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Original Article

A long road to recovery: dynamics and ecology of the marbled rockcod (*Notothenia rossii*, family: Nototheniidae) at South Georgia, 50 years after overexploitation

Philip R. Hollyman [1,*], Simeon L. Hill [1], Vladimir V. Laptikhovsky [2], Mark Belchier[1,3], Susan Gregory[1,3], Alice Clement[1], and Martin A. Collins [1]

[1] *British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK*
[2] *Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK*
[3] *Government of South Georgia and the South Sandwich Islands, Stanley FIQQ 1ZZ, Falklands*

[*] *Corresponding author: tel: +44(0) 1223 22130; e-mail:phyman@bas.ac.uk*

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Exploitation is one of the major drivers of change in marine ecosystems. Following discovery in 1775, South Georgia saw sequential overexploitation of living resources, including seals, whales, and fish. Although exploitation is now tightly regulated, the ecosystem is still recovering. Marbled rockcod, *Notothenia rossii* (Richardson 1844), was the first fish species to be commercially exploited and high catches between 1967 and 1972 resulted in dramatic stock decline. Here, we use 30 years of trawl survey data to provide the first evidence of a sustained increase in the *N. rossii* population starting two decades after the prohibition of targeted fishing in 1985. The way species respond to change is mediated in part by trophic relationships with other organisms. We present the first multi-year, spatially-resolved comparison of adult *N. rossii* diet at South Georgia, highlighting a variable diet with less reliance on Antarctic krill than previously thought. Life history factors and possible heavy predation on early life stages might have delayed their recovery while diet plasticity potentially supported recent population growth. Due to the dynamic ecosystem at South Georgia and questions over catch reports from the period of heaviest exploitation, it is unlikely the current ecosystem could support a recovery to estimated pre-exploitation levels.

Keywords: Diet analysis, Nototheniidae, *Notothenia rossii*, Over-exploitation, Trawl survey

Introduction

Overexploitation of marine resources is an issue found throughout the world's oceans, with an estimated 34.2% of fish stocks unsustainably fished as of 2017 (FAO, 2020). As the demand for seafood is increasing with a growing global population (Cochrane, 2021), the best approach to tackle overexploitation is effective fisheries management (Hilborn *et al.*, 2020), which often includes reductions in fishing mortality (Cochrane, 2021). Whilst some fish stocks may be resilient to moderate overexploitation and recover quickly, for many stocks this recovery has been slow due to a combination of ongoing fishing mortality and the intensity and duration of the initial exploitation (Neubauer *et al.*, 2013). For heavily overexploited stocks, recovery may well take several decades (Neubauer *et al.*, 2013).

Some parts of the Southern Ocean historically experienced serial overexploitation of marine resources, resulting in the establishment of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, a dual conservation and management body) in 1982. The sub-Antarctic island of South Georgia is found within the CAMLR Convention area, and before

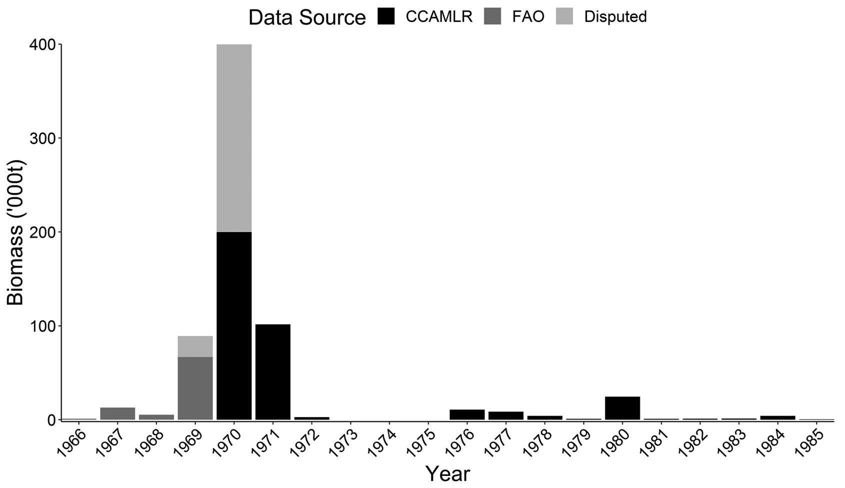

Figure 1. Catches of *Notothenia rossii* at South Georgia (CCAMLR subarea 48.3) from 1966 to 1985. Data are reported from records held by CCAMLR (1970–1985) and the FAO (1966–1969). Catches highlighted by Agnew, (1995) as potentially not *N. rossii* are labelled as "disputed".

1982 was the location of extensive overfishing of available finfish species (Ainley and Blight, 2009), evident in a dramatic reduction in demersal fish biomass (Myers and Worm, 2003). One such species is the marbled rockcod, *Notothenia rossii*, an upper trophic level fish distributed around islands and on continental shelves in the Southern Ocean between 45°S and 65°S (Gon and Heemstra, 1990). It was the first fish species to be commercially targeted in the Southern Ocean and was the focus of a short period of heavy exploitation in the early 1970s (Kock *et al.*, 2004). This exploitation was particularly intensive around South Georgia (Figure 1), where the reported catch was 500 000 tonnes in just 2 years between 1969 and 1971 (Myers and Worm, 2003; Kock *et al.*, 2008; CCAMLR, 2019). Earlier catches of *N. rossii* taken between 1966 and 1969 were attributed to South Georgia by Agnew, (1995) using data from the Fisheries and Aquaculture Organization (FAO, 2019). These data highlighted relatively intensive fishing in the years preceding the largest catch in 1970 (Figure 1). Catches between 1969 and 1976 were often recorded as "Unspecified Demersal Percomorphs" and were only later classified as *N. rossii* (Everson, 1978). Subsequent work suggested significant portions of these reported catches may have been comprised of species other than *N. rossii* (Kock, 1992; Agnew, 1995). Revised estimates suggest that up to 50% of the catch in 1970 and 25% of the catch in 1969 may have in fact been other species (largely mackerel icefish, *Champsocephalus gunnari*, Figure 1) (Agnew, 1995) but there is no way to retrospectively confirm this.

There was also targeted exploitation of *N. rossii* at the sub-Antarctic islands in the Indian Ocean sector (CCAMLR area 58), and at both the South Shetland (CCAMLR subarea 48.1) and South Orkney Islands (CCAMLR subarea 48.2) until fishing for *N. rossii* was prohibited in 1985 (CCAMLR, 1985; Duhamel and Williams, 2011; Duhamel *et al.,* 2017; CCAMLR, 2019). Between 1970 and 1985, the biomass of *N. rossii* extracted from South Georgia accounted for 60% of the total harvested biomass of this species (CCAMLR, 2019). These unregulated catches appear to have depleted the stocks and subsequent reports suggested that the stock at South Georgia remained well below pre-exploitation levels (Kock *et al.,* 2004).

The marine ecosystem around South Georgia has experienced significant environmental and ecological change. This includes historic overexploitation of marine mammals and fish (Murphy *et al.,* 1998; Croxall and Nicol, 2004), rapid ocean warming (Whitehouse *et al.*, 2008), and a possible decline in the abundance of a key prey species, Antarctic krill, *Euphausia superba*, as its distribution has contracted southwards (Atkinson *et al.,* 2019). Some previously exploited species have recovered (e.g. fur seals), or are now showing signs of recovery (e.g. baleen whale species; Trathan *et al.* 2012; Zerbini *et al.*, 2019; Calderan *et al.,* 2020). Understanding a species' role in the food web is critical for understanding how it responds to such ecosystem change (Abrams *et al.*, 1996). Despite its abundance and commercial importance, knowledge of the ecology of *N. rossii* at South Georgia is limited and based on relatively few studies.

The life cycle of *N. rossii* at South Georgia was first described by Burchett (1983c). After spawning at depths of 100–400 m in April–May (Shcherbich, 1975; Burchett, 1983a), hatching occurs offshore between September and October (Shcherbich, 1975; Burchett *et al.,* 1983), where the larvae remain for several months until moving to the fjords as blue phase fingerlings (35–68 mm) in January–February (Burchett, 1983c, d). These blue fingerlings become demersal and develop the typical brown colouration of juvenile fish by April (48–106 mm) (Burchett, 1983d). Juveniles remain in the shallow (< 100m) coastal kelp habitats (Burchett, 1982) for around 5 years until migrating into the deeper water of the shelf, presumably with the onset of maturity (Burchett, 1983d). The life cycle of *N. rossii* is similar at Kerguelen, although spawning at this location is roughly a month later in June (Duhamel, 1982a,b).

The diet of *N. rossii* at South Georgia varies with ontogeny, with blue phase fingerlings predating on planktonic organisms (e.g. fish and crustacean larvae, amphipods), switching to predominantly small fish and amphipods by the time they reach the juvenile phase (Burchett, 1983b). Previous studies on the diet of adult *N. rossii* at South Georgia all reported that Antarctic krill was a major component of the adult diet (Tarverdiyeva, 1972; Naumov and Permitin, 1973; Chekunova and Naumov, 1982; McKenna, 1991). Tarverdiyeva, (1972) reported *E. superba* as an important dietary component of adult samples collected in the winter (May), but in a sample from earlier in the year (March), ctenophores were dominant. In contrast, on the Kerguelen Plateau, mackerel icefish (*Champsocephalus gunnari*), hyperiid amphipods, cnidaria, and

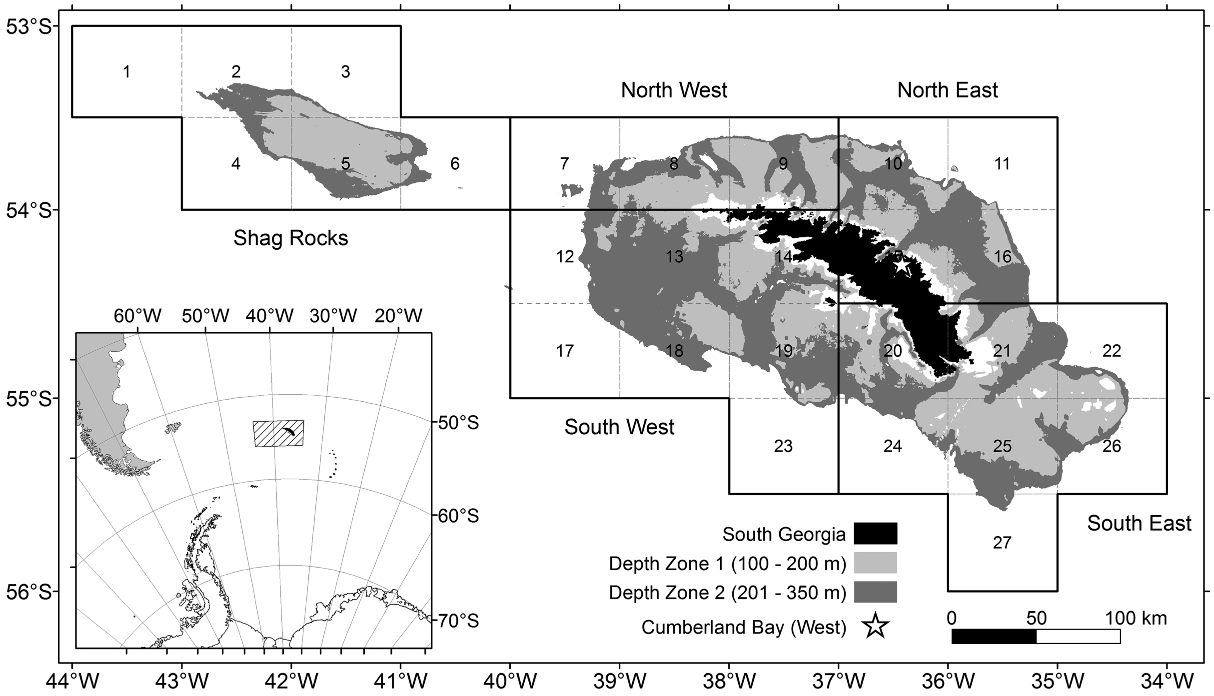

Figure 2. A map of the area covered by the South Georgia ground fish surveys. The inset highlights the area of interest in the wider South Atlantic. The five sectors are denoted by thick black outlines with numbered subdivisions (grid squares) outlined in grey. The two depth zones are represented by light grey (Depth Zone 1: 100–200m) and dark grey (Depth Zone 2: 201–350 m) shading.

ctenophora are all important components of adult *N. rossii* diet (Duhamel and Hureau, 1985).

This study is the first to investigate the status of the *N. rossii* stock at South Georgia since the early 2000s (Kock *et al.*, 2004) and is the first to describe the trophic role of adult *N. rossii* on the South Georgia shelf as the ecosystem changes, responding to recovery of previously exploited species and climate change. The dietary analysis uses a multi-annual dataset to characterize spatial, temporal, and ontogenetic variability in the diet. We provide evidence of an increase in *N. rossii* abundance and biomass during the 21st century and discuss the factors which may have influenced this increase and their implications for recovery to pre-exploitation levels.

Methodology

Sample collection

Trawl surveys

Data on the abundance and distribution of *N. rossii* were collected during 23 ground fish surveys conducted mainly during the austral summer (Nov–Mar) at South Georgia and Shag Rocks, between 1987 and 2019. Whilst originally undertaken to assess the state of fish populations following heavy exploitation between 1969 and 1985 (McKenna and Saila, 1991), the ground fish surveys at South Georgia are now the primary source of data for stock assessment of mackerel icefish, *Champsocephalus gunnari* (Earl, 2019; Gregory *et al.*, 2019). The survey design has remained constant throughout the time series despite changes in survey vessel. From the 1991 survey onwards, gear was standardized (commercial sized otter trawl FP-120, wingspread 18–20 m, headline height 3–6 m, cod end mesh 40 mm), before this, broadly similar gear was used on each of the early surveys (Belchier *et al.*, 2015). 30-min trawls at a speed of 3–4 knots were carried out in a random-stratified design split into five sectors (sub divided into grid squares) and two depth zones (depth zone 1: 100–200 m; depth zone 2: 201–350 m) (Figure 2). In earlier surveys, three depth zones were used (100–200 and 201–300 and >300 m), for the purposes of this analysis, all >300 m trawls were re-classified as Depth Zone 2 and hauls > 350 m were removed from the analysis for comparability.

During each survey, the total catch of *N. rossii* in each trawl was recorded and, where possible, fish were measured (total length, TL) to the nearest cm below. In general, all individuals in a haul were measured, but for large catches random subsampling was employed. At this stage, where possible, individuals not used for further analysis were released alive. For a maximum of 30 randomly selected individuals from each haul, total weight (to the nearest gram) was recorded using a top loading motion compensated balance along with a macroscopic maturity assessment based on Everson, 1977 (SM Table 2). Both size at sexual maturity (using stages 2–5 which may include both maturing virgins and repeated spawners) and size at first spawning (using stages 3–5 comprised exclusively of spawning animals from the current season) were calculated (Kock, 1989; Kock and Kellermann, 1991). These calculations were made using logistic regression in the sizeMAT package in R (Torrejon-Magallanes, 2020).

Trammel netting

Juvenile *N. rossii* were collected between 2001 and 2003 using trammel nets deployed in the shallow (10–100 m), inshore waters of Cumberland Bay on a monthly basis (Figure 2). The nets were deployed for a minimum of 6 hours before being recovered, all fish contained within the net were identified to species level. All *N. rossii* were measured (TL, cm), weighed and assessed for maturity using the methods described above.

Stomach sampling

Whole stomach samples were collected opportunistically during the 2005, 2006, 2007, and 2010 surveys. A targeted collection effort was undertaken during the 2017 and 2019 surveys, where up to 20 (mean 6 +/- SD: 5.1) randomly selected whole stomach samples were collected from each haul when available. Stomach samples were placed in individually labelled ziplock bags and frozen for later analysis.

Stomach samples were analysed at the King Edward Point Laboratory, South Georgia or the British Antarctic Survey, Cambridge. After defrosting at room temperature, whole stomach weight was taken to the nearest 0.01 g including any liquid. The stomach was then removed and weighed again, minus liquid. Stomach contents were identified to the lowest possible taxonomic resolution using a range of identification guides (Gon and Heemstra, 1990; Reid, 1996; Boltovskoy, 1999; Rauschert and Arntz, 2015). Individuals of species were counted, weighed as a species group and visually assessed for digestion. Any prey items (mainly fish) that had not undergone any visible digestion were assumed to be net feeding and discounted from further analyses (Main *et al.*, 2008).

Length measurements were taken from a maximum of 20 individuals of fish and krill species when possible (heavily digested items were not measured). For larger prey items such as fish, individual weights were recorded. When numerous small crustaceans were encountered in single stomach, subsampling was employed to estimate the total number. For heavily digested crustacean species, the number of eyes were counted and divided by two to give an estimate of abundance. Heavily digested fish were identified using otoliths where possible (Reid, 1996).

Data analysis

CPUE

Catch per unit effort (CPUE) was calculated as the number of tons of *N. rossii* caught in an hour of trawling (t/h), with the duration of each trawl used to scale the catch values and any trawls less than 15 minutes in duration were removed (after Kock *et al.*, 2004). CPUE data were split in to two time periods, early period: 1987–2002 and later period, 2004–2019. These time periods were chosen to allow easier comparison against an earlier study by Kock *et al.*, (2004) which only used the data from 1987–2002. Splitting the data set in 2002 also gives roughly the same number of hauls in each period (749 in the early period and 820 in the later period).

Biomass estimates

Biomass estimates were calculated using a swept area method utilizing catch densities from individual hauls, along with the estimated seafloor area covered by the net during the deployment (calculated using wing spread and tow distance). Mean densities were calculated for each of the two depth zones (100–200 and 201–350 m) within each of the five sectors. These mean values are then multiplied by the total available seafloor area for the associated depth zone and sector, calculated from swath bathymetry (Fretwell *et al.*, 2009). Confidence intervals were estimated using a bootstrap resampling method with 10 000 re-samples (Efron and Tibshirani, 1993). This method was used to generate biomass estimates for the whole South Georgia shelf area, as well as the five individual sectors.

Prey-Specific Index of Relative Importance (%PSIRI)

Prey were categorized into broad groups for further analysis. %PSIRI was used to calculate the importance of broad prey groups in the diet of *N. rossii*. These data were then used for comparison between years, sectors, and fish size. Size classes of fish were selected by equally splitting the available size range, (small: 200–400 mm; medium: 401–600 mm; large: 601–800 mm).

$$\%PSIRI_i = \frac{\%FO_i\ x\ (\%PN_i + \%PW_i)}{2},$$

where %FO is the percentage frequency of occurrence, %PN is the prey specific abundance, and %PW is the prey specific biomass (Brown *et al.*, 2012). %PSIRI was used in place of %IRI which can overrepresent abundant prey and underrepresent rare prey items (Brown *et al.*, 2012).

Results

CPUE and biomass estimates

During the 23 ground fish surveys, 1776 individual hauls were completed (see SM Table 1). Of these hauls, 1680 had a duration of >15 min and a depth of < 350 m, with *N. rossii* recorded in 641 (38.2%). No *N. rossii* were recorded deeper than 335 m and very few mature/adult individuals were collected in waters < 100 m during trammel net sampling, this suggests the preferred depth range for adults at South Georgia is ∼100–350 m. In the early period (1987–2002), *N. rossii* were recorded in 31.3% of hauls (total hauls = 806) and for the later period (2004–2019), this rose to 44.5% (total hauls = 874). These percentages are significantly different (binomial test, P < 0.001). The individual trawl CPUE (t/h) of *N. rossii* around South Georgia and Shag Rocks shows an increase in large hauls (>1 t/h) between the early and later period (Figure 3). There was also an increase in the number of hauls containing *N. rossii* at Shag Rocks. The reduction in effort in the South West and South East sectors in the later period, was a consequence of rough ground which is unsuitable for trawling. Many of these unsuitable grounds were identified in the early surveys (1987–1989) and not visited in subsequent years.

The proportion of hauls containing *N. rossii* over time for each sector all show an increasing trend (Figure 4a), specifically since the mid-2000s. The biomass of *N. rossii* was calculated for the combined survey area and each individual sector (Figure 4b). There was an overall increase in estimated biomass over the survey time series, much of which appears to be driven by an increase in the South East sector.

Life history

There were distinct differences in the length frequency of *N. rossii* caught between 2001 and 2003 in Cumberland Bay (shallow <100 m trammel nets) and the ground-fish survey (100–400 m; Figure 5). Estimates of the size at maturity and first spawning of both males (402 and 464 mm TL, respectively) and females (434 and 547 mm TL, respectively) have been overlaid, size at maturity values fall between the clear peaks in length frequency of the trammel net and trawl caught fish.

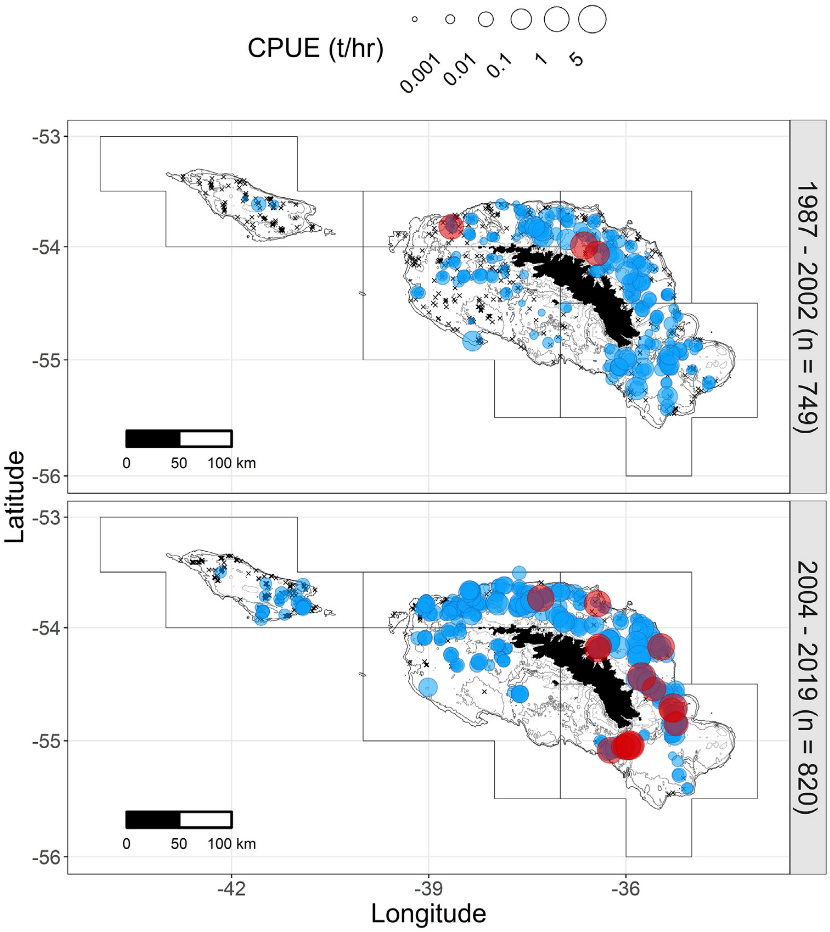

Figure 3. Catches of *Notothenia rossii* over the ground-fish survey time series. Data are presented as tonnes per hour of hauling (blue circles), red circles represent hauls with over 1 t of *N. rossii* caught. Black crosses represent hauls with no *N. rossii* caught.

Dietary analysis

In total, 511 stomachs were collected and analysed for diet composition, of these, 31 were empty (Table 1). A wide array of prey items were identified including both pelagic and benthic taxa (e.g. ophiuroids, tunicates), with evidence of occasional scavenging (e.g. fur seal, *Arctocephalus gazella*, remains), suggesting a highly generalist diet (see SM Table 3). There was no clear trend or pattern in the diversity of prey items between sectors and years.

Broad prey groups displayed a high degree of spatial and temporal variability (Figure 6). Whilst the most important prey were fish, mysids (*Antarctomysis* sp.), hyperiid amphipods (*Themisto* sp.), and euphausiids (*Euphausia* spp.), the relative importance of these groups was highly variable in time and space.

Discussion

Whilst our results indicate a gradual increase in the population of *Notothenia rossii* at South Georgia since 2005, there is no evidence that the stock has returned to pre-exploitation levels. The most recent biomass estimate of around 113 000 t is less than half the reported annual catch between 1969 and 1971 and around 18% of a minimum estimate of pre-exploitation biomass (600 000 t; Agnew, 1995). Our results, which show evidence of recovery only after 2005, are consistent with Kock *et al.,* (2004) who found no evidence of a recovery in the period to 2002.

The biomass estimate has large confidence intervals, indicative of a patchy distribution (Kock *et al.,* 2004) which has also been reported for this species in other areas such as the Kerguelen Plateau (Duhamel *et al.,* 2017). Kock *et al.* (2004) noted that *N. rossii* were regularly found in large aggregations, which were present in the same locations in multiple years and questioned the validity of a stratified survey design, which assumes an even distribution when calculating biomass estimates. Acoustic methods are often used for highly aggregated species (e.g. mackerel, herring), but as *N. rossii* lack a swim-bladder, it would not be straightforward to distinguish them from mackerel icefish or Antarctic krill, which are abundant in the area.

The aggregations of *N. rossii* described by Kock *et al.* (2004) were often found in submarine canyons off the SE coast and extending from Cumberland Bay. In early German-led surveys, conducted before the ground-fish survey time series, catches > 10 t/h were observed from submarine canyons around South Georgia (Kock, 1978, 1979). The canyons off the SE coast had consistent high catches of *N. rossii* for almost 25 years (Kock *et al.,* 2004) although little sampling effort was dedicated to these particular canyons in the later years of the survey (2004–2019). In later surveys, other canyons to the south were eventually sampled, and resulted in re-

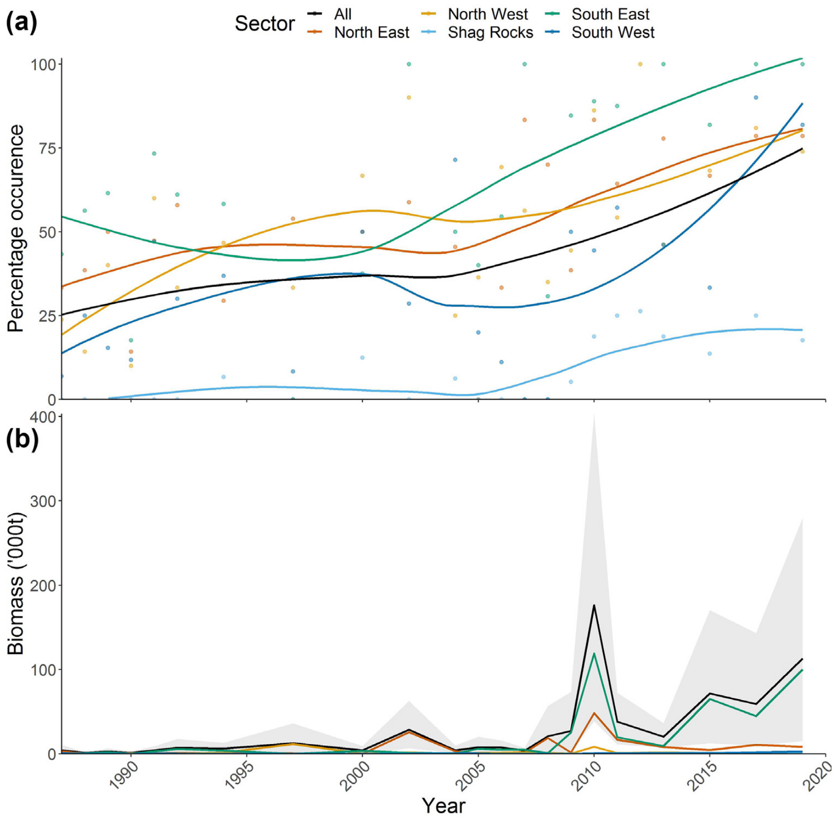

Figure 4. (a) Proportion of hauls in a given sector containing *Notothenia rossii* over the ground fish survey time series. Individual points are displayed by circles. Lines have been fitted to data from each sector using LOESS to show change over time. (b) Fishable biomass of *N. rossii* on the South Georgia shelf calculated from density estimates obtained from the ground fish survey time series. Both the combined biomass (black line) and individual sector biomasses (coloured lines) are shown. The grey shaded area represents the 95% CI of the combined biomass. CI values for individual sectors are not displayed for clarity.

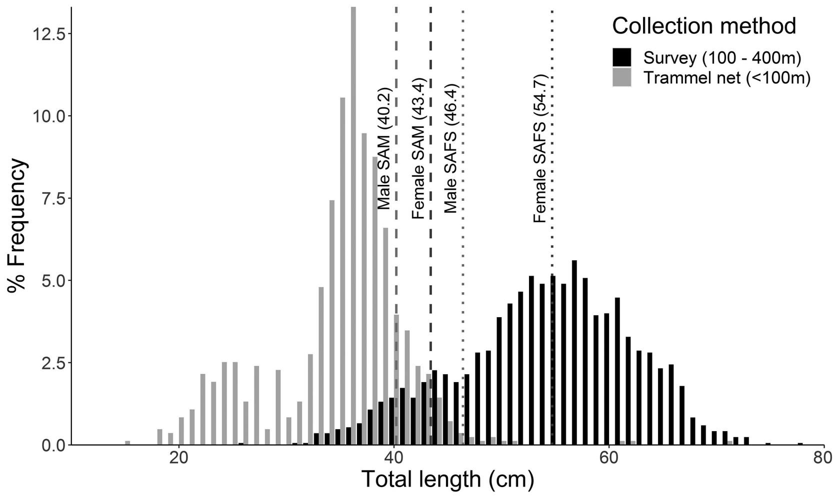

Figure 5. Length frequency of shallow water (grey, trammel net < 100m) and deeper water (black, survey 100–400 m) *Notothenia rossii* collected between 2001 and 2003. Size at maturity (SAM) and size at first spawning (SAFS) have been overlaid for males and females.

peated high catches in multiple years, along with the maximum CPUE values from the entire time series (9.3 and 8.6 t/h in 2010 and 2019, respectively). Similar aggregations of *N. rossii* were found at Elephant Island (South Shetland Islands), but here were associated with gently sloping topography (Kock *et al.*, 2004), the same has also been observed on the Kerguelen Plateau (Duhamel, 1987). The German-led surveys in 1978 and 1979 were conducted as part of semi-commercial fishing activities which actively targeted fish con-

Table 1. The number of stomachs samples processed from each sector, along with richness of prey species.

Year	Sector	n	% empty	Prey species Richness
2005	NW	20	0	15
	SE	31	0	12
	SW	11	0	8
2006	NE	10	0	9
	NW	5	0	5
	SE	32	31.25	13
2007	NE	11	9.09	8
	NW	11	0	12
2010	NE	15	0	8
2017	NE	8	12.50	9
	NW	88	3.41	33
	SE	47	14.89	19
	SR	6	0	6
	SW	26	0	9
2019	NE	70	8.57	21
	NW	77	1.30	22
	SE	17	0	5
	SR	1	0	1
	SW	25	8	17

centrations whenever they were detected (Kock *et al.*, 2004). Despite these uncertainties associated with the sampling design, we consider that our analysis provides strong evidence of a sustained period of higher occurrence and biomass since about 2005.

In parallel with the observed recovery, the spatial distribution of *N. rossii* also appears to be changing, most notably on the Shag Rocks shelf, where the frequency of catches has increased since 2009. This small population at Shag Rocks may reflect the limited shallow inshore habitat (just 91 km^2) which is necessary for juvenile development (Burchett, 1983c), although Young *et al.*, (2018) suggested that there is no resident spawning population there, with these fish being expatriates from South Georgia. The apparent expansion of *N. rossii* to Shag Rocks is unexpected for this cold-water species, as sea surface temperature at Shag Rocks is consistently warmer than the South Georgia shelf (SM figure 3). There is no obvious trend in seawater temperatures at South Georgia or Shag Rocks since the expansion began (~2009, SM Figures 4 and 5), suggesting that the migration may be driven by other environmental (e.g. passive transport in currents) or ecological factors (e.g. feeding or intraspecific competition), rather than temperature.

The two-decade lag between the cessation of fishing and signs of recovery at South Georgia is similar to delays in recovery reported in other areas where *N. rossii* was exploited (i.e. Kerguelen and the South Shetlands) (Marschoff *et al.*, 2012; Barrera-Oro *et al.*, 2017; Duhamel *et al.*, 2017). On the Kerguelen Plateau, the estimated biomass has increased from 7500 tonnes in 2006 to 193 000 tonnes in 2017 (Duhamel *et al.*, 2017), whilst in the South Shetland Islands, there was an order of magnitude an increase in survey catches between 2003 (Jones *et al.*, 2003) and 2007 (Kock *et al.*, 2007). The delayed recovery at Kerguelen was attributed to late first maturity (6–7 year at Kerguelen for females; Duhamel, 1982b; 1987) and a complex life cycle. In the South Shetland Islands, data suggest that recruitment has increased and is now similar to 1983 levels (Marschoff *et al.*, 2012). An expansion in the range of *N. rossii* was also reported at Kerguelen, with the adult *N. rossii* expanding to new areas. These expansions were often congruent with the distribution of their prey species (Hunt *et al.*, 2011; Duhamel *et al.*, 2017).

The evidence of an increase in biomass and shifting distribution of the South Georgia *N. rossii* population, may be indicative of broader ecosystem change. Since the end of exploitation of *N. rossii* at South Georgia (1985) there has been enough time for 3–4 full generational cycles up to 2005 (maturity at 5–6 years). Assuming at least a portion of the population reproduces each year, it seems unlikely that age at maturity alone would be the cause for such a protracted delay in any detectable recovery.

It is possible that predation pressure has played a role in slowing the recovery of *N. rossii*. Whilst Antarctic fur seals (*Arctocephalus*

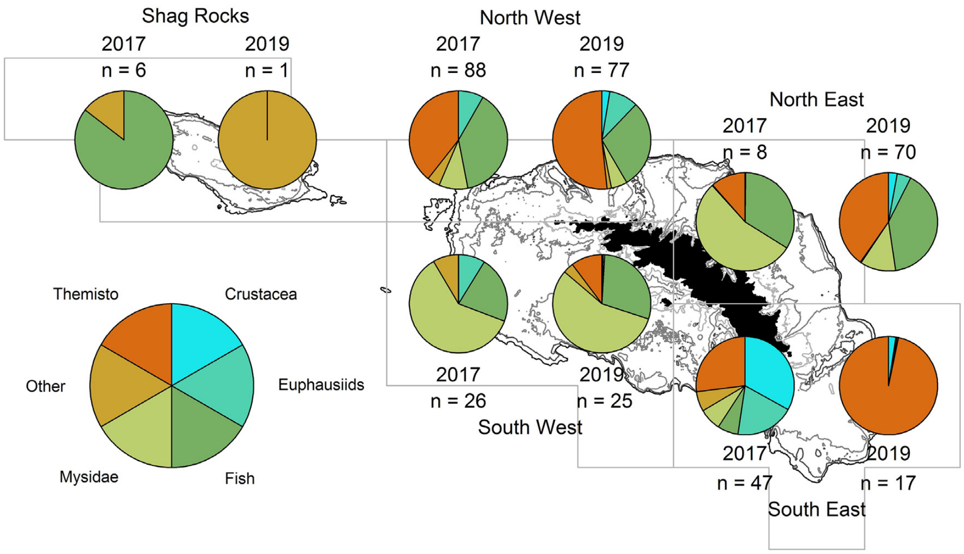

Figure 6. %PSIRI values of broad prey groups from *Notothenia rossii* stomachs collected during the 2017 and 2019 ground fish surveys displayed over the corresponding sector.

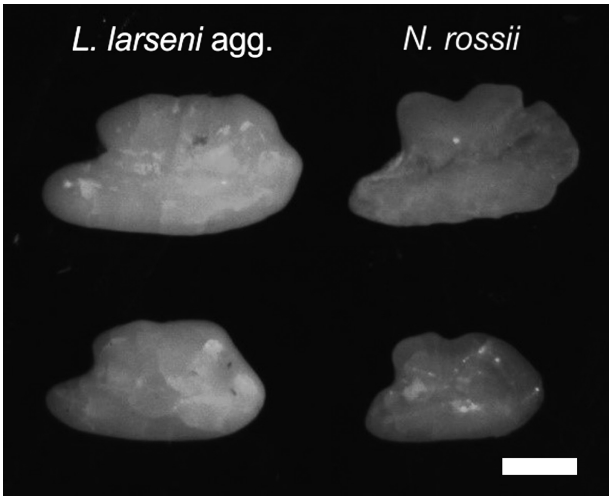

Figure 7. An example of large (top) and small (bottom) otoliths of *Lepidonotothen larseni* agg. taken from routine *Arctocephalus gazella* scat sampling, and *Notothenia rossii*, taken from live specimens. Scale bar 2 mm. Photo courtesy of K. Owen.

gazella) largely feed on krill at South Georgia (Reid and Arnould, 1996), they also feed on fish, including *N. rossii* (North *et al.*, 1983), particularly when krill is in short supply. Whilst the frequency of *N. rossii* otoliths reported in scats is low (BAS, unpublished data), it is possible that *N. rossii* otoliths are recorded as "*Lepidonotothen larseni* aggregate (agg.)" or "*Notothenia* sp." which are generic classifications for otoliths of several difficult to distinguish nototheniid species (North *et al.*, 1983; Reid and Arnould, 1996). Otoliths of small (juvenile) *N. rossii* look very similar to otoliths recorded as *L. larseni* agg. (Figure 7) and the distinction can become even more difficult when the otoliths are partially digested. Several hundred *L. larseni* agg. and *Notothenia* sp. otoliths are recorded each year (BAS, unpublished data), suggesting that *N. rossii* may be significantly underrepresented in this data set. The conspicuous absence of a common shallow water species (juvenile phase) in fur seal diets has also been noted in previous studies (North *et al.*, 1983). Genetic analysis of scat samples from *A. gazella* could help to identify the frequency of samples containing *N. rossii*, along with the full diversity of prey items found in scats (Casper *et al.*, 2007).

Extreme overexploitation in the 19th century reduced the fur seal population at South Georgia. Antarctic fur seals were scarce and restricted to Bird Island at the western end of South Georgia (Payne, 1977), with few reports of fur seals on mainland South Georgia in the 1960s and 1970s. Since the 1970s, the fur seal population has dramatically recovered, increasing at ~10% per year between 1975 and 1991 with population estimates of ~2.7 million in 1991 (Boyd, 1993), and over 4.5 million by 2000 (SCAR, 2008). If Antarctic fur seals are important inshore predators of *N. rossii*, the scarcity of fur seals in the early to mid 20th century, possibly allowed an increase in the *N. rossii* population exploited in the 1970s. Given that the recovery of the fur seal breeding population started in the west and has gradually extended east, the high densities of *N. rossii* in the SE may be linked to reduced predation pressure on juveniles in inshore areas (Boyd, 1993; Trathan *et al.*, 2012). Even with a low level of predation, this number of fur seals may well have slowed the recovery of *N. rossii* through juvenile predation in shallow waters in the years following the end of exploitation. *A. gazella* numbers also increased over the same time period in other areas reporting slow *N. rossii* recovery, such as the Kerguelen Plateau (Page *et al.*, 2003; SCAR, 2008) and the South Shetlands (Boveng *et al.*, 1998; SCAR, 2008). The pre-exploitation population size of *A. gazella* at South Georgia was thought to be around 2.5 million, which is similar to estimates from recent decades (Foley and Lynch, 2020). If this was the case, then it is unlikely that the present day population of *N. rossii* could grow to the size of the historically exploited stock with the current predation pressure.

The recovery of *Champsocephalus gunnari* stocks also experienced a protracted delay at South Georgia following exploitation in the 1970s and 1980s (Everson *et al.*, 1999). The recovery of *C. gunnari* was expected to be quick as they reach maturity much younger than other fish in the same region (~3 years) (Kock and Everson, 1997). It has been suggested that ecological interactions with both prey (*E. superba*) and predator (*A. gazella*) populations are reasons for the delay in recovery (Everson *et al.*, 1999; Reid *et al.*, 2005), with the latter eating more *C. gunnari* when there is reduced abundance of their main prey (*E. superba*). This effect is two-fold, as the reduced *E. superba* abundance also appears to negatively impact the body condition of *C. gunnari* (Everson and Kock, 2001).

The available distribution data coupled with biological information support early work by Olsen (1954) and Burchett (1983c) outlining the life cycle of *N. rossii* at South Georgia, with an offshore migration following maturity. The size of fish caught in shallow water trammel nets between 2001 and 2003 were consistent with those reported by Burchett (1982), but contrast with the offshore survey data, indicating an ontogenetic offshore migration (Figure 5). Size at maturity estimates, calculated from all available data between 2001 and 2007, were similar to the length at which all *N. rossii* are thought to migrate offshore (410 mm; Burchett, 1983a). Males mature younger (Olsen, 1954) and first spawn at a smaller size than females, and are thought to migrate to deeper water a year before their female counterparts (Burchett, 1983a). The clear differences between size at first maturity and size at first spawning also indicate that *N. rossii* are not in reproductive condition when they undergo their offshore migration. Males may well be able to spawn within a year of their offshore migration, whereas females may take a year or more after migration before they can spawn. The data suggest that South Georgia *N. rossii* reach maturity at smaller sizes than conspecifics at Kerguelen (Duhamel, 1982b) and the South Shetlands (Cali *et al.*, 2017). Males at South Georgia are ~30 mm smaller at maturity and females ~50 mm smaller than the population at Kerguelen (Duhamel, 1982b). It has previously been presumed that the life cycle of *N. rossii* is similar between populations (Kock *et al.*, 1985; Barrera-Oro, 2002; Cali *et al.*, 2017). However, analysis of daily growth increments in otoliths of *N. rossii* in the South Shetland Islands has highlighted two annual cohorts, with hatching events in both July and February (Barrera-Oro *et al.*, 2014). There is no evidence of multiple annual cohorts at South Georgia, and it is assumed that there is only one hatching period around September (Burchett, 1983c; North, 2001).

The dietary analysis represents the most comprehensive overview of adult *N. rossii* feeding to date at South Georgia and indicates a high degree of spatial, temporal, and ontogenetic variability. This variation in diet suggests that *N. rossii* are generalist feeders, which is consistent with the variable diet seen in the early life stages (Burchett, 1983b). Krill (order Euphausiacea), predominantly *E. superba*, made a relatively low contribution to the diet in the years with the greatest sampling intensity (2017 and 2019). It is likely that previous studies lacked the temporal and spatial resolution to fully explore the variability in *N. rossii* diet.

For example, McKenna (1991) only analysed 25 *N. rossii* stomachs, whilst our 2010 diet data in this paper (n=15) all came from a single haul and showed a high degree of krill feeding, highlighting the importance of widespread sampling effort (SM Figure 1). Fish, mysid shrimp and the hyperiid amphipod, *Themisto gaudichaudii*, were all important in diets in both 2017 and 2019 with krill appearing to be more important in earlier seasons in certain sectors (Figure 9, SM Figure 1). Fish size also appears to influence prey with larger *N. rossii* containing more fish in their diets and smaller *N. rossii* containing more *T. gaudichaudii* and mysid shrimp (SM Figure 2). There was also evidence of benthic feeding, with ophiuroids, tunicates, and isopods all found in adult diets, albeit at low frequency (SM Table 3). Several instances of algae, which is a prominent component of juvenile diet (Burchett, 1983b; Barrera-Oro *et al.*, 2019), were also recorded. Scavenging behaviour was evident with fur seal (*A. gazella*) fur identified in two stomachs. Reported diets from the northern Kerguelen Plateau also show a high degree of spatial variability, with *Champsocephalus gunnari* and salps more important in the north, and hyperiid amphipods, gelatinous zooplankton, and a different fish species (*Gobionotothen acuta*) more important in the south (Duhamel *et al.,* 2017).

The main crustacean prey of *N. rossii* (*T. gaudichaudii,* mysids, and krill) are important in diets of other demersal fish species at South Georgia (Kock *et al.*, 2004; Reid *et al.,* 2007; Collins *et al.,* 2008; Main *et al.*, 2008). The common, swarming hyperiid amphipod *T. gaudichaudii* (Watts and Tarling, 2012) was an important prey item for *N. rossii* in several sectors and in several years (particularly the NW in 2005, 2017, and 2019, SM Figure 1) with over 3000 individuals in some stomachs. *T. gaudichaudii* is an important prey item for other species on both the South Georgia and Patagonian shelves (Murphy *et al.*, 1998; Padovani *et al.,* 2012) and the Kerguelen Plateau (Duhamel *et al.*, 2017). At South Georgia *T. gaudichaudii* predators include mackerel icefish, *Champsocephalus gunnari* (Kock *et al.*, 1994; Main *et al.*, 2008) and macaroni penguins, *Eudyptes chrysolophus* (Murphy *et al.,* 1998; Waluda *et al.,* 2012). However, the importance of *T. gaudichaudii* in the diet of these species varies between years and may be related to the availability of other prey items such as *E. superba* (Kock *et al.,* 1994; Waluda *et al.,* 2012). Our data clearly indicate that krill are not a major component in the diet of adult *N. rossii* across the South Georgia shelf and that *N. rossii* are generalist feeders. The diet includes pelagic, demersal, and benthic species but it is unclear where the majority of feeding occurs since many of the prey items migrate between different parts of the water column (e.g. *T. gaudichaudii;* Atkinson *et al.* 1992).

Gelatinous plankton, such as cnidarians, ctenophores, and salps, all of which have been previously reported in *N. rossii* diets at South Georgia (Tarverdiyeva, 1972; Hoshiai, 1979; Burchett, 1983b; Davenport, 1998) and in other areas (Hunt *et al.,* 2011; Duhamel *et al.,* 2017), were notably absent from our data. The absence is likely due to the method of preservation, with gelatinous prey disintegrating during the freeze/thaw process as ctenophores in particular were routinely spotted in fresh stomachs. Tarverdieva, (1972) processed fresh *N. rossii* stomachs from South Georgia and reported that over 95% contained ctenophores. Previous analyses of fatty acid signatures in *N. rossii* tissue also suggest that gelatinous zooplankton are a part of the diet in this species (Stowasser *et al.,* 2012). For further dietary analysis of this species, stomach samples should be analysed when fresh or fixed in formalin to preserve tissues before preservation. Molecular methods may also be useful in identifying cryptic prey and improving the overall identification of prey species (Amundsen and Sánchez-Hernández, 2019). With the knowledge that this prey is missing, it is important to consider that there may well have been other important components to the PSIRI analysis that are absent. However, the carbon content in the wet weight of ctenophores and cnidarians is roughly 1/40th and 1/20th of that found in crustaceans, respectively (Kiørboe, 2013), and the energetic content of fish tissue is largely higher (per unit of dry weight) than that of crustaceans (Schaafsma *et al.*, 2018). Therefore, crustacean and fish prey are likely have a significantly higher energetic input to *N. rossii* diet than gelatinous zooplankton, even if the latter are relatively abundant.

Southern Ocean ecosystems, particularly those around South Georgia, are changing as a result of the combined effects of historic overexploitation and ongoing climate change (Whitehouse *et al.*, 2008; Forcada and Hoffman, 2014; Atkinson *et al.,* 2019) and many previously overexploited species are showing signs of recovery (Zerbini *et al.,* 2019; Calderan *et al.*, 2020). The diverse diet of *N. rossii* likely allows it to adapt to changing prey availability and therefore facilitate a degree of recovery. We have two strands of evidence for partial recovery: (i) the sustained trend in the biomass estimates and catch data and (ii) the apparent expansion of the population onto the Shag Rocks shelf. However, the recovery to date is modest compared to estimates of pre-exploitation biomass (600–900 000 t; Agnew, 1995). Comparisons between the current situation and that in the 1970s are hampered by scarce and uncertain data for the earlier period. Nonetheless, there are several factors that suggest that recovery to over 600 000t is unlikely. First, it is possible that early catch data include catches of other species or *N. rossii* from other areas, both of which would inflate the pre-exploitation biomass estimate. Second, the ecological conditions in the 1970s could plausibly have supported a higher biomass than is possible today. In particular, prey reources might have been more abundant (Atkinson *et al.* 2019) and potential predators more scarce, whilst at an earlier stage of recovery from overexploitation (Zerbini *et al.*, 2019; Calderan *et al.,* 2020; Foley and Lynch, 2020).

In its current state, the South Georgia ecosystem likely has a much lower carrying capacity for *N. rossii* than it did in 1970. The ecosystem continues to change with the recovery of previously depleted species, a changing climate, and continued (although well-managed) fishing for krill, toothfish, and icefish. In these conditions, there may still be capacity for further population growth; although the current trajectory does not look like a return to the estimated pre-exploitation biomass.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data Availability Statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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