in the longline fisheries across the Kerguelen Plateau. *B. murrayi* is the smallest of the three species and can grow to 70 cm TL. It is found at 30 to 650m, but is more common at shallower depths (Duhamel et al., 2005).

Skates are known to be long-lived, late-maturing and with relatively low fecundity, making them susceptible to over-exploitation, even when taken as by-catch (Stevens et al., 2000; Dulvy et al., 2000). Tagging experiments by Australian scientists have shown that the skates at HIMI generally did not move very far, and were recaptured on average only 4 M (7.5 km) from their release point, even though the majority had been at liberty for several years (Nowara et al., 2013). This is another characteristic which can make them vulnerable to localised depletion. Few studies have looked at survival rates of skates in fisheries where skates are not targeted but are returned to the water after being incidentally caught (Endicott and Agnew, 2004; Laptikhovsky, 2004).

Preliminary stock assessments of by-catch species at HIMI used a Generalised Yield Model to calculate a sustainable catch limit for *Bathyraja* spp. of 50–210 t (Constable et al., 1998). This work led to CCAMLR setting an annual catch limit of 120 t for the HIMI fishery (SC-CAMLR, 1997). A limit on the catch of skates has been in place since the commencement of an Australian fishery, with the current catch limit not to exceed 120 t in any one season (1 December to 30 November in the next year) (CCAMLR, 2014a; Conservation measure 33-02). A 'move on' rule also applies, so that if skate by-catch in any one haul exceeds 2 t then the vessel must not use that method of fishing within 5 M of the area for 5 days (CCAMLR, 2014a; Conservation measure 33-02). The Kerguelen fishery also has a move on rule based on observer monitoring. If the catch rate of skates is greater than 50 per 1000 hooks, the captain must set the next line at least 2 nautical miles from the previous haul.

The aim of this study was to look at the occurrence of skates across the Kerguelen Plateau to describe the abundance, distribution, and depth pattern of the three species. The changes in abundance over time were examined in order to evaluate the impact that fisheries were having on the skate populations on the Kerguelen Plateau.

2. Methods

2.1. On-board data collection

At HIMI, geographical coordinates, time of setting and hauling, effort, and the duration of the trawl net tow or longline set were recorded for each haul. Catch numbers for the entire haul and biological measurements of a sub-sample of the toothfish, icefish and by-catch were taken. Skates in the trawl fisheries were identified to species and measured (total length and wing span) when they came aboard in the net and a biological sub-sample was weighed, sexed and assigned a gonad stage.

In the HIMI longline fishery, the counting and identification of skates involved two separate processes because most skates were cut off the line and returned to the water, either before they come over the side or shortly after, to maximise their chance of survival. Random biological sampling of up to ten skates occurred for each haul (Supplementary material S1.1). Skates taken for biological samples were always identified to species. Secondly, observations for 40% of each line during hauling recorded catch (numbers) by species or taxon grouping. Skates were identified to species level where possible, but sometimes only to genus level (*Bathyraja* sp.) or order level (Rajiformes).

In addition, similar data to those collected in the trawl fisheries were collected during an annual trawl survey, the Random Stratified Trawl Survey (RSTS), which is a biological survey to examine the abundance of toothfish, icefish and by-catch species in HIMI waters down to 1000 m. Approximately 150 hauls are carried out across the plateau and have been conducted in each year since the commencement of the Australian fishery in 1997.

The trawl net used in both the commercial toothfish fishing and during the RSTS at HIMI has remained consistent throughout the duration of the trawl fishery. A Champion 4-panel bottom trawl with a headline height of 38.5 m and a mesh size of 152 mm (Nowara et al., 2006) was used for 95% of the hauls. The same Champion net with a small mesh cod end liner (50–60 mm mesh size) was used during all RSTS survey hauls (Nowara et al., 2006). In the longline fishery at HIMI, auto longline gear with an integrated weight line was standard for the duration of the fishery, except for the first three trips where there was a mixture of integrated weight line and externally weighted line.

All vessels in the Kerguelen longline fishery have operated using a standardised integrated weight auto longline since observers began collecting reliable data on skate by-catch in 2008. Prior to December 2014, most skates caught were kept and retained, though some were cut off the line and did not come on board, or were later discarded. From the 2014/15 CCAMLR year (1 December 2014–30

November 2015), skates (except those kept for biological sampling) have been cut off and returned to the sea. Observers identified skates while observing 25% of the hooks hauled for each line. Similar data to those taken at HIMI on location, timing and biological measurements were collected.

In addition biomass surveys named POissons de KERguelen (POKER) cruises were conducted in 2006 (POKER 1), 2011 (POKER 2) and 2013 (POKER 3) in the bathymetric range 100–1000 m off the Kerguelen Islands, sampling 200 bottom trawl stations (shelf, slope, surrounding banks). The trawl net used during the POKER surveys was a 35/39 bottom trawl with a large vertical opening with a head rope length of 35 m and a ground rope length of 39 m (Ets Le Drezen ref: G2035013). A codend liner with mesh size of 40 mm was used for POKER 1 and 2; POKER 3 used a 90 mm codend liner. By-catch of skates were analysed during these surveys (Duhamel and Hautecoeur, 2009; Duhamel et al., 2014).

2.2. Data coverage

Data were available for the duration of the HIMI fisheries for all methods, toothfish trawling, icefish trawling and longlining. Data from the toothfish and icefish trawl fisheries at HIMI covered the years from the start of the fishery in 1997–2014. Longline fishing data from HIMI are presented from commencement in 2003–2014. Data from the RSTS ranged over the years of the fishery (1997–2014). French data from the Kerguelen fishery were available for 2008–2014 (Martin and Pruvost, 2007), but not from the commencement of the fishery, as earlier data for skates were considered to be unreliable.

Annual data were grouped on the basis of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) fishing year (season) which runs from 1 December in one year to 30 November in the next year, with the label consisting of the second year.

2.3. CPUE calculation

2.3.1. HIMI fishery data breakdown

At HIMI, trawl data and longline data were collected differently and therefore required different processing to calculate a catch per unit effort (CPUE). The trawl data were divided into those shots targeting toothfish, those targeting icefish and the annual RSTS. Trawl data were recorded for the entire catch, mostly to species level, and the CPUE was calculated per swept area in square kilometres (km^2). Hauls where skates were not identified to species (4% of records, mostly from 1997 and 1998) were excluded from the analysis. Although trawl data were generally recorded on a haul by haul basis, by-catch of skates was sometimes unable to be processed before the next haul came on board and skates from several hauls were stored together before being processed. These records were identified and pooled together (see Supplementary methods S1.2.1).

Longline data required distribution of counted numbers of skates to species level. The species specific skate catch for each haul was estimated using the proportion of each species in the biological sample to allocate the observer counts of 40% of the line to species. For hauls where there were less than ten individuals in the biological sample, the species composition was based on that of the nearby hauls in the same year, using the method described in the Supplementary methods (S1.2.2). Although the biological sub-sample was smaller than the counted catches, identification was considered to be more accurate because distinguishing between the species when seen only briefly during line observations is challenging, but straightforward when they have been landed. For the longline data catch numbers related to the percentage of line observed and were presented in numbers per 1000 hooks ($n\,kh^{-1}$).

2.3.2. Kerguelen longline

Skate counts from the Kerguelen longline fishery were based on the numbers of each species in the line haul observations (25% of each line) made by observers. CPUE data were calculated from counts by species divided by the number of hooks, and were recorded in the same units as the HIMI data ($n\,kh^{-1}$). An estimate of the fate of all skates caught was available for the years 2008–2010. In those years, 75% of skates were processed on board, 22% were brought on board but not processed, and 3% were cut-off and returned to the water.

2.4. Spatial distribution

The HIMI trawl CPUE data for each haul (1997–2014) were interpolated using Spatial Analyst in ArcMAP for each of the three species caught by toothfish trawl combined with the RSTS hauls, with an inverse distance weighted model with an interpolation distance of 0.1°.

The HIMI longline data (2003–2014) and the French Kerguelen longline data (2008–2014) were combined in spatial plots showing interpolated CPUE (numbers per 1000 hooks), using the same method as for trawl data, for the two main species.

2.5. Biomass estimates

Data from the annual RSTS were used to provide an estimate of biomass (numbers and tonnes) of the three species of skates at HIMI. The numbers and weights of the skates in the survey hauls were scaled to the area of the strata to provide estimates of numbers and biomass across the survey area. Uncertainty was estimated using a stratified non-parametric bootstrap (resampling the data; Efron and Tibshirani, 1994), with 10,000 iterations. The same method was used to estimate biomass in Kerguelen waters from three French fishery independent (POKER) surveys.

2.6. Temporal modelling of CPUE

Skate data for each of the three species from the toothfish and icefish commercial trawl fisheries, and the longline data from the entire HIMI area and separately for the Kerguelen fishery, were modelled and examined for the trend in relative abundance over the duration of the fisheries (see Section 2.2). For each species with each fishery the catch (numbers) per haul was standardised to account for the effects of the covariates CCAMLR fishing year (CCYear), month, depth, latitude and longitude, vessel and log transformed catch of target species (icefish or toothfish) using the following process. Firstly a Generalised Additive Model (GAM) containing a bivariate smooth of fishing location (latitude and longitude) was fitted using the R package mgcv (Wood, 2006) to determine whether smoothing of fishing locations was appropriate. In cases where the initial GAM failed to adequately represent the spatial aspects of the fishery, fishing locations were separated into strata and trends in relative abundance were evaluated using Generalised Linear Models (GLM; McCullagh and Nelder, 1989) fitted with R (R Core Team, 2014; Venables and Ripley, 2002; Zeileis et al., 2008).

Both the GAMs and the GLMs assumed skate counts were either Poisson or Negative Binomially distributed with a log-link function with Negative Binomial models used when there was over-dispersion in the skate counts (Hilbe, 2011). To account for variability in fishing effort, the log of the swept area for trawl or log of the number of hooks was included as an offset for the trawl and longline fisheries respectively. The combination of using catch numbers, log-link and this offset was equivalent to modelling the expected value of CPUE conditional on effort (Maunder and Punt, 2004; McCullagh and Nelder, 1989; Wood, 2006).

Where there was a high percentage of zero hauls (>45%), the zero catch hauls were accounted for using a zero-inflated modelling approach (Zeileis et al., 2008) where the additional zero component was represented by a binary model (either GAM or GLM) with a logistic link. Zero-inflated GAMs from mgcv were fitted using the EM algorithm to iterate between maximising the binary and count models (Minami et al., 2007) (https://github.com/AustralianAntarcticDataCentre/zipgam). As Wald based confidence intervals from the EM algorithm based fitting procedure are unreliable, uncertainty was estimated using a parametric bootstrap (resampling the residuals; Efron and Tibshirani, 1994) with 900 iterations. Zero-inflated GLMs were fitted using the R package pscl (Zeileis et al., 2008) with uncertainty estimated using a non-parametric bootstrap with 10,000 iterations. For ease of interpretation we have presented the confidence intervals of the optimal model only.

For each gear/species combination a stepwise model selection procedure was applied to select the optimal model. Terms were either added sequentially to the null model (CCAMLR fishing year only) or subtracted from the saturated model until the Akaike Information Criteria (AIC; Burnham and Anderson, 2002) was minimised. When multiple models were within 2 AIC units of one another, they were all considered optimal. Additional information on the details of each analysis is provided in the Supplementary methods, S1.3.

2.7. Temporal modelling of total length

Data from biological sampling at HIMI were analysed for trends in total length over time. A Gaussian GAM with an identity link function was fitted to the total lengths of each species for the two gears, trawling and longlining. The explanatory variables included in the model were CCAMLR year, depth, latitude and longitude.

Kernel density estimates of length distributions were plotted in representative years against the length at maturity.

2.8. Length at maturity

Biological data were used to estimate the length at maturity for females and males of each of the three skate species using a binomial GLM (logistic regression). The maturity assessment was based on external examination of males and internal macroscopic examination of the gonads for females. The maturity scale recommended for CCAMLR fisheries was used (CCAMLR, 2011), a three point scale (1- immature; 2- maturing; 3- mature).

2.9. Growth

A linear regression model was fitted to the change in length over time for skates from the HIMI tag return data to estimate the annual growth rate. Sufficient data (from skates that had been at liberty for at least 62 days) were available for only one species, *B. eatonii.*

3. Results

3.1. Fishing effort

At HIMI, the commercial toothfish trawl fishery had an average of 751 hauls per year, while the icefish trawl fishery averaged 91 hauls per year (Table 1). For longline, the average annual number of hauls at HIMI was 442, nearly one-sixth of the average for Kerguelen (2613 per year). In the trawl fisheries the mean and the range of depths for fishing was shallower for the icefish trawl than for toothfish trawl, while longline fisheries occurred at much deeper depths (Table 1). A comparison of fishing effort (% hooks) by depth in the longline fisheries at HIMI and Kerguelen (Fig. 1) shows that in both fisheries a large proportion of the effort (49 and 62% respectively) was in the 900–1500 m depth range. At HIMI almost all the remainder (33%) occurred between 1500 and 2000 m. Proportionally more fishing occurred in shallower depths (500–900 m) at Kerguelen than at HIMI, but a substantial amount (18%) occurred from 1500 m down to 1700 m at Kerguelen.

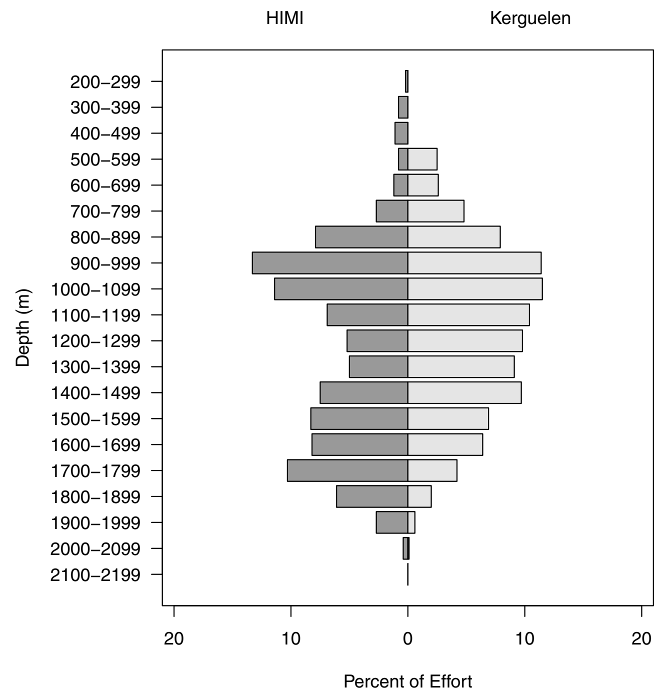

Fig. 1. Percent effort (hooks) by depth in the HIMI (2003–2014) and Kerguelen (2008–2014) longline fisheries.

3.2. Species compositions and bathymetric ranges

3.2.1. Proportions of each species by method

The toothfish trawl fishery at HIMI caught high percentages (by number) of *B. eatonii* (45%) and *B. murrayi (*50%), and a small percentage of *B. irrasa* (Table 1). In contrast, the icefish trawl fishery took predominately *B. eatonii* (84%), and smaller proportions of *B. murrayi* and *B. irrasa* (Table 1).

In the HIMI longline fishery, of those skates identified to species level from the catch sampling, 89% (by number) were *B. irrasa* and 11% were *B. eatonii* (Table 1). Few *B. murrayi* (<1%) were reported. In the Kerguelen longline fishery, 62% of the skates landed (by number) in the seven years from 2008 to 2014 were *B. irrasa*, and the remaining 38% were *B. eatonii*. An average of only 58 individuals of *B. murrayi* were reported in the catches per year (Table 1). The trawl fisheries caught numbers up to in the thousands of each species annually, with many more (around 65,000) *B. irrasa* taken annually in the longline fisheries.

3.2.2. Mean numbers and weights

The average estimated number of each species (excluding zero hauls) taken per haul is presented in Fig. 2. *B. eatonii* were taken in greatest numbers per haul in the icefish trawl and the Kerguelen longline fisheries. B. *irrasa* were taken in greatest numbers per haul in the longline fisheries. The estimated numbers of *B. murrayi* taken per haul when not zero was generally similar for trawls at HIMI, but few were taken in the longline fisheries (Fig. 2).

Table 1
Mean and range of yearly effort (number of hauls), mean and range (5% & 95% quantiles) of depth of fishing for the trawl and longline fisheries at HIMI and for the Kerguelen longline fishery, and mean annual estimated by-catch of skates (numbers) and percentage (by number) of each skate species in the by-catch for the trawl and longline fisheries (including those returned to the sea) at HIMI and Kerguelen.

	HIMI icefish trawl	HIMI toothfish trawl	HIMI longline	Kerguelen longline
Period of study	1997–2014	1997–2014	2003–2014	2008–2014
Mean annual no. hauls (range)	91 (0–280)	751 (46–1467)	442 (94–463)	2613 (2060–3007)
Mean depth (m) of fishing	271	571	1248	1195
Range of depth of fishing (m) 5%–95% quantiles	214–384	450–744	534–1849	617–1744
Period of study	2000–2014	1999–2014	2003–2014	2008–2014
Bathyraja eatonii Mean annual catch – no. (Percent)	3283 (84)	1396 (45)	1406 (11)	33,260 (38)
Bathyraja irrasa Mean annual catch – no. (Percent)	74 (2)	158 (5)	10,982 (89)	54,089 (62)
Bathyraja murrayi Mean annual catch – no. (Percent)	556 (14)	1529 (50)	15 (<1)	58 (<1)

Table 2
Mean individual weight (kg) and sample size of skates caught by each fishing method at HIMI from biological measurements.

Species	Icefish trawl			Toothfish trawl			Longline		
	n	Mean	se	n	Mean	se	n	Mean	se
Bathyraja eatonii	9907	2.48	0.022	18037	3.87	0.02	3420	6.21	0.05
Bathyraja irrasa	904	3.39	0.136	2836	7.56	0.103	24677	8.52	0.022
Bathyraja murrayi	2419	0.46	0.005	17587	0.43	0.002	55	0.58	0.016

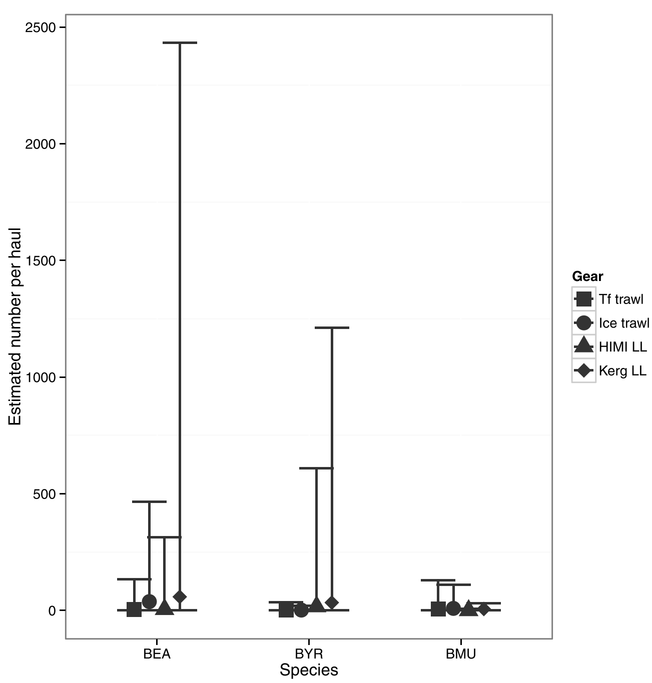

Fig. 2. Mean, minimum and maximum numbers of skates caught per haul (excluding zero hauls) by species and fishing method at HIMI, and in the Kerguelen longline fishery. Numbers for HIMI and Kerguelen longline are estimated. BEA = *B. eatonii*, BYR = *B. irrasa* and BMU = *B. murrayi*. Tf trawl = Toothfish trawl (HIMI), Ice trawl = Icefish trawl (HIMI), LL = Longline, Kerg LL = Kerguelen longline.

Mean individual weights of skates were available for each species from the biological sampling at HIMI, from 1997 to 2014 in the trawl fisheries and 2003–2014 in the longline fishery (Table 2). The mean weight of individual *B. eatonii* was greater on longlines than in trawls, but for *B. irrasa* the weights taken by toothfish trawls and longlines were similar, and much smaller ones of this species were taken by the icefish trawl. The *B. murrayi* taken by longlines weighed more on average than those taken by either of the trawls.

3.2.3. Depths of capture

B. eatonii were caught from 270 m to just over 1000 m depth in the trawl fisheries, but also on longlines set at ~1800 m. *B. irrasa* were caught in waters from 150 m to over 1500 m in trawl fisheries, but in recent years have been captured at depths greater than 2000 m on longline gear at both HIMI and at Kerguelen. *B. murrayi* were caught down to ~1400 m in the trawl fishery and even deeper (>1500 m) in the longline fisheries (Fig. 3a). However, the depths for longlines are only indicative as longlines are typically set down a slope and the depth recorded is the mean of the start and finish depth. The exact position of skate catches on the line (and its depth) are not recorded.

3.2.4. Modelled abundance with depth

The RSTS data showed *B. eatonii* was the most abundant species caught in trawls at HIMI in depths of 200 m (40 n km^2) then declining to less than 10 n km^2 from 700 to 1000 m (Fig. 3b). *B. irrasa* peaked in abundance at 400–500 m at 16–20 n km^2, with numbers dropping to around 5 n km^2 in shallower and deeper trawls (Fig. 3b). *B. murrayi* was caught in consistent numbers (19 n km^2) between 200 and 500 m, then decreasing with depth to less than one n km^2 at 1000 m (Fig. 3b).

In the longline fishery at HIMI, *B. irrasa* was caught in abundances between 2 and 3 n kh^{-1} from a depth of 500 m to 1600m, declining subsequently to <1 n kh^{-1} by 2300 m (Fig. 3b). At Kerguelen, *B. irrasa* were caught in highest numbers at similar depths to HIMI (700–1000 m), but at Kerguelen they decreased in abundance with depth much sooner than at HIMI (Fig. 3b). For Kerguelen the numbers were below one n kh^{-1} and have been multiplied by 100 to be visible on the graph.

3.3. Bathyraja eatonii

3.3.1. Spatial distribution and abundance with depth

At HIMI, the skates *B. eatonii* were caught in the toothfish trawl fishery in highest abundance (up to, and sometimes above 50 individuals (n km^{-2})) to the north and northeast of Heard Island, both on the plateau and on the slopes, mainly to a depth of 500 m (Fig. 4). The distributions of skate CPUE in the HIMI and Kerguelen longline fisheries across the Kerguelen Plateau showed mostly

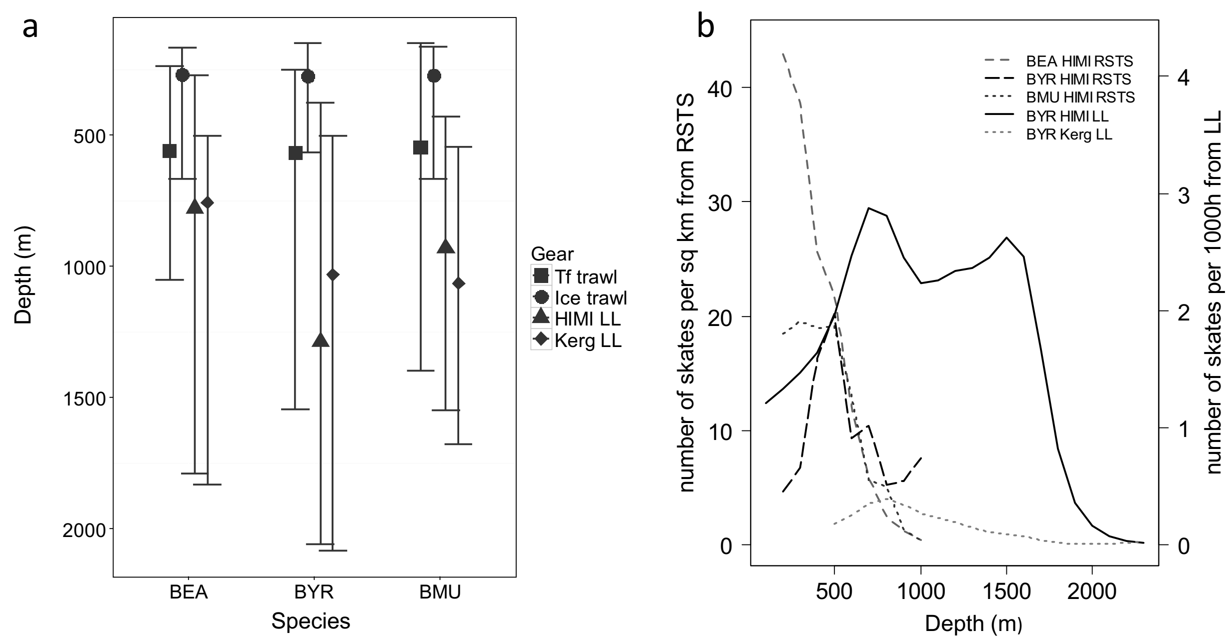

Fig. 3. (a) Mean (weighted), minimum and maximum depths (m) where skates were caught, by species and fishing method at HIMI and in the Kerguelen longline fishery (for legend see Fig. 2) and (b) Skate abundance (mean number) with depth from the RSTS and predicted numbers from the best models for the HIMI longline fishery and Kerguelen longline fishery (numbers ×100).

a low (0–5 n kh^{-1}) abundance for *B. eatonii* throughout most of the areas fished, including around HIMI, but areas of higher abundance (5–30 n kh^{-1}) occured in the east and northeast of Kerguelen Island, with some hot spots of >30 n kh^{-1} in those areas (Fig. 4).

3.3.2. Temporal trends in biomass and abundance

3.3.2.1. Biomass estimates from RSTS and POKER surveys.
AT HIMI, numbers for *B. eatonii* peaked in 2009 at approximately 5 million (M), while remaining at a more constant lower level (approx. 1.5 M) before and after that time, except for an early peak in 1998 (Fig. 5). When the biomass estimates for HIMI were calculated in tonnes, *B. eatonii* had the highest biomass of the three species, peaking in the first few years at nearly 8 thousand tonnes (kt), then remaining at below 3 kt until 2006 where it increased to between 4 and 5 kt since then (Fig. 5). The peaks were associated with much greater uncertainty than the smaller estimates (Supplementary results, Fig. S2.2).

At Kerguelen biomass estimates from three fishery independent surveys (POKER) showed *B. eatonii* were the most abundant in both numbers (6–7 M) and biomass (15–18 kt) (Fig. 5).

3.3.2.2. B. eatonii *abundance from HIMI toothfish trawl.*
The trends in abundance models with the lowest AIC for *B. eatonii* from the toothfish trawl fishery were two Poisson and one Negative Binomial models (Fig. 6, Table 3). For the Poisson models, the full model for both the count and the binary models and one with a polynomial on depth in the count model and without depth in the binary model had AIC's within two units. The optimal Negative Binomial fit was with the full model on both count and binary models with depth as a polynomial on both (Table 3).

The proportion of hauls with zero catch of *B. eatonii* declined from the beginning of the fishery from around 70% to between 40% and 50% from 2007 onwards (not shown). The catch of *B. eatonii* increased gradually to peak at around 4 skates per haul in 2008 for the Poisson models and at 5 for the Negative Binomial model (Fig. 6). All models then show a decrease to around 2 skates per haul in 2014. The overall trend in catch rates is similar to that seen in the un-standardised arithmetic mean.

3.3.2.3. B. eatonii *abundance from HIMI icefish trawl.*
The proportion of hauls in the icefish fishery that had no *B. eatonii* catch declined over time, from around 40% in the years 1997–2003 to less than 5% for the latter years (2007–2014) with the exception of 2009 where it was about 80% (not shown). The two optimal models for catch rates of *B. eatonii* (with AIC's within two units) included CCYear and month with or without depth. They showed a similar pattern over time, with catches of less than 70 per haul except in two high years where the catches were closer to 150 per haul (Fig. 6, Table 3).

3.3.2.4. B. eatonii *abundance from HIMI longline.*
For *B. eatonii* in the longline fishery, the best models for the duration of the fishery 2003–2014 showed catches between 0 and just over 1 n kh^{-1}. Models for 2006–2014 showed catches of less than 0.2 n kh^{-1} until 2011 when they rose to between 0.3 and 0.6 n kh^{-1} for the next two years before falling again. (see Supplementary results S2.3.1, Figs. S2.3 & S2.4).

3.3.2.5. B. eatonii *from Kerguelen longline.*
For *B. eatonii* from the Kerguelen longline fishery, the saturated Poisson model omitting the toothfish catch and the full Negative Binomial model were optimal. There was a small increase in the number of *B. eatonii* n kh^{-1} over the time period (2008–2014; Fig. 6).

3.3.3. Biological information

3.3.3.1. Changes in total length and length at maturity.
For *B. eatonii* from HIMI trawl fisheries there was a significant decline in mean total length from 950 mm to 764 mm between 1998 and 2011, with an increase to 835 mm by 2014 (Fig. 7, Table 4). In the longline fishery at HIMI, although the GAM was significant for *B. eatonii*, the total lengths did not vary a great deal except for the first two years, where a small number of large and small fish respectively, were measured (Fig. 7). The analysis of total length of skates at HIMI took into account the effects of depth and geographic location (latitude and longitude) in each case.

The length at 50% maturity (LM_{50}) for *B. eatonii* showed that females matured at a greater length than males (Table 5). The ker-

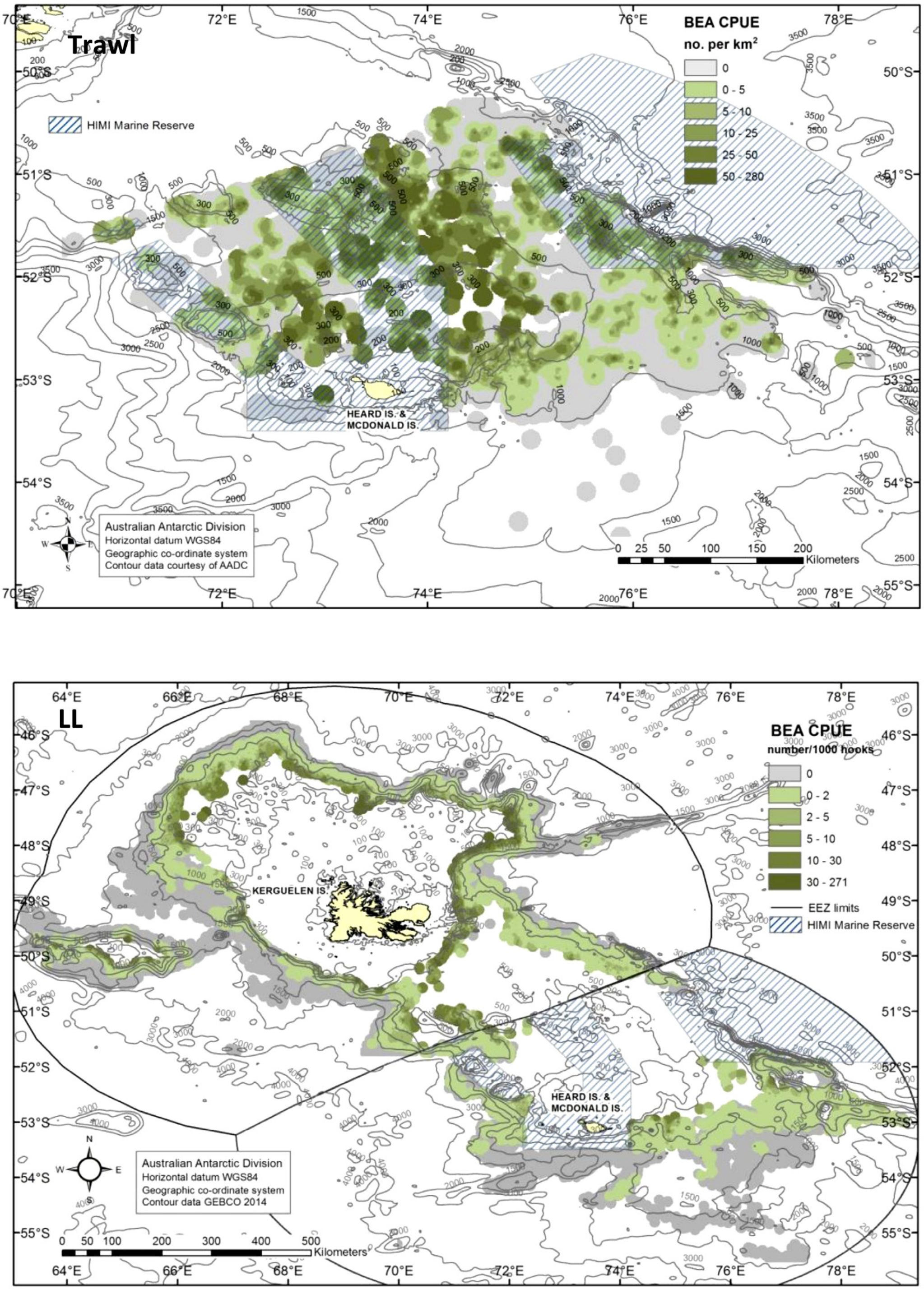

Fig. 4. Distribution and abundance of *B. eatonii* taken in the toothfish trawl fishery and RSTS at HIMI (1997–2014) (Trawl) and in the Kerguelen (2008–2014) and HIMI (2003–2014) toothfish longline fisheries (LL).

nel density plots of total length of skates from selected years with the length at maturity marked showed that *B. eatonii* from the toothfish trawl fishery are taken mostly before they are mature (Fig. 8). *B. eatonii* taken in the longline fishery were larger on average than those taken in the trawl fishery and were mostly mature (Fig. 9).

3.3.3.2. Growth rate.
For *B. eatonii* a significant relationship between growth rate and time at liberty (adjusted $R^2 = 0.66$, intercept = −1.27, slope = 17.14) indicated linear growth was estimated to be ∼20 mm per year for skates 600–1000 mm TL, indicating maximum ages greater than 20 years (Fig. 10).

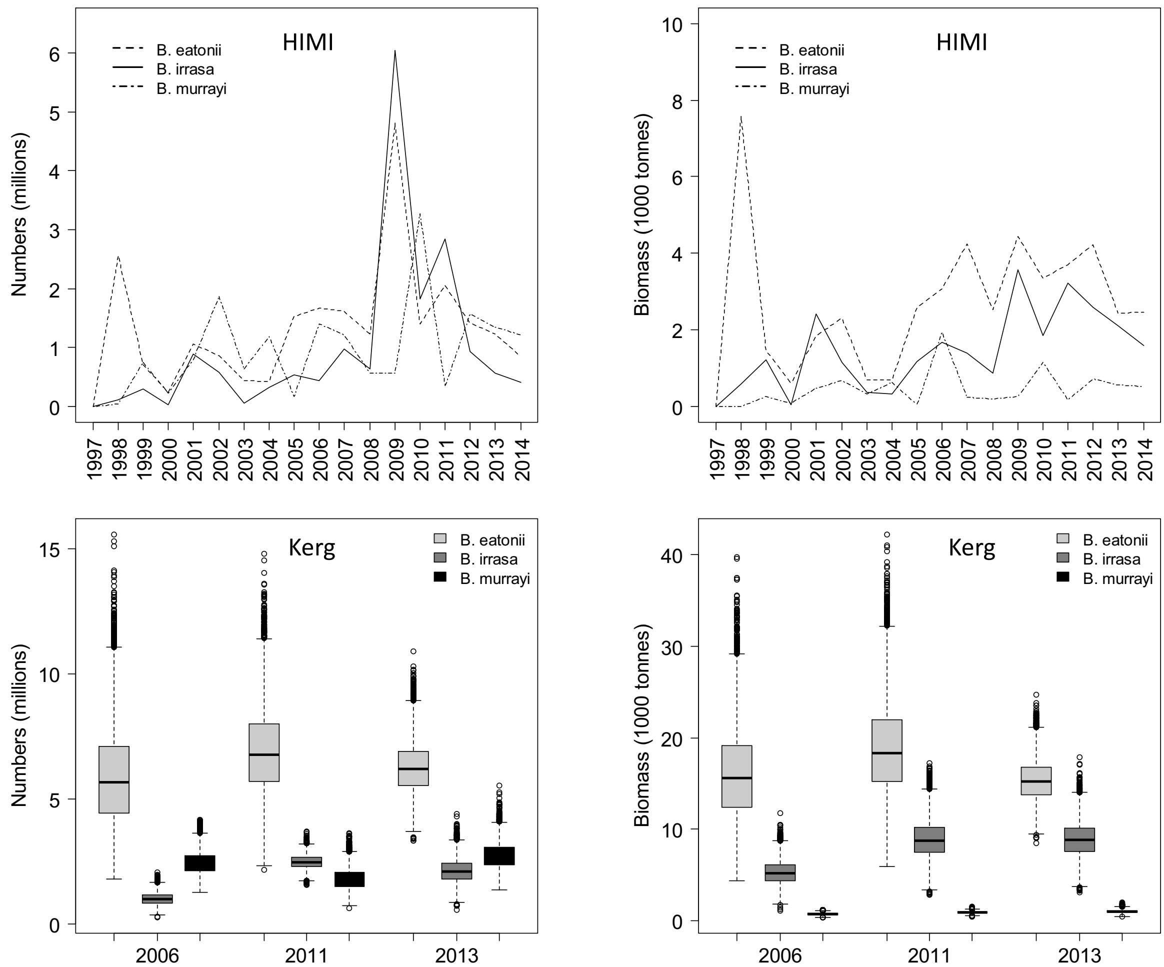

Fig. 5. Estimate of the biomass in numbers (left) and tonnes (right) of the three skates species from the RSTS surveys at HIMI (HIMI) and POKER surveys at Kerguelen (Kerg).

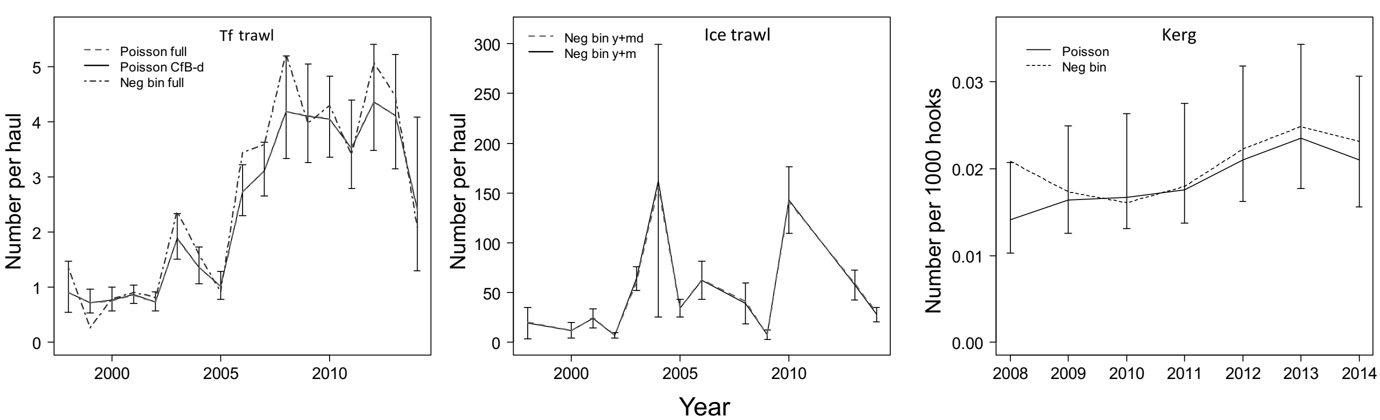

Fig. 6. Catch rate of *B. eatonii* (numbers per haul) from the optimal models for the toothfish trawl fishery at HIMI (Tf trawl), the two optimal negative binomial models for from icefish trawl at HIMI (Ice trawl) and the trend (smoothed) in number of *B. eatonii* per 1000 hooks over years from the optimal poisson and Negative Binomial gam models for the Kerguelen longline fishery, 2008–2014 (Kerg).

3.4. *Bathyraja irrasa*

3.4.1. *Spatial distribution and abundance with depth*

At HIMI, *B. irrasa* catches from trawls indicated an abundance generally of 0–25 n km^{-2} around the shallower plateau except for some hot spots (of over 100 n km^{2}) to the north and northwest of Heard Island at depths between 300–500 m (Fig. 11).

The distribution of skate CPUE in the longline fisheries across the Kerguelen Plateau for *B. irrasa* showed abundances between just above 0 and 10 n kh^{-1} for much of the fished areas, but greater numbers (10–150 n kh^{-1}) occur to the northwest and northeast of Kerguelen Is. and in fishing areas to the east and in an arm extending along the southeast to the edge of the French EEZ. Around HIMI the most abundant areas for this species were to the northwest of Heard

Table 3
Model covariates and AIC's for *B. eatonii* from the toothfish trawl fishery and the icefish trawl fishery at HIMI (Y – yes; N – no).

Model	AIC	Covariates CCYear	Month	Vessel	Strata	Depth	Log (toothfish wt)
Toothfish trawl fishery							
Poisson CfB-d count	53566.47	Y	Y	Y	Y	Y(poly)	Y
Binary		Y	Y	Y	Y	N	Y
Poisson full count	53567.22	Y	Y	Y	Y	Y(poly)	Y
Binary		Y	Y	Y	Y	Y	Y
Neg bin full count	34129.34	Y	Y	Y	Y	Y (poly)	Y
Binary		Y	Y	Y	Y	Y (poly)	Y
Icefish trawl fishery							
Neg bin y + m	10534.8	Y	Y	N	N	N	N
Neg bin y + md	10534.8	Y	Y	N	N	Y	N

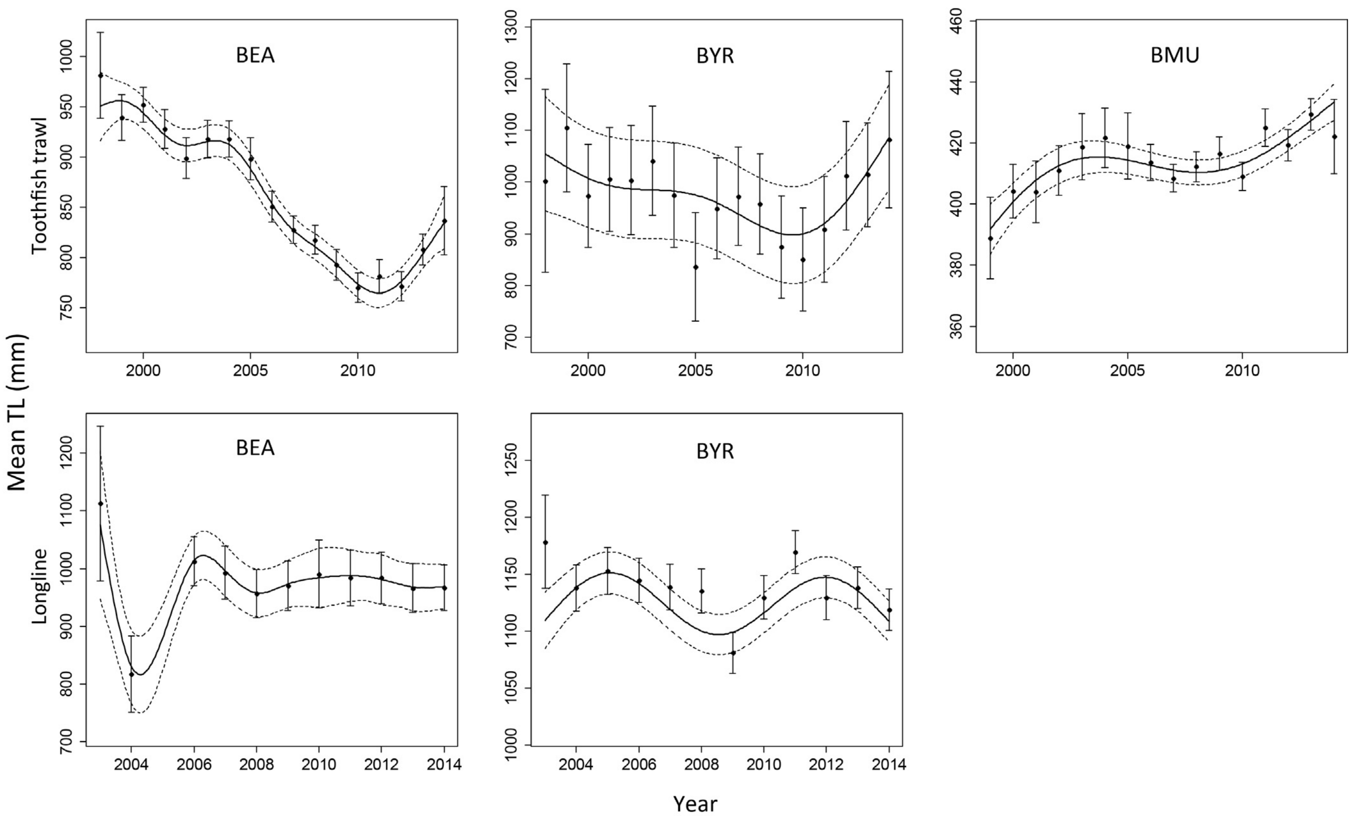

Fig. 7. GAM plots of mean total length (TL) by CCAMLR year for *B.eatonii* (BEA), *B.irrasa* (BYR) and *B. murrayi* (BMU) from the HIMI toothfish trawl fishery (1997–2014) (top) and longline fishery (2003–2014) (bottom). All plots have other variables at fixed values.

Table 4
Results of the GAM analysis for total length of the species of skates taken by longline at HIMI and at Kerguelen.

	Model	Model df	p	Deviance expl	n
Tf trawl					
B. eatonii	TL_mm ~ s(CCYear) + s(Depth) + s(Long, Lat)	46.4	<0.001	18.8	17719
B. irrasa	TL_mm ~ s(CCYear, k = 5) + s(Depth) + s(Long, Lat)	39	<0.001	58.1	2833
B. murrayi	TL_mm ~ s(CCYear, k = 5) + s(Depth) + s(Long, Lat)	41.1	<0.001	5.2	17494
Longline					
B. eatonii	TL_mm ~ s(CCYear) + s(Depth) + s(Long, Lat)	45.5	<0.001	19.1	3399
B. irrasa	TL_mm ~ s(CCYear, k = 5) + s(Depth) + s(Long, Lat)	41.83	<0.001	8	24689

Table 5
Length at 50% maturity (LM_{50}, mm) of the species of skates taken by longline at HIMI. UCL – upper confidence limit, LCL – lower confidence limit.

Species	Female				Male			
	n	LM_{50}	LCL	UCL	n	LM_{50}	LCL	UCL
B. eatonii	1300	1072	952	1226	2433	986	910	1077
B. irrasa	6673	1124	1069	1186	7397	1069	1017	1127
B. murrayi	617	434	389	490	1294	449	369	574

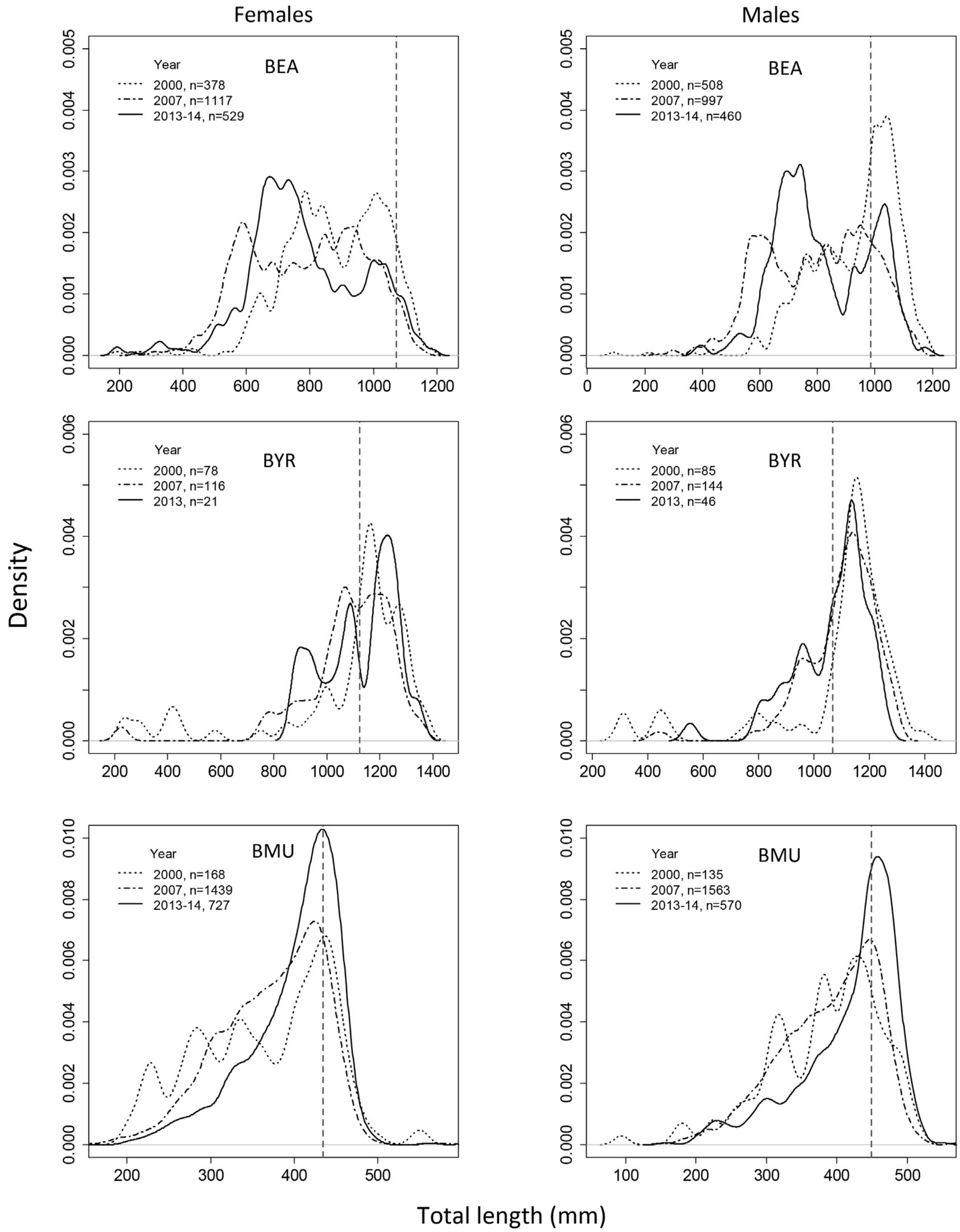

Fig. 8. Kernel densities for length (TL) for *B. eatonii* (BEA), *B. irrasa* (BYR) and *B. murrayi* (BMU) taken by toothfish trawl at HIMI for selected years of the fishery (females on left, males on right). The dashed vertical line indicates the length at maturity (LM_{50}).

Is. near the edge of the EEZ, a couple of patches to the east of Heard Is., and two to the west (Fig. 11).

3.4.2. Temporal trends in biomass and abundance

3.4.2.1. Biomass estimates from RSTS and POKER surveys.

At HIMI, estimated *B. irrasa* numbers were below 1 M each year up until 2009 when numbers rose sharply to approx. 6 M, before dropping to below half of that for the next two years and returning to pre-2009 levels in 2013 and 2014 (Fig. 5). When the biomass estimates for HIMI were calculated in tonnes, biomass of *B. irrasa* had increased in the latter years (2009 onwards) to 3–4 kt from <3 kt. The peaks in each case were associated with much greater uncertainty than the smaller estimates (Supplementary results, Fig. S2.2). At Kerguelen biomass estimates from the POKER surveys showed *B. irrasa* rose to approx. 2.5 M in the two latter surveys, making up a biomass of between 5–10 kt (Fig. 5).

3.4.2.2. B. irrasa *from HIMI longline.*

For the modelled catch rates of *B. irrasa* from the longline fishery, the best fit models for both Poisson and Negative Binomial

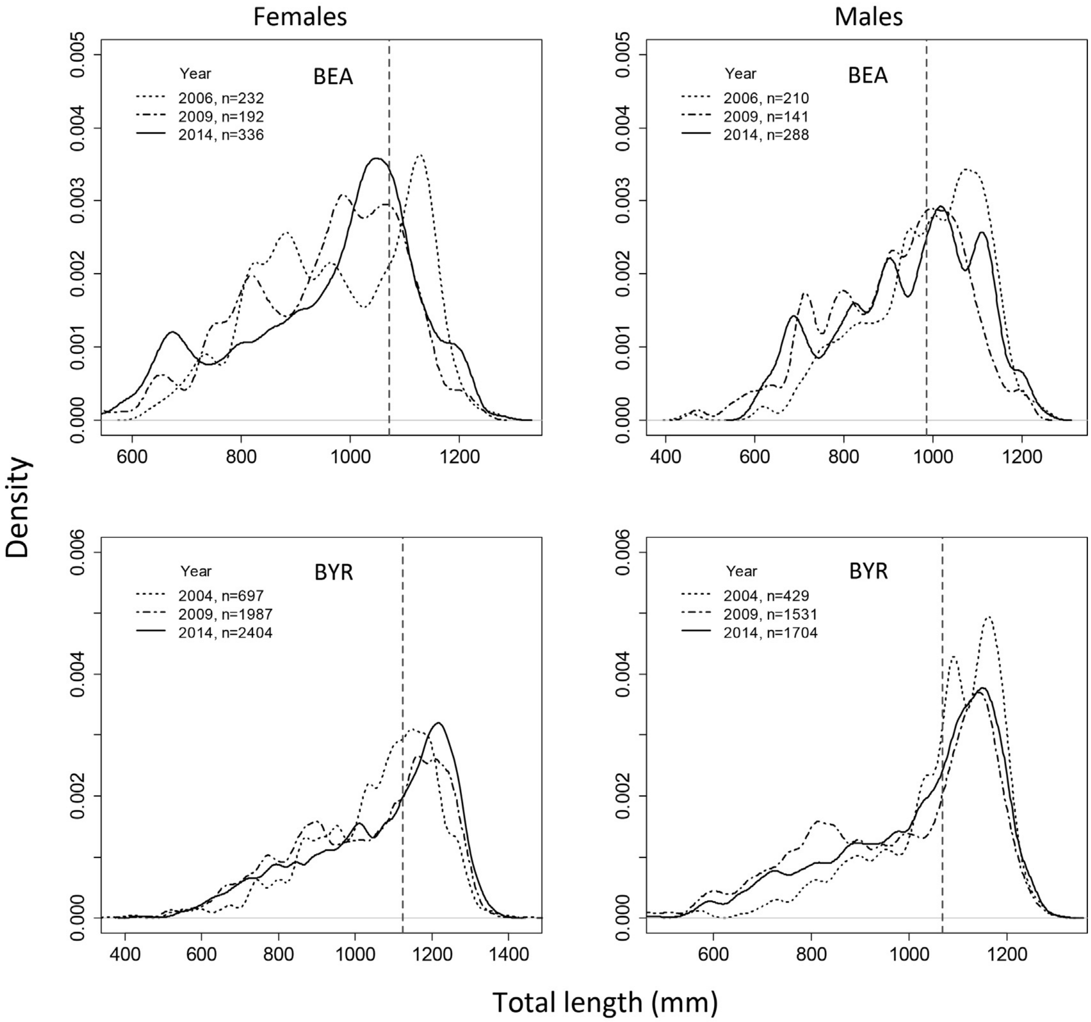

Fig. 9. Kernel densities for length (TL) for *B. eatonii* (BEA) and *B. irrasa* (BYR) taken by longline at HIMI for selected years of the fishery (females on left, males on right). The dashed vertical line indicates the length at maturity (LM_{50}).

Table 6
Model covariates and AIC's for *B. irrasa* from the longline fishery at HIMI (Y – yes; N – no).

Time period Model	AIC	Covariates CCYear	Month	Vessel	s (Depth)	s (Lat, Long)	Log (toothfish number)
2003–2014							
Poisson full	73292	Y	Y	Y	Y	Y	Y
Neg bin full	33088	Y	Y	Y	Y	Y	Y
2006–2014							
Poisson full	61424	Y	Y	Y	Y	Y	Y
Neg bin full	29168	Y	Y	Y	Y	Y	Y
Neg bin -vess	29168	Y	Y	N	Y	Y	Y

models included full models, while the Negative Binomial model for 2006–2014 without vessel showed a similar AIC. However, the models for the Poisson and Negative Binomial distributions showed dissimilar results. The Poisson model for the full time period (2003–2014) showed a peak of around $4\,n\,kh^{-1}$ in 2006 falling sharply in the next two years to just above $2\,n\,kh^{-1}$ then declining to fewer than $2\,n\,kh^{-1}$ by 2014. When the analysis was restricted to 2006–2014, the trend was similar but remained above $2\,n\,kh^{-1}$ in 2014 (Fig. 12, Table 6). The Negative Binomial models, however, showed more stability in the relative abundance over time. The model for 2003–2014 was about $3\,n\,kh^{-1}$, while the model from 2006 to 2014 declines only slightly from just above to just below $4\,n\,kh^{-1}$ by 2014 (Fig. 12, Table 6).

3.4.2.3. B. irrasa *from Kerguelen longline.*
For *B. irrasa* the saturated (full) model had the best AIC. The CPUE for *B. irrasa* from Kerguelen did not show a trend in the years analysed, with around 0.0015 per 1000 hooks throughout the time period (Fig. 12).

3.4.2.4. B. irrasa *from HIMI toothfish and icefish trawl.*
For *B. irrasa* the catch from the toothfish trawl fishery was less than 0.5 per haul for all years except 2006 and 2008 when it was closer

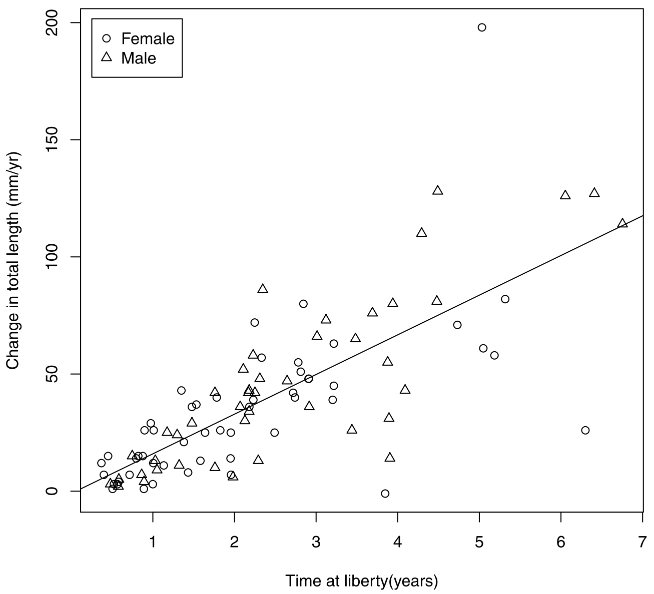

Fig. 10. Change in total length (TL) by sex between release and recapture while at liberty for tagged *B. eatonii* from the HIMI fishery. The line shows the linear regression of change in length over time at liberty independent of sex.

to 1 per haul (see Supplementary results Fig. S2.5). Catches of *B. irrasa* from the icefish trawl started at 2–8 per haul (depending on the model) in 2000 but the models were more consistent at below 4 per haul for the rest of the time (see Supplementary results S2.3.2, Fig. S2.6).

3.4.3. Biological information

3.4.3.1. Changes in total length and length at maturity.

The GAM analyses of mean TL over time from 1997 to 2014 at HIMI showed that for trawl caught *B. irassa* there was a significant decline from the start of the fishery at 1055 mm to 899 mm in 2010 but then a gradual increase in the mean length each year to 1087 mm in 2014 (Fig. 7, Table 4).

For *B. irassa* in the HIMI longline fishery, a significant result in the GAM showed little change in the long term trend of total length (Fig. 7). The analysis of total length of skates at HIMI took into account the effects of depth and geographic location (latitude and longitude).

The length at 50% maturity (LM_{50}) for *B. irrasa* from HIMI showed that females matured at a greater length than males (Table 5). The kernel density plots of total length of skates from selected years with the length at maturity marked showed that *B. irrasa* taken in the toothfish trawl are mostly mature (Fig. 8), as were those taken in the longline fishery, although they were larger on average than those taken in the trawl fishery (Fig. 9).

3.5. Bathyraja murrayi

3.5.1. Spatial distribution and abundance with depth

At HIMI, *B. murrayi* were fairly evenly dispersed to the north, northwest and northeast of Heard Island down to about 1000 m, generally with numbers up to 100 n km^{-2} (Fig. 13). The places where *B. murrayi* were most abundant (with patches of >100 n km^{-2}) were in waters shallower than 300 m close to the northern side of Heard Island.

The spatial map of skate CPUE of *B. murrayi* in the HIMI and Kerguelen longline fisheries showed distribution was patchy in both the Australian and the French EEZ's on the Kerguelen Plateau, with small reported catches in total. Relative abundances were very low in comparison to the other species; at HIMI abundances were mostly below 0.1 n kh^{-1}, with a few small points of greater abundance (but never >0.4 n kh^{-1}) to the northwest of Heard Is. near the edge of the EEZ (Supplementary material Fig. S2.1).

3.5.2. Temporal trends in biomass and abundance

3.5.2.1. Biomass estimates from RSTS and POKER surveys.

At HIMI, *B. murrayi* numbers were generally estimated to be less than 2 M except for 2010 when there were over 3 M. Biomass estimates in tonnes of *B. murrayi* have remained at less than 1 kt except for an exceptionally high year in 2006 of around 2 kt (Fig. 5). The peaks were associated with much greater uncertainty than the smaller estimates (Supplementary results, Fig. S2.2). The biomass estimates at Kerguelen showed consistent estimates of *B. murrayi* at around 1 kt (Fig. 5).

3.5.2.2. B. murrayi *from HIMI toothfish trawl.*

For the modelled catch rates of *B. murrayi* from the HIMI toothfish trawl fishery, the Poisson model omitting vessel in the count model and the Poisson full model with polynomial depth term in both the count and binary models were both considered optimal by AIC. The optimal Negative Binomial model was the saturated model omitting toothfish catch from the count model and depth from the binary model. These three models showed similar patterns.

The proportion of zero hauls declined over time for this species, starting at around 80% until about 2007, then fluctuating between 40 and 50% for the remaining years (not shown). For *B. murrayi* the modelling showed increased numbers in the latter years of the fishery, from less than one per haul prior to 2006 to fluctuating between 3 and 8 per haul after that (Fig. 14, Table 7).

3.5.2.3. B. murrayi *from HIMI icefish trawl.*

The catch per haul of *B. murrayi* in the icefish trawl fishery ranged between 0 and 10 over the years of the fishery but did not show any temporal trend (see Supplementary results Fig. S2.7).

3.5.3. Biological information

3.5.3.1. Changes in total length and length at maturity.

For *B. murrayi* at HIMI the GAM analysis of the toothfish trawl fishery showed that the mean total length increased significantly over the time span (1997–2014) from 352 mm in 1999 to 384 mm in 2014 (Fig. 8, Table 4). The length at 50% maturity (LM_{50}) showed that for HIMI *B. murrayi* males matured at greater length than females (Table 5). The kernel density plots of total length of skates from selected years with the length at maturity marked, showed that male *B. murrayi* from the toothfish trawl fishery are taken mostly before they are mature, and to a lesser extent also females (Fig. 8).

4. Discussion

4.1. Spatial distribution and abundance

The distribution of skates in the HIMI area showed high concentrations of *B. eatonii* and *B. irrasa* on the plateau to the north and northwest of Heard Island out to the edge of the Australian EEZ. Some higher, but localised, concentrations of *B. murrayi* also occurred in this area. Large parts of these areas of high abundance are within the HIMI Marine Reserve, where commercial fishing is prohibited, thus providing a refuge for these species. In the area to the east and southeast of Heard Island, where the majority of the longline fishery operates, skate abundances were patchy. The abundances were highest around the underwater banks to the northwest of Heard Island near the edge of the Australian EEZ. The main species caught in this area, *B. irrasa*, formed the majority of the skate catch by longlines. *B. irrasa* and *B. eatonii* had a widespread

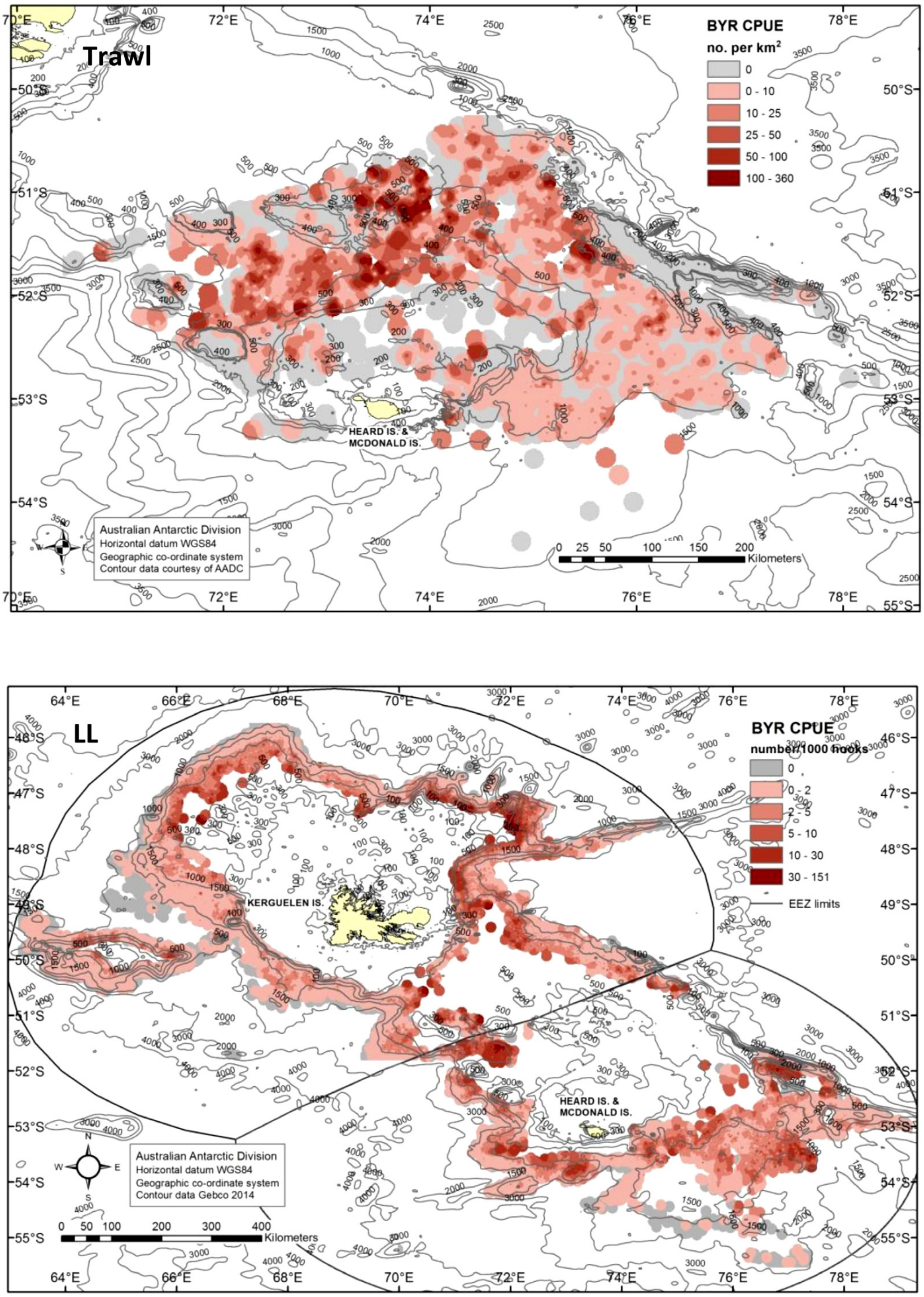

Fig. 11. Distribution and abundance of *B. irrasa* taken in the toothfish trawl fishery and RSTS at HIMI (1997–2014) (Trawl) *and* in the Kerguelen (2008–2014) and HIMI (2003–2014) toothfish longline fisheries (LL).

Table 7
Model covariates and AIC's from the best models for *B. murrayi* (Y – yes; N – no).

Model	AIC	Covariates CCYear	Month	Vessel	Strata	Depth	Log (toothfish wt)
Poisson poly count	42374.04	Y	Y	Y	Y	Y (poly)	Y
binary		Y	Y	Y	Y	Y (poly)	Y
Poisson C-vBf count	42374.23	Y	Y	N	Y	Y (poly)	Y
binary		Y	Y	Y	Y	Y (poly)	Y
Neg bin C-tB-d count	27770.90	Y	Y	Y	Y	Y (poly)	N
binary		Y	Y	Y	Y	N	Y

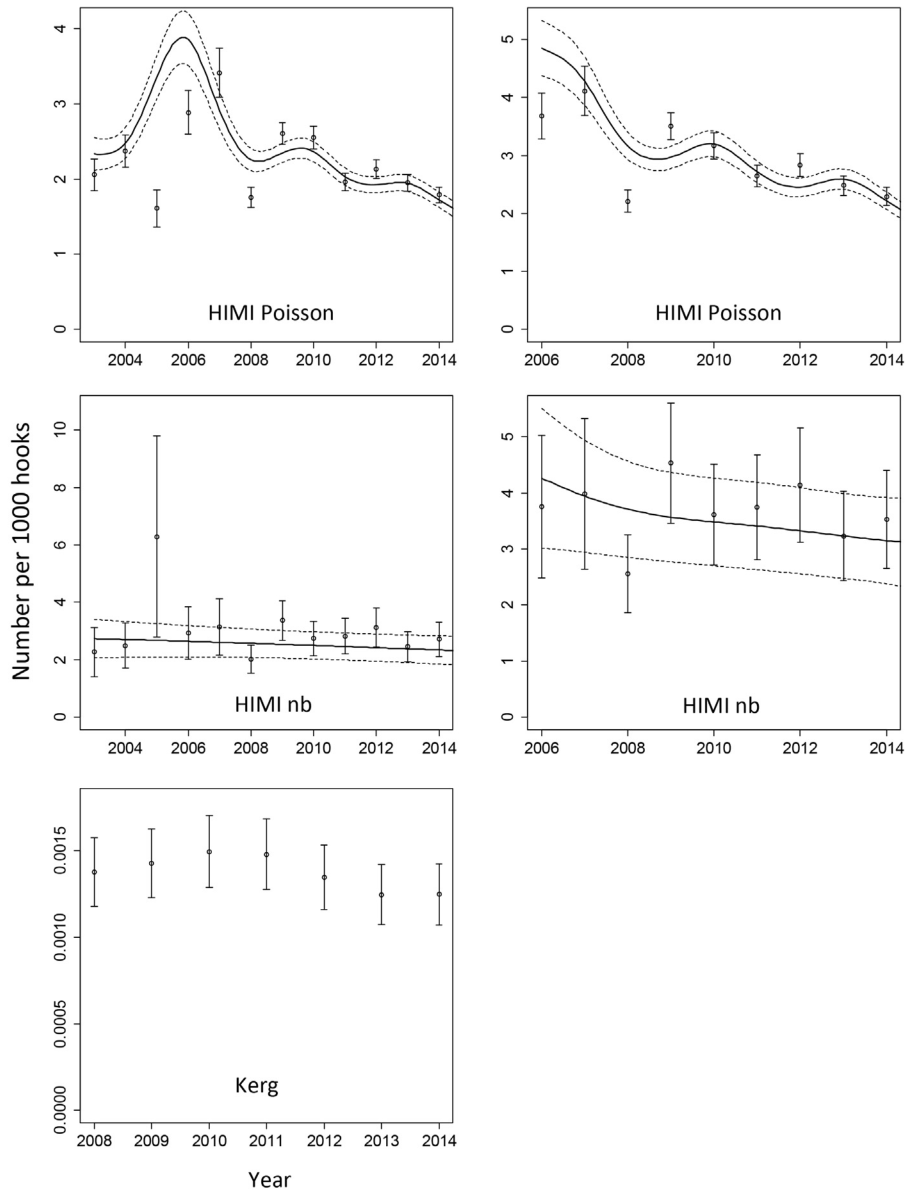

Fig. 12. The trend in number of *B. irrasa* per 1000 hooks over years at HIMI from the optimal Poisson gam models (HIMI Poisson) and negative binomial models (HIMI nb), 2003–2014 on the left and 2006–2014 on the right, and the trend in number of *B. irrasa* per 1000 hooks over years from the Negative Binomial gam model for the Kerguelen longline fishery, 2008–2014 (Kerg).

distribution across the entire Kerguelen Plateau, as shown by the combined HIMI and Kerguelen data. Abundances of *B. eatonii* in the catches are higher around Kerguelen Island than at HIMI. *B. murrayi* was caught in low densities in the HIMI longline fishery and in the Kerguelen longline fishery. The longline fisheries mostly operate in depths beyond where this species is most abundant. At Kerguelen a ban on fishing at depths less than 500 m affords protection to skates in a large area off the Kerguelen Islands.

4.2. Species composition and bathymetric ranges

This study extends the range previously reported about the depth distribution of these skate species. *B. eatonii* were commonly caught down to 560 m in the trawl fisheries, but in lower abundances down to 1790 m in the longline fishery, extending the range reported in Duhamel et al. (2005). *B. irrasa* had previously been caught down to depths of 1800 m in the HIMI region, but they were recently reported on longlines down to 2059 m, again extending the range previously reported in Duhamel et al. (2005). *B. murrayi* were most abundant at around 550 m, at shallower depths than the other two species. This is similar to the reported depths in Duhamel et al. (2005), although they were brought up in much smaller numbers from deeper set (to 1548 m) longlines at HIMI. For skates on longlines depth of capture is only approximate as the mean depth of the line is recorded and longlines are usually set down a slope.

B. eatonii were caught in greater numbers per year on average in the icefish trawl fishery than in the toothfish trawl fishery at HIMI, despite lower effort in the icefish trawl fishery. This can be explained when the depth of fishing by the two methods is taken into account. Icefish fishing occurred primarily at depths of 200–400 m, where *B.eatonii* are most common, while most of the toothfish trawl effort was concentrated in the 450–750 m range.

The longline fishery from the Kerguelen area showed a different species composition of skates in the by-catch compared to that at

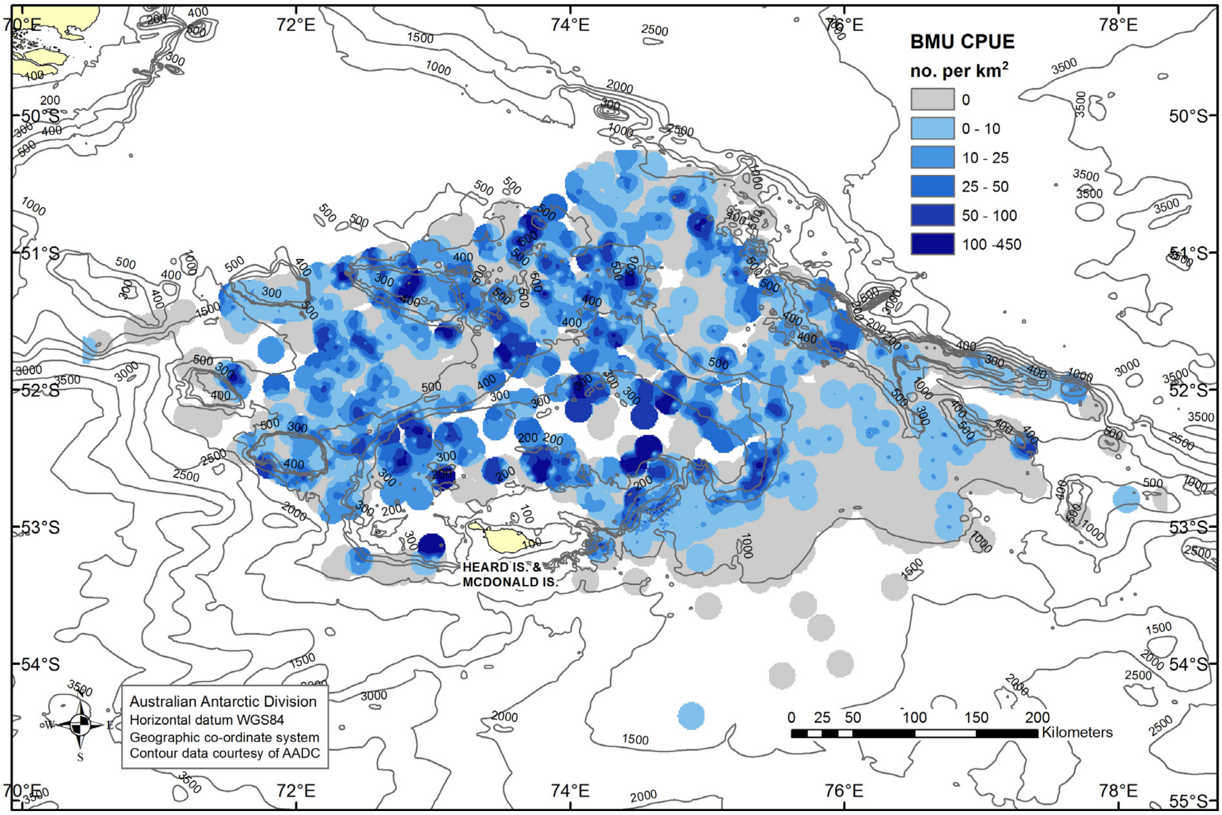

Fig. 13. Distribution and abundance of *B. murrayi* taken in the toothfish trawl fishery and RSTS at HIMI (1997–2014).

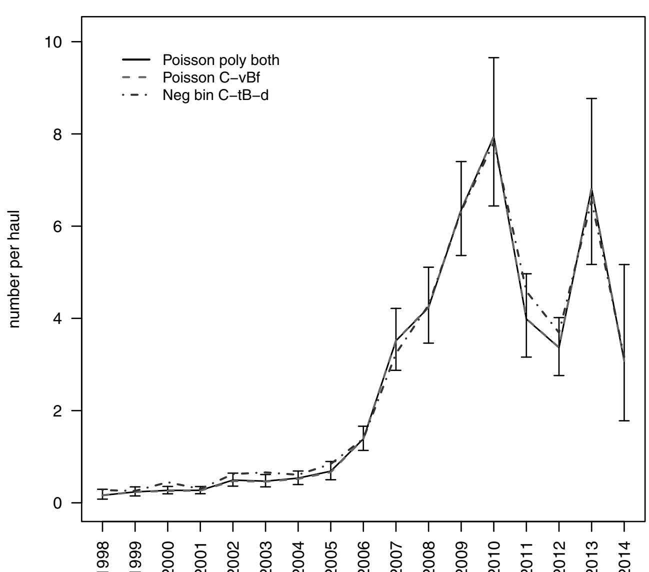

Fig. 14. The catch rate (number per haul) for *B. murrayi* from the toothfish trawl fishery at HIMI.

HIMI. While both fisheries predominantly take *B. irrasa*, the Kerguelen fishery data showed a much higher percentage of *B. eatonii* than at HIMI. If these data are representative of the underlying populations, then there may be a gradient of distribution occurring with the large changes in latitude that occur from north to south (46° to 54°S) across the Kerguelen Plateau. Both fisheries took few *B. murrayi*.

4.3. Temporal trends in biomass

Estimates for the biomass (numbers of skates) for the three species at HIMI from the annual RSTS were generally stable except for the period 2009–2011 where they increased substantially. The increase of skates in the toothfish fishery corresponded with increased abundance of skates in the RSTS, but it is unknown whether the scale of the increase in the RSTS is real or represents sampling variability. The biomass estimates in the RSTS, however, returned to previous levels in 2011 or 2012, not reflected in the catch rates until 2014. The RSTS results indicate that the increased abundance in the fishery is at least partly reflecting increased abundances in the population. Biomass estimates from the Kerguelen POKER surveys showed much larger populations of *B. eatonii* and *B. irrasa* than at HIMI. The total biomass, especially of *B. irrasa*, and to a lesser extent *B. eatonii*, was likely to be higher than estimated because the bathymetric range of the RSTS and POKER surveys were limited to 1000 m and the species are observed to occur deeper (to 2000 m).

4.4. Temporal trends in abundance

The modelling of the CPUE of *B. eatonii*, one of the two species caught in greatest numbers on the shallower parts of the plateau around HIMI by the toothfish trawl fishery, showed an increase in relative abundance (numbers per haul) since 2006. At the same time, the mean total length of *B. eatonii* taken in the trawls has declined significantly since the commencement of the fishery. Their large size at maturity means that most individuals are caught before they reach reproductive age. All skates (apart from those processed for biological sampling) are released, however survival rates in the longer term are unknown. The decrease in the average length may be due to a strong pulse of recruitment, or alternatively, it may be that fishing pressure has reduced the number of larger individuals in the population. The HIMI toothfish fishery has been transitioning from trawling to longlining and by 2015 this had mostly been completed, thus reducing the potential for future impacts on *B. eatonii,* since this species is not caught as often on longlines. Such a transition (through a ban of toothfish trawling) already occurred at Kerguelen in 2001 (Duhamel et al., 2011).

The abundance of the other common species in the toothfish trawl fishery, *B. murrayi,* has similarly shown an increase in abundance from 2006. Unlike *B. eatonii*, this species has shown an increase in average total length over the duration of the fishery, even though the majority landed in the trawls are not yet reproductively mature. It is possible that the species composition has shifted from the large species (*B. eatonii*) to the smaller species (*B. murrayi*) over time, as has been reported in fisheries in the North Sea (Walker and Hislop, 1998) and in the Irish Sea (Dulvy et al., 2000) and presumed to be due to competitive release. In the Irish Sea the removal of the larger skates may have led to greater availability of resources for the smaller skates, due to dietary overlap between the species (Dulvy et al., 2000). However, the overall catches of skate species remained stable over this period, highlighting the need to monitor by-catch rates by species. On the Kerguelen Plateau, studies showed that the skates, particularly *B. eatonii* and *B. murrayi* fed on similar prey items, small fish and benthic invertebrates (Duhamel et al., 2005; Pshenichnov, 2013).

Walker and Hislop (1998) have shown in a long-term study of the North Sea that fishing has had an effect on the length-frequency composition, as well as a marked change in species composition of skate and ray populations. The larger length classes of all but one (starry ray) of seven species have become much less abundant in surveys of the latter part of the 20th century compared to the first half. The smallest species (starry ray) has become more abundant in the ecosystem.

In the deeper waters where the longline fishery operates (>1000 m), the modelling for *B. eatonii* showed little change in abundance over time, but this species was caught in much smaller numbers and seldom occurs at depths greater than 1500 m.

The CPUE of *B. irrasa*, the main species caught in the longline fishery at HIMI, showed a small decrease in relative abundance from 2006 to 2014, with the Poisson model showing a greater decrease than the Negative Binomial model. When the less reliable data from 2003 to 2005 were included, the two models differed more, with the Poisson model showing a peak in 2006 and the Negative Binomial model not fitting to the high catch rate in 2005 so showing little trend over time. The average length of this species taken over time, while fluctuating, does not show a substantial decrease, so overall there is little evidence that the longline fishery has impacted this species to date.

Catch rates for the two species of skates taken in the Kerguelen longline fishery have remained relatively constant, showing only a slight rise and no change in CPUE for *B. eatonii* and *B. irassa* respectively over the seven years. However, the many years of fishing prior to the start of the data available in this analysis make it unclear how the current catch rates compare with earlier years.

The waters of the Kerguelen Plateau have been subject to illegal, unreported and unregulated (IUU) fishing in the past. In the late 1990's at HIMI and early 2000's around Kerguelen Is., IUU catches of toothfish sometimes exceeded legal catches, but there are no estimates available for skate catches (CCAMLR, 2014b,c). Although IUU fishing subsequently declined and was virtually eliminated from 2005 at both HIMI and Kerguelen Is. (Duhamel and Williams, 2011), there were undoubtedly impacts on the skate populations as well as on toothfish. Any IUU catches before the recording of skate by-catch in the legal fisheries would have resulted in lower indices of relative abundance than if none had occurred. Where IUU fishing overlapped with the recording of skate catches by the legal fishery the unreported catch would likely be represented in the Year term in the CPUE analysis.

4.5. Factors influencing survival and mortality

Although the majority of skates (except those taken for biological sampling) caught in fisheries on the Kerguelen Plateau are released alive, it is not known whether those returned to the sea have a good survival rate. There have been few studies of survival of rajid skates after capture in fisheries. Enever et al. (2009) found that rajid skates in demersal trawls from the Bristol Channel skate fishery had a good survival rate after 72 h if they were in good condition when they were brought onboard, with good condition being related to a lighter codend. When alternative configurations of codend meshes were tested, larger diamond and square mesh codends reduced the volume of by-catch over the industry standard net and increased the survivorship of by-catch (Enever et al., 2010). For longline fisheries, Endicott and Agnew (2004) investigated the post-haul survivorship of rajids from the South Georgia toothfish longline fishery. Short-term (12 h) survival proved to be inversely related to the depth of capture, decreasing from 75% to 24% with depth. Further studies on post-capture survival and the effect of gear modifications on skate injuries or mortalities on the KP would be valuable.

Because the limited data available prevents more comprehensive stock assessments, several studies have attempted to define characteristics that could be used to identify species of skate which are susceptible to declines in population (Dulvy and Reynolds, 2002; Dulvy et al., 2000; Walker and Hislop, 1998). Dulvy and Reynolds (2002) examined characteristics of skates which had already disappeared from substantial parts of their ranges. The characteristic which best explained the pattern of local extinctions of some skates was large body size, which correlates with life-history characteristics such as late age of maturity. McPhie and Campana (2009) studied four common species of Rajid skates off Eastern Canada and found that the relationship between the maximum age and the age of maturity was the best predictor of population growth rate. The species which had the highest ratio had the lowest predicted growth rate, and this corresponded to the species *Leucoraja ocellata*, which has experienced the greatest population decline on the eastern Scotian Shelf. Considering that two of the species caught on the Kerguelen Plateau grow to a large size, continued close monitoring of populations would be advisable, even though large conservation areas occur both at HIMI and Kerguelen Islands.

5. Conclusions

This study provides the first comprehensive analysis of the skate distribution and by-catch from scientific surveys and the fisheries in the two areas (HIMI and Kerguelen) of the greater Kerguelen Plateau. Scientific surveys suggested little change in the abundance of the three species over time, however, the uncertainty in these estimates is high. Analysis of the trawl fisheries suggested some species may have suffered localised depletion, however, the level of trawling at HIMI has decreased since the longline fishery began in 2003. It has been timely to review the status of skate at HIMI because two changes in the fisheries in 2015 (an increase in longline effort and the phasing out of trawling) may change the dynamics of impacts on by-catch. We recommend ongoing monitoring of species specific by-catch levels, and further research to determine the life history parameters of these species, particularly for *B. irrasa* which is taken both in the trawl and the longline fisheries, and hence is at highest risk of adverse impacts from fishing. Studies to better understand and, if necessary, reduce by-catch and/or discard mortality are required.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2016.07.022.

References

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer Science & Business Media.

CCAMLR, 2011. Scheme of International Scientific Observation: Scientific Observers Manual. CCAMLR, Hobart, Australia. https://www.ccamlr.org/en/document/publications/scientific-observers-manual-%E2%80%93-2011 (accessed 30.06.16.).

CCAMLR, 2014a. Schedule of Conservation Measures in Force, 2014/15 season. CCAMLR, Hobart, Australia: 289 pp.

CCAMLR, 2014b. Fishery Report 2014: Dissostichus eleginoides Heard Island Australian EEZ (Division 58.5.2). CCAMLR, Hobart, Australia. www.ccamlr.org/node/85876 (accessed 30.06.16.).

CCAMLR, 2014c. Fishery Report 2014: Dissostichus eleginoides Kerguelen Islands French EEZ (Division 58.5.1). CCAMLR, Hobart, Australia. www.ccamlr.org/node/85877 (accessed 30.06.16.).

Constable, A.J., Williams, R., de la Mare, W.K., 1998. Assessment of by-catch in trawl fisheries at Heard and McDonald Islands. CCAMLR Sci. 5, 231–243.

Duhamel, G., Hautecoeur, M., 2009. Biomass, abundance and distribution of fish in the Kerguelen Islands EEZ (CCAMLR division 58-5-1). CCAMLR Sci. 16, 1–32.

Duhamel, G., Williams, R., 2011. History of whaling, sealing, fishery and aquaculture trials in the area of the Kerguelen Plateau: 15–28. In: Duhamel, G. and Welsford, D. (Eds) The Kerguelen Plateau: marine ecosystem and fisheries. Paris: Société française d'ichtyologie.

Duhamel, G., Gasco, N., Daviane, P., 2005. Poissons des Iles Kerguelen et Crozet. Guide régional de l'océan Austral. Muséum national d'Histoire naturelle, Paris, 419 p. (Patrimones naturels, 63).

Duhamel, G., Pruvost, P., Bertignac, M., Gasco, N. Hautecoeur, M., 2011. Major fishery events in Kerguelen Islands: Notothenia rossii, Champsocephalus gunnari, Dissostichus eleginoides – Current distribution and status of stocks. In: Duhamel, G., Welsford, D., (Eds) The Kerguelen Plateau: marine ecosystem and fisheries. Paris: Société française d'ichtyologie.

Duhamel, G., Hautecoeur, M., Sinegre, R., 2014. 2006–2013 fish distribution and biomass in the Kerguelen EEZ (CCAMLR Division 58-5-1) for the bathymetric range 100–1000 m. Document WG-FSA-14/07, SC-CAMLR-XXXIII, CCAMLR, Hobart, Australia.

Dulvy, N.K., Reynolds, J.D., 2002. Predicting extinction vulnerability of skates. Conserv. Biol. 16, 440–450.

Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., Reynolds, J.D., 2000. Fishery stability, local extinctions, and shifts in community structure in skates. Conserv. Biol. 14, 283–293.

Efron, Tibshirani, 1994. An Introduction to the Bootstrap. CRC Press.

Endicott, M., Agnew, D.J., 2004. The survivorship of rays discarded from the South Georgia longline fishery. CCAMLR Sci. 11, 155–164.

Enever, R., Catchpole, T.L., Ellis, J.R., Grant, A., 2009. The survival of skates (Rajidae) caught by demersal trawlers fishing in UK waters. Fish. Res. 97, 72–76.

Enever, R., Revill, A.S., Caslake, R., Grant, A., 2010. Discard mitigation increases skate survival in the Bristol Channel. Fish. Res. 102, 9–15.

Gasco, N., 2011. Contributions to marine science by fishery observers in the French EEZ of Kerguelen. In: Duhamel, G., Welsford, D., (Eds) The Kerguelen Plateau: marine ecosystem and fisheries. Paris : Société française d'ichtyologie.

Hilbe, J.M., 2011. Negative Binomial Regression, second edition. Cambridge University Press, New York, 553 pp.

Laptikhovsky, V.V., 2004. Survival rates for rays discarded by the bottom trawl squid fishery off the Falkland Islands. Fish. Bull. 102 (4).

Lord, C., Duhamel, G., Pruvost, P., 2006. The patagonian toothfish (*Dissostichus eleginoides*) fishery in the kerguelen islands (Indian ocean sector of the southern ocean). CCAMLR Sci. 13, 1–25.

Martin, A., Pruvost, P., 2007. Pecheker, relational database for analysis and management of fisheries and related biological data from the French southern ocean fisheries monitoring scientific programs, Muséum National d'Histoire Naturelle.

Maunder, M.N., Punt, A.E., 2004. Standardising catch and effort data: a review of recent approaches. Fish. Res. 70, 141–159.

McCullagh, Nelder, 1989. Generalised Linear Models. Chapman and Hall.

McPhie, R.P., Campana, S.E., 2009. Reproductive characteristics and population decline of four species of skate (Rajidae) off the eastern coast of Canada. J. Fish Biol. 75, 223–246.

Minami, M., Lennert-Cody, C.E., Gao, W., Román-Verdesoto, M., 2007. Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. Fish. Res. 84, 210–221.

Nowara, G.B., Williams, R., Lamb, T., 2006. Report on a random stratified trawl survey to estimate distribution and abundance of *Dissostichus eleginoides* and *Champsocephalus gunnari* conducted in the Heard Island region (Division 58.5.2), May-June 2006. Document WG-FSA-06/42 rev 1., SC-CAMLR-XXV, CCAMLR, Hobart, Australia.

Nowara, G.B., Lamb, T.D., Welsford, D.C., 2013. Skate tagging in the Heard Island and McDonald Island (Division 58.5.2) toothfish fishery up to 2013. Document WG-FSA-13/22, SC-CAMLR-XXXII, CCAMLR, Hobart, Australia.

Pshenichnov, L.K., 2013. Biological characteristics of by-catch fish species during trawl fishing on the shelf of Kerguelen Islands (Indian Ocean, Sub-Antarctic) Trudy YugNIRO, 51: 91–106 (Russian), In: Ellis, J.R., McCully, S.R., Laptikhovsky, V.V. Scott, R. (2013) An overview of the elasmobranch fish of the Southern Ocean, Document WG-FSA-13/28, SC-CCAMLR-XXXII, CCAMLR, Hobart, Australia.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

SC-CAMLR, 1997. Report of the Sixteenth Meeting of the Scientific Committee (SC-CAMLR-XVI). CCAMLR, Hobart, Australia: 438 pp.

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57, 476–494.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth edition. Springer, New York.

Walker, P.A., Hislop, J.R.G., 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES J. Mar. Sci. 55, 392–402.

Wood, S.N., 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. J. Stat. Softw. 27.