



Distribution, hosts and long-term decline in abundance of the Patagonian lamprey inferred from diet assessment of albatrosses

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Received: 1 December 2022 / Accepted: 7 May 2023 / Published online: 26 May 2023
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Abstract Knowledge of lampreys during their marine phase is limited, and for the southern hemisphere species was gleaned from their predators (albatrosses) in the 1970s. Taking advantage of new methodologies and long-term data on predator diet and distributions, we infer diverse aspects of lamprey distribution and ecology. DNA analyses indicated that albatrosses at South Georgia prey on Patagonian lamprey *Geotria macrostoma*, originating from Argentina. Their core pelagic distribution when free swimming appears to be the Antarctic Polar Frontal zone (APFZ), and not South Georgia waters as assumed previously. If so, the APFZ would be the first known hotspot in abundance of an anadromous lamprey in oceanic waters. We could not identify a teleost fish that would be a likely host. Instead, we infer that the lamprey may prey on baleen whales, based on comparison of stable isotope ratios in lamprey with candidate host species, timing of appearance in albatross diets coincident with whale migrations,

and circumstantial evidence (unexplained scarring recorded during the whaling era). We suggest that the lamprey do not tolerate cold Antarctic waters, and detach from southerly-migrating whales at the thermal boundary of the APFZ, where they become accessible to albatrosses in surface waters. Given strong evidence that relative importance of prey in seabird diets reflects availability in foraging areas, the steep decrease in the annual consumption of lamprey by albatrosses at South Georgia from > 550 tonnes in 1975–1976 and 1986, to very low levels in most years since 2012, is likely to indicate a major population decrease. Despite our unconventional means of assessing the population trend, there is a compelling case for listing of Patagonian lamprey at least as Near threatened by the International Union for the Conservation of Nature, and an urgent need to better understand anthropogenic threats in Argentina.

Keywords Anadromy · Baleen whale · Biogeography · Diet determination · *Geotria macrostoma* parasitism · South Georgia stomach contents

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11160-023-09786-3>.

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Introduction

Lamprey (order Petromyzontiformes) are an ancient order of agnathan (jawless) fish. There are ~43 extant species recognised, including 18 that are parasitic (Potter et al. 2015). Of the 18 parasitic species, 10

are anadromous, migrating from marine to freshwater environments to spawn (Quintella et al. 2021). Information is very limited on the distribution, ecology and abundance of lampreys during their marine phase, although some species are known to travel very large distances in the open ocean and take several years to mature (Silva et al. 2014; Potter et al. 2015; Quintella et al. 2021). The hosts of many species also remain little-known, e.g., only in the last decade were an extra 19 hosts added to the list for the sea lamprey *Petromyzon marinus*, taking the total number up to 54, including Chondrichthyes (cartilaginous fish), Osteichthyes (bony fish) and cetaceans (Silva et al. 2014), and an extra six hosts discovered for the Arctic lamprey *Lethenteron camtschaticum* from DNA barcoding of gut contents (Shink et al. 2019).

There are four species of anadromous parasitic lamprey in the southern hemisphere, including the pouched lamprey *Geotria australis*, previously considered to be the only member of its family (Geotriidae), which appeared to have a very wide spawning distribution; rivers south of 32°S in Australia (including Tasmania), New Zealand, Chile and Argentina (Neira et al. 1988). However, environmental DNA (eDNA), and molecular and morphological studies have revealed a cryptic taxon in Argentina, revalidating the original description in 1868 of the Patagonian (or Argentinian pouched) lamprey *G. macrostoma* (Nardi et al. 2020; Riva-Rossi et al. 2020; Baker et al. 2021, Riva-Rossi et al. 2022). This corroborates studies indicating that *Geotria* populations in Argentina, Chile and Australasia are morphologically distinct (Neira et al. 1988), and is in accordance with the suggestion by Potter et al. (1979) that, following the direction of the prevailing currents, young adults from Argentina should move south and east in their marine phase, and those from Chile should move north. Although the hosts of *Geotria* remain unknown (Miller et al. 2021), based on dentition, they feed on flesh rather than on carrion or blood as in some other parasitic lamprey species (Renaud et al. 2009).

Seabirds and seals are known to eat lamprey, sometimes in very high numbers, in rivers and estuaries (Clemens et al. 2019), and pouched lamprey are consumed by coastal predators in the Southern Hemisphere (Miller et al. 2021). However, lamprey are very rarely recorded as prey of pelagic predators even though several species are presumably common in the open ocean. The one exception is the high incidence

of lamprey—originally identified as *Geotria australis*—in the diet during chick-rearing of grey-headed albatrosses *Thalassarche chrysostoma*, and to a lesser extent black-browed albatrosses *T. melanophris* breeding at Bird Island, South Georgia from the 1970s to 2000s (Potter et al. 1979; Mills et al. 2020a, b; Xavier et al. 2003a, b; Xavier et al. 2013). Knowledge of parasitic lamprey up until the late 1970s was based mainly on the landlocked form of the sea lamprey in the Great Lakes region, until Potter et al. (1979) used the samples from albatrosses to make a number of inferences about the life cycle and ecology. That study concluded that huge numbers were present in surface waters around South Georgia, of which an estimated 1,800,000 and 100,000 individuals were consumed annually by grey-headed and black-browed albatrosses, respectively, and that they were caught when free swimming near the sea surface rather than attached to a host. In addition, two hosts were tentatively proposed—southern blue whiting *Micromesistius australis* and Patagonian toothfish *Dissostichus eleginoides*—because they were abundant and had distributions thought to overlap with the lamprey, but recognising that these were not substantiated by observations of attacks. Finally, based on sizes of lamprey eaten by albatrosses compared with metamorphosing and downstream migrants in Chile and elsewhere, Potter et al. (1979) concluded that lamprey consumed around South Georgia had been at sea for more than a year and were in the latter stage of the adult parasitic phase.

Knowledge of *Geotria* at sea has progressed little in the decades since Potter et al. (1979). However, annual monitoring of diets of grey-headed and black-browed albatrosses at Bird Island has continued, providing more data on lamprey incidence, and specimens for stable isotope and pollutant analysis (Anderson et al. 2009, 2010). In addition, diet sampling and deployment of tracking devices has provided unprecedented detail on distributions and diets of many seabirds and seals in this region (Frankish et al. 2020; Wakefield et al. 2011; Phillips et al. 2008; Reid and Arnould 1996; Waluda et al. 2017, 2012; Mills et al. 2021; Moreno et al. 2016). Forensic methods of diet determination have become available, including stable isotope analysis of predator tissues to determine trophic level and carbon source of prey (Peterson and Fry 1987), as well as the trophic levels and hosts of sea

lamprey in the Great Lakes (Harvey et al. 2008). The ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}$) increases by 2 to 4‰ per trophic level in the marine environment (Vanderklift and Ponsard 2003; Seyboth et al. 2018). The ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) increases to a lesser extent ($\leq 1\text{‰}$) with trophic level, but indicates carbon source, which reflects spatial variation, particularly water mass or latitude, in pelagic regions of the Southern Ocean (Phillips et al. 2009; Jaeger et al. 2013; France and Peters 1997; Ceia et al. 2015). In addition, analyses of mitochondrial DNA markers are often used to determine phylogenetic relationships, including among lamprey (Riva-Rossi et al. 2020; Espanhol et al. 2007).

Our study takes advantage of these methodological developments, improved knowledge of distribution and foraging ecology of predators, and ongoing diet sampling, to examine long-term changes in the consumption of *Geotria* by albatrosses at South Georgia. We test conclusions from Potter et al. (1979), and infer other aspects of the *Geotria* life cycle. Our objectives were to: (i) determine if the lamprey consumed by albatrosses at South Georgia is the nominate *G. australis* or the newly revalidated Patagonian lamprey *G. macrostoma*, (ii) analyse changes in the occurrence and estimated total consumption of lamprey by grey-headed and black-browed albatrosses over the last four decades, (iii) test for changes with month in the incidence of lamprey in albatross diets, which would indicate seasonality in availability in the upper water column, (iv) identify the main area of occurrence of *Geotria* in pelagic waters of the southwest Atlantic, inferred from high-resolution tracking data now available from albatrosses and other predators, and (v) identify the most likely candidate host species, by examining co-occurrence with other taxa in diet samples, and by comparing stable isotope ratios in lamprey with bony fish and cetaceans in the region. The results are discussed in the context of the distribution, abundance, ecology and conservation of lamprey in the southwest Atlantic Ocean.

Methods

Sampling methods

Diet samples (stomach contents) were obtained via induced regurgitation of grey-headed and black-browed albatross chicks in 1959–1961, 1975–1976, 1986, 1994 and 1996–2022, and adults in 1975–1976 at Bird Island, South Georgia (54°00'S, 38°03'W). For details of sample collection and processing, see Tickell (1964), Prince (1980), Reid et al. (1996) and Mills et al. (2020a, b). Induced regurgitation has no significant effect on chick survival or fledging mass (Phillips 2006), and no chicks were sampled more than once. The vast majority of sampling (99.0% and 96.5% for black-browed and grey-headed albatrosses, respectively) was in February to April, during the chick-rearing period. Briefly, the samples were drained through sieves to separate the liquid and solid fractions, and the latter separated into major dietary component (cephalopods, fish, Antarctic krill *Euphausia superba*, lamprey, carrion [mostly penguin feathers or seal fur], and other [mostly other crustaceans and non-food items such as fishing debris and tussac grass *Poa flabellata*]). Within each major dietary component, prey items were further identified, where possible, using reference material and published guides. Lamprey were recorded in samples as whole animals, heads only, teeth only or not specified.

Genetic analyses

Muscle tissue from seven lamprey collected in 2002 to 2011 was stored frozen, then later transferred to 70% ethanol and sent for analysis at the University of Otago. DNA was extracted successfully from four specimens using a Qiagen DNeasy Blood and Tissue kit. The DNA extracts were quantified via Qubit Fluorometer (Thermo Fisher Scientific) and the cytochrome c oxidase I (COI) region was amplified using the FishFI and FishR1 primers following the protocol described by Ward et al. (2005). Exonuclease I and shrimp alkaline phosphatase (https://www.nucleics.com/DNA_sequencing_support/exonucleaseI-SAP-PCR-protocol.html) were used to purify the PCR products that were then sequenced (reverse and forward directions) on an Applied Biosystems 3730xl DNA Analyzer (Applied Biosystems). All available *Geotria* COI sequences were downloaded

from NCBI GenBank and 19 New Zealand *G. australis* sequences were downloaded from the Aotearoa Genomics Data Repository (AGDR). These previously published COI sequences were then combined with the newly sequenced COI samples for downstream analyses (Supplementary Material Table S1). Geneious Prime v2020.1.1. was used to inspect and edit (e.g. low-quality bases) the raw sequences before they were aligned using MAFFT (Katoh and Standley 2016) with the E-INS-I strategy. Uncorrected distances and sequence similarity were then evaluated using Geneious and BLAST, respectively. Haplotype networks (median joining; Bandelt et al. 1999) were created using PopART (Leigh and Bryant 2015). The new sequences were deposited into NCBI GenBank.

Lamprey consumption

The presence of lamprey in the diet of each albatross species was quantified in terms of percentage occurrence (%O), and percentage by mass (%M; available for adults in 1975–1976 and chicks from 1986 to 2022). Percentage occurrence was compared among months (February to April) to test for seasonality in lamprey availability in the albatross foraging areas. That analysis only included years in which data were available for all three months (1997, 1999–2010 and 2012–2022).

The total mass of lamprey consumed by adults and chicks each year was estimated for each albatross species at South Georgia. The approach of Prince (1980) was used for chicks, although with some changes to parameter values. The estimated mass of all prey consumed by chicks was calculated as the mathematical product of annual breeding population size and breeding success, which approximates to the total number of chicks raised, mean chick-meal mass and the number of days on which a meal is provided. Annual breeding population sizes were estimated by indexing the total breeding population at South Georgia in the all-island surveys in 2003/04 (Poncet et al. 2006) to the proportional change in breeding pairs each year in study colonies monitored annually at Bird Island. The clutch size in albatrosses is one egg, and breeding success was calculated as chicks fledged divided by eggs laid. The values used for mean meal mass were 0.616 kg and 0.569 kg for grey-headed and black-browed albatrosses, respectively, based on data from automatic balances deployed in 1990–1996 (Huin

et al. 2000). These values were slightly higher than those used by Prince (1980), which were 0.596 kg and 0.537 kg, based on weighing chicks before and after feeds in 1959–1961. The calculations were repeated using the mean mass fed per day to chicks on the automatic nest balances (Huin et al. 2000), and the duration (in days) of chick-rearing, but results were very similar and only the former are presented. The total mass of lamprey eaten by chicks was calculated from the estimated total mass of all prey, multiplied by the annual percentage by mass of lamprey.

The total mass of lamprey consumed by adult albatrosses during chick-rearing each year was estimated using a simple bioenergetics model. Mean body masses during chick-rearing of grey-headed and black-browed albatrosses at Bird Island were 3290.5 g and 3356.5 g, respectively (Phillips et al. 2004). Field metabolic rate ($\text{kJ}\cdot\text{day}^{-1}$) was estimated from body mass using allometric equations for Procellariiformes in Shaffer et al. (2011), and used to calculate the total energy required (in kJ) during chick-rearing for both parents at nests where the chick fledged. As lamprey are around twice as energy dense as other prey (Clarke and Prince 1980), their percentage contribution in terms of energy was estimated from the percentage mass ($\%M_{\text{Lamprey}}$) in the diet according to the following equation, $(2 \times \%M_{\text{Lamprey}})/(1 + \%M_{\text{Lamprey}})$. The total mass of lamprey consumed by adults was then calculated as their total energy requirement multiplied by the percentage contribution of lamprey each year, divided by the mean energy density of lamprey (11.53 kJ/g; Clarke and Prince 1980).

Co-occurrence of lamprey and other prey species

As co-occurrence of lamprey and another species in diet samples might indicate that the latter was a potential host, we used chi-square tests to compare the proportion of samples in which lamprey was recorded along with other species of fish and squid, with the expected proportion if there was no association. Analyses were restricted to taxa that were found in the same sample as lamprey on at least 10 occasions. Although these other prey included both squid and fish, as far as we are aware, squid have never been recorded as hosts for any lamprey species from analysis of DNA or morphological remains in their guts (Clemens et al. 2019; Shink et al. 2019; Silva et al. 2014).

Stable isotope comparisons

Stable isotope ratios of muscle from lamprey obtained from albatross diet samples at Bird Island were presented by Anderson et al. (2009), but with no discussion of implications in terms of hosts. Lipids had been extracted from these samples over a 4 h period using Soxhlet apparatus containing 1:1 methanol to chloroform solvent mixture, prior to isotope analysis. We compared isotope ratios of lamprey with those of muscle, baleen or skin of potential hosts, including southern blue whiting and Patagonian toothfish (both considered to be candidate hosts by Potter et al. 1979), the fish species that co-occurred most frequently with the lamprey in the albatross diet samples (mackerel icefish *Champscephalus gunnari* and the myctophids *Protomyctophum choriodon*, *Electrona antarctica*), and migratory cetaceans in the region, given previous circumstantial evidence (from scarring), and recent confirmation of lamprey parasitism of several cetaceans (Samarra et al. 2012; Nichols and Tschertter 2011; Nichols and Hamilton 2004; Pike 1951; Mackintosh and Wheeler 1929). Where possible, values were taken from studies in the southwest or south Atlantic Ocean. Interpretation of differences in stable isotope ratios between lamprey and the candidate hosts requires that ^{15}N and ^{13}C enrichment with trophic level be taken into consideration, the mean values for which range from 2.5 to 3.4 ‰, and ≤ 1 ‰, respectively, in marine environments, reflecting diverse factors (Vanderklift and Ponsard 2003; France and Peters 1997).

Unless indicated otherwise, all means are presented in results \pm SD.

Results

Taxonomic identification

The 589 bp trimmed COI region from the four sequenced lamprey collected from the albatross stomach contents were nearly identical (99.66 pairwise similarity) to the published Argentina Patagonian lamprey sequences on GenBank (MT478622–43). This confirmed that the lamprey found in the stomach contents were Patagonian lamprey (*G. macrostoma*). In addition, the sequences from these lamprey demonstrated pairwise similarity of $\sim 87.78\%$ (72–74 fixed

substitutions), $\sim 86.8\%$ (77–78 fixed substitutions), and $\sim 87.1\%$ (78 fixed substitutions) to the 2 Chile, 12 Western Australia, and 25 New Zealand + Australia (not including Western Australia) sequences, respectively (Fig. 1).

Annual and seasonal variation in lamprey consumption

In total, 1422 and 1410 stomach contents were collected from grey-headed and black-browed albatrosses during the chick-rearing period from 1959–1961 to 2022 (Table 1). The vast majority were collected directly from chicks, and the remainder from adults intercepted before the chick was fed. Including years from 1997 onwards in which samples were collected in all three months, the mean percentage occurrence (%O) of lamprey in stomach contents in February and March was similar, and around twice as high as in April in both grey-headed albatrosses (33.0%, 33.9% and 18.8%, respectively) and black-browed albatrosses (3.9%, 3.1% and 1.4%, respectively).

The contribution of lamprey in the diet was very similar within species in samples from adults and chicks in 1975–1976, and so samples were pooled in all comparisons. Mean annual %O from 1959–1961 to 2022, and percentage wet mass (%M) from 1975–1976 to 2022 of lamprey was $27.0 \pm 16.6\%$ and $3.02 \pm 3.20\%$, respectively, in diet samples from grey-headed albatrosses, which was 9–10 \times higher than in samples from black-browed albatrosses ($2.58 \pm 2.69\%$ for %O and $0.33 \pm 0.63\%$ for %M) (Table 1). Samples were only available for one or two years per decade prior to 1994, and lamprey %M was unavailable for 1959–1961. As such, long-term trends in the importance of lamprey until the mid 1990s are uncertain given the high annual variability in subsequent years. Nevertheless, in grey-headed albatrosses, mean annual percentage occurrence and percentage mass of lamprey from 2012 to 2022 were less than one half and one twentieth, respectively, of the values in previous decades (mean %O of 34.7 ± 13.8 in 1959–1961 to 2011 vs 14.2 ± 13.8 in 2012–2022, and mean %M of 4.62 ± 2.99 in 1975–76 to 2011 vs 0.25 ± 0.53 in 2012–2022) (Fig. 2). Long-term trends in black-browed albatrosses similarly show a decline in importance in 2012 to 2022 to less than one half and one eighth of values in previous years (mean %O of 3.32 ± 2.96 in 1959–1961 to 2011 vs 1.52 ± 1.74

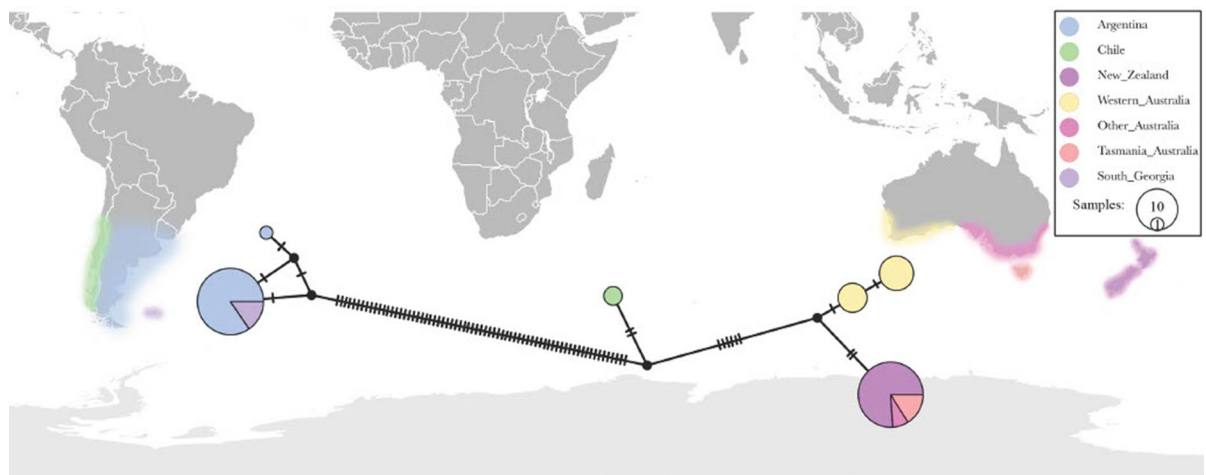


Fig. 1 Median joining haplotype network of newly-sequenced lamprey collected from the stomachs of albatrosses and combined with published *Geotria* cytochrome c oxidase I (COI) sequences (for full sample list see Table S1). Colours corre-

spond to locations, sizes of circles correspond to the frequency of the sequences belonging to a haplotype, and the hashes (|) along the lines correspond to the number of fixed substitutions (mutations) between haplotypes

in 2012–2022, and mean %M of 0.48 ± 0.74 in 1975–1976 to 2011 vs 0.06 ± 0.20 in 2012–2022) (Fig. 2).

The estimated total consumption of lamprey each year by adult albatrosses was $2.6 \times$ that of chicks (range $2.44\text{--}2.70 \times$ and $2.55\text{--}2.60 \times$ in grey-headed and black-browed albatrosses, respectively) from 1975–76 to 2022. Annual consumption was highly variable, ranging from 0 to 358.4 t (mean 57.6 ± 95.9 t) for adults, 0 to 179.5 t (mean 28.1 ± 47.8 t) for chicks, and 0 to 538.0 t (mean 85.7 ± 143.7 t) in total for grey-headed albatrosses (Table 2). Values were from 0 to 77.1 t (mean 8.7 ± 17.9 t) for adults, 0 to 31.8 t (mean 3.55 ± 7.35 t) for chicks and 0 to 109.0 t (12.2 ± 25.2 t) in total for black-browed albatrosses (Table 3). On average, grey-headed albatrosses consumed around $7 \times$ as much lamprey as black-browed albatrosses, despite having a breeding population at South Georgia around 55% of the size. Total consumption of lamprey by grey-headed albatrosses was very high in 1975–76 and 1986, low to intermediate from 1994 to 2011, and then nil or low to 2022 (Fig. 3). Consumption of lamprey by black-browed albatrosses has been nil since 2013 (Fig. 3, Table 3).

Co-occurrence of lamprey and other prey species

Lamprey co-occurred significantly more often than expected with eight squid taxa, *Moroteuthopsis longimana*, *Gonatus antarcticus*, *Filippovia knipovitchi*, *Alluroteuthis antarcticus*, *Histioteuthis B*, *Chiroteuthis* sp., *Chiroteuthis veranyi*, *Batoteuthis skolops* and *Mastigoteuthis psychrophila* but no fish species, in the diet of grey-headed albatrosses (Table 4). There was no significant co-occurrence with other prey species in the diet of black-browed albatrosses.

Stable isotope ratios of lamprey and potential hosts

Mean values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in muscle of lamprey ($n=11$) sampled in 2001/02 were -22.27 ± 2.08 ‰ (range -25.11 to -17.60 ‰) and 8.45 ± 0.57 ‰ (range 7.90 to 9.49 ‰), respectively. The values for $\delta^{13}\text{C}$ in the lamprey correspond broadly to those of a wide range of fish and cetaceans sampled from continental shelf, subantarctic and Antarctic waters, but in two lamprey exceed those in southern blue whiting, gaptooth lanternfish *Protomyctophum choriodon*, and mackerel icefish *Champscephalus gunnari* (Table 5, Fig. 4). The values for $\delta^{15}\text{N}$ in the lamprey are considerably lower than in killer whales *Orcinus orca*, Patagonian toothfish, southern blue whiting and gaptooth lanternfish *Protomyctophum choriodon*, but

Table 1 Lamprey in the diet of grey-headed and black-browed albatrosses in chick-rearing (February to April) at Bird Island, South Georgia (1959–1961 to 2022). Source ¹Tickell (1964), ²Prince (1980), ³Reid et al. (1996)

Year	Age group	Grey-headed albatross				Black-browed albatross			
		N_{tot}	$N_{lamprey}$	%O	%M	N_{tot}	$N_{lamprey}$	%FO	%M
1959–1961 ¹	Chick	111	24	21.4		109	0	0	0
1975–1976 ²	Chick	170	56	32.9		170	8	4.7	
1975–1976 ²	Adult	132	45	34.1	10.4	138	6	4.3	1.5
1986 ³	Adult	40	5	12.5	10.7	43	1	2.3	0.9
1994 ³	Adult	37	1	2.7	2.4	38	0	0	0
1996	Chick	35	9	25.7	5.2	20	1	5.0	0.3
1997	Chick	40	12	30.0	3.0	39	0	0	0
1998	Chick	38	10	26.3	7.4	46	0	0	0
1999	Chick	40	19	47.5	2.8	30	2	6.7	trace
2000	Chick	120	61	50.8	4.5	120	4	3.3	0.1
2001	Chick	34	9	26.5	3.8	31	1	3.2	0.7
2002	Chick	34	18	52.9	7.1	39	3	7.7	2.4
2003	Chick	30	11	36.7	1.8	30	1	3.3	0
2004	Chick	30	9	30.0	3.8	30	2	6.7	0.1
2005	Chick	30	12	40.0	3.0	30	3	10.0	2.1
2006	Chick	30	13	43.3	3.6	30	0	0	0
2007	Chick	30	13	43.3	1.3	30	1	3.3	trace
2008	Chick	31	11	35.5	7.0	27	1	3.7	0.6
2009	Chick	30	8	26.7	7.9	30	1	3.3	0.5
2010	Chick	30	18	60.0	0.7	30	0	0	0
2011	Chick	20	7	35.0	1.7	20	0	0	0
2012	Chick	30	0	0	0	30	1	3.3	0.7
2013	Chick	30	0	0	0	30	1	3.3	trace
2014	Chick	30	6	20.0	0.7	30	1	3.3	trace
2015	Chick	30	8	26.7	trace	30	0	0	0
2016	Chick	30	2	6.7	trace	30	0	0	0
2017	Chick	30	0	0	0	30	0	0	0
2018	Chick	30	4	13.3	trace	30	1	3.3	trace
2019	Chick	30	7	23.3	trace	30	0	0	0
2020	Chick	30	0	0	0	30	0	0	0
2021	Chick	30	9	30	1.7	30	0	0	0
2022	Chick	30	11	36.7	0.2	30	1	3.3	trace

N_{tot} No. diet samples collected, $N_{lamprey}$ no. samples with lamprey, %O = percentage occurrence ($N_{lamprey}/N_{tot}$), %M—percentage wet mass

around or above the means for various baleen whales (Table 5, Fig. 4). Given the expected trophic enrichment factors of 2.5 to 3.4 ‰, and ≤ 1 ‰ for ¹⁵N and ¹³C, respectively, it is highly unlikely that killer whale, Patagonian toothfish, southern blue whiting or lanternfish are host species.

Discussion

This study is the first in over 40 years to address key questions about the distribution, abundance,

hosts and other aspects of the life cycle of *Geotria* lamprey in the open ocean, taking advantage of methodological developments and long-term diet studies of the main seabird predators. Although there were only four samples, the DNA analyses (targeted marker COI) of muscle tissue indicate that all were the Patagonian lamprey *Geotria macrostoma*, which was confirmed only recently as a separate species from the pouched lamprey *G. australis* (Nardi et al. 2020; Riva-Rossi et al. 2020). Lamprey are not recorded in rivers at South Georgia, and are extremely rare in the Falklands

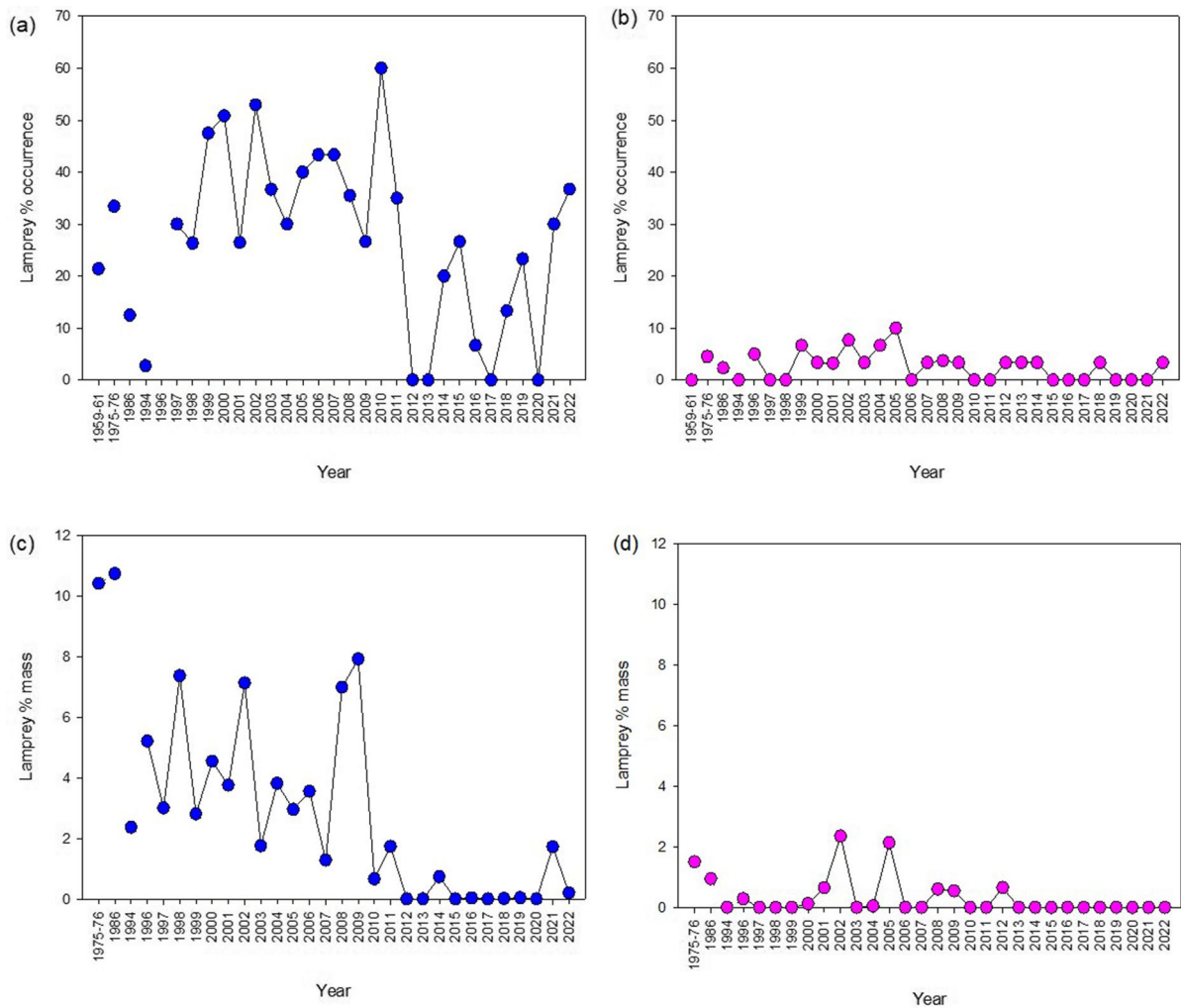


Fig. 2 Long-term trends in the relative importance of lamprey in the diet of grey-headed (GHA) and black-browed albatrosses (BBA) in chick-rearing (February to April) at Bird Island, South Georgia (1959–1961 to 2022). **a** % occurrence of lam-

prey in GHA diet, **b** % occurrence of lamprey in BBA diet, **c** percentage wet mass of lamprey in GHA diet, and **d** percentage wet mass of lamprey in BBA diet

(McDowall et al. 2001), and so our identification corroborates the conclusion of Potter et al. (1979) that the lamprey consumed by the albatrosses originate from Argentina and likely dispersed east from the Patagonian Shelf with the prevailing currents, either swimming or on their hosts. A Chilean origin is far less likely given the coastal currents flow in a different direction. In addition, we infer the core pelagic distribution of the Patagonian lamprey from improved knowledge of the distributions and diets of albatrosses and other marine predators at

South Georgia. We propose a potential new group of hosts from a comparison of stable isotope ratios, and by the timing of host movements coincident with monthly changes in incidence of lamprey in albatross diets. We also document what appears to be a steep decline in the consumption of lamprey since 2012, for which there are several potential explanations.

Table 2 Estimated annual consumption of lamprey by grey-headed albatrosses in chick-rearing (February to April) at Bird Island, South Georgia (1975–1976 to 2022)

Year	Breeding pop. (pairs)	Breeding success	Chicks fledged	Lamprey %M	Lamprey %E _{Ad}	Lamprey consumed (t)		
						Chicks	Adults	All birds
1975–1976	85,795	0.460	39,466	10.40	18.84	179.5	358.4	538.0
1986	62,392	0.590	36,811	10.72	19.36	172.6	343.6	516.2
1994	50,310	0.305	15,345	2.36	4.61	15.8	34.1	49.9
1996	74,480	0.506	37,663	5.20	9.89	85.7	179.5	265.1
1997	49,379	0.556	27,457	3.00	5.83	36.0	77.1	113.1
1998	57,153	0.061	3465	7.36	13.71	11.2	22.9	34.1
1999	68,556	0.485	33,254	2.80	5.45	40.7	87.3	128.1
2000	35,352	0.150	5303	4.54	8.69	10.5	22.2	32.7
2001	50,325	0.310	15,601	3.75	7.23	25.6	54.4	80.0
2002	50,740	0.292	14,838	7.12	13.29	46.2	95.1	141.3
2003	45,349	0.249	11,296	1.75	3.44	8.6	18.7	27.4
2004	47,674	0.133	6351	3.81	7.34	10.6	22.5	33.1
2005	39,499	0.098	3867	2.95	5.73	5.0	10.7	15.7
2006	40,728	0.097	3955	3.55	6.86	6.1	13.1	19.2
2007	38,358	0.106	4083	1.28	2.53	2.3	5.0	7.3
2008	39,765	0.630	25,052	6.98	13.05	76.5	157.6	234.1
2009	38,344	0.675	25,889	7.91	14.66	89.6	183.0	272.5
2010	34,034	0.403	13,702	0.66	1.31	4.0	8.7	12.6
2011	29,176	0.219	6400	1.73	3.40	4.8	10.5	15.3
2012	34,774	0.265	9227	0	0	0	0	0
2013	25,207	0.208	5235	0	0	0	0	0
2014	28,909	0.305	8815	0.73	1.45	2.8	6.2	9.0
2015	33,293	0.175	5824	0	0	0	0	0
2016	21,564	0.370	7981	0.03	0.06	0.1	0.2	0.3
2017	21,297	0.138	2939	0	0	0	0	0
2018	23,593	0.373	8800	0.01	0.02	<0.1	0.1	0.1
2019	22,556	0.336	7579	0.04	0.08	0.1	0.3	0.4
2020	22,497	0.462	10,393	0	0	0	0	0
2021	25,029	0.387	9686	1.72	3.38	7.3	15.8	23.1
2022	21,460	0.361	7747	0.20	0.40	0.7	1.5	2.2

For details of calculations, see text. %M—percentage wet mass of lamprey; %E_{Ad}—percentage energy contribution of lamprey to adult diet

Lamprey pelagic distribution

Multiple years of tracking since the 1990s indicate that during chick-rearing, grey-headed albatrosses from South Georgia predominantly forage in sub-antarctic waters in the Antarctic Polar Frontal Zone (APFZ; the water mass between the sub-Antarctic Front and the APF), and to a lesser extent in Antarctic waters, whereas black-browed albatrosses mainly feed in Antarctic waters (Wakefield et al. 2011; Phillips

et al. 2004; Catry et al. 2004; Xavier et al. 2003a, b). These two albatross species are similar morphologically and consume similar types of prey but in different proportions (Mills et al. 2020a, b). Given that they are far more common in the diet of grey-headed than black-browed albatrosses, the Patagonian lamprey are likely to have been caught in the APFZ (see Fig. 5). Without the benefit of seabird tracking studies, Potter et al. (1979) understandably concluded that the lamprey were found around South Georgia. However,

Table 3 Estimated annual consumption of lamprey by black-browed albatrosses in chick-rearing (February to April) at Bird Island, South Georgia (1975–1976 to 2022)

Year	Breeding pop. (pairs)	Breeding success	Chicks fledged	Lamprey %M	Lamprey %E _{Ad}	Lamprey consumed (t)		
						Chicks	Adults	All birds
1975–1976	93,760	0.490	45,942	1.50	2.96	22.4	54.6	76.9
1986	93,760	0.310	29,066	0.94	1.86	8.9	21.8	30.6
1994	99,167	0.075	7438	0	0	0	0	0
1996	86,337	0.430	37,125	0.28	0.56	3.4	8.3	11.7
1997	103,438	0.355	36,721	0	0	0	0	0
1998	89,390	0.030	2682	0	0	0	0	0
1999	90,467	0.485	43,876	0	0	0	0	0
2000	84,480	0.360	30,413	0.12	0.24	1.2	2.9	4.1
2001	85,811	0.365	31,321	0.65	1.29	6.6	16.3	22.9
2002	84,386	0.495	41,771	2.35	4.59	31.8	77.1	109.0
2003	90,809	0.150	13,621	0	0	0	0	0
2004	75,500	0.275	20,763	0.05	0.10	0.3	0.8	1.2
2005	73,118	0.265	19,376	2.13	4.17	13.4	32.5	45.9
2006	70,516	0.195	13,751	0	0	0	0	0
2007	70,185	0.495	34,742	0	0	0	0	0
2008	76,075	0.495	37,657	0.60	1.19	7.3	18.1	25.4
2009	72,811	0.520	37,862	0.54	1.07	6.6	16.4	23.0
2010	72,361	0.190	13,749	0	0	0	0	0
2011	67,228	0.350	23,530	0	0	0	0	0
2012	66,306	0.320	21,218	0.65	1.29	4.5	11.0	15.5
2013	61,433	0.411	25,249	0	0	0	0	0
2014	58,689	0.403	23,622	0	0	0	0	0
2015	64,200	0.518	33,256	0	0	0	0	0
2016	63,869	0.238	15,201	0	0	0	0	0
2017	57,056	0.168	9585	0	0	0	0	0
2018	56,607	0.293	16,586	0	0	0	0	0
2019	56,252	0.249	14,007	0	0	0	0	0
2020	54,171	0.253	13,705	0	0	0	0	0
2021	55,140	0.508	28,011	0	0	0	0	0
2022	52,136	0.438	22,836	0	0	0	0	0

For details of calculations, see text. %M—percentage wet mass of lamprey; %E_{Ad}—percentage energy contribution of lamprey to adult diet

although there is a record of lamprey in South Georgia waters (Ivanova-Berg 1968), the species must be extremely rare as none have been caught in nets during numerous fisheries surveys using non-selective demersal trawls at depths from 100 m to > 350 m, nor trammel nets set in shallow inshore waters (10–100 m depth) starting in summer 1986/87 (Mark Belchier and Martin Collins *pers. comm.*), or recorded in any diet study of piscivorous species that feed in South Georgia waters or elsewhere south of the APF,

including giant petrels *Macronectes* spp., white-chinned petrels *Procellaria aequinoctialis*, macaroni penguins *Eudyptes chrysolophus*, gentoo penguins *Pygoscelis papua*, Antarctic fur seals *Arctocephalus gazella*, Patagonian toothfish, myctophids or notothenioids (Waluda et al. 2017, 2012; Mills et al. 2021; Berrow and Croxall 1999; Davis et al. 2006; Collins et al. 2010, 2007; Saunders et al. 2015; Hollyman et al. 2021).

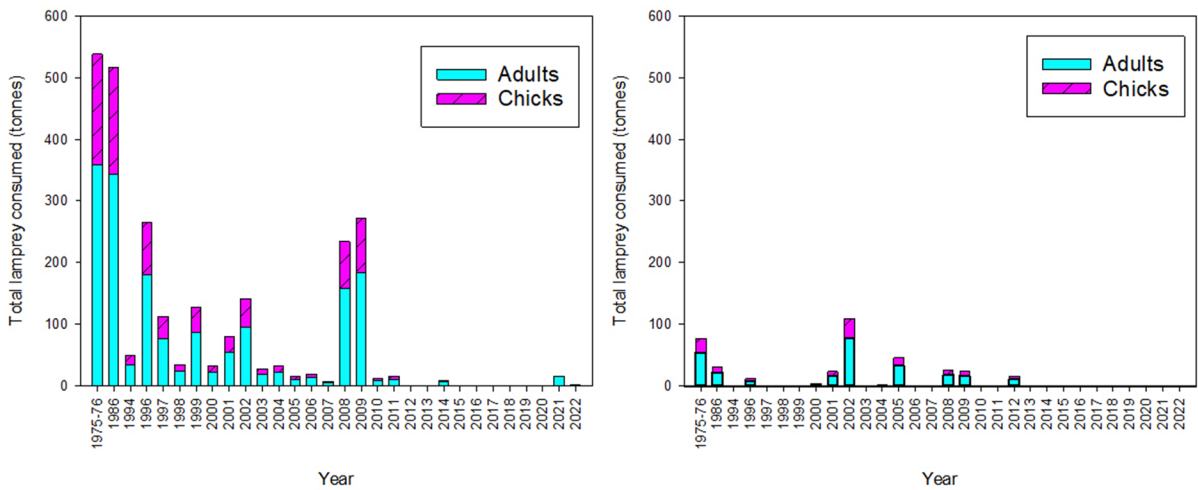


Fig. 3 Long-term trends in the consumption of lamprey by adults and chicks in **a** grey-headed albatrosses, and **b** black-browed albatrosses in chick-rearing (February to April) at Bird Island, South Georgia (1975–1976 to 2022)

Table 4 Co-occurrence of lamprey with other prey in the diet of grey-headed albatrosses and black-browed albatrosses in chick-rearing (February to April) at Bird Island, South Georgia (1996–2022)

	No. of samples in which present	No. of diet samples co-occurring with lamprey	No. of diet samples expected to co-occur with lamprey	χ^2
<i>Grey-headed albatross</i>				
Squid				
<i>Galiteuthis glacialis</i>	637	219	196.2	2.66
<i>Martialia hyadesi</i>	554	187	170.6	1.58
<i>Moroteuthopsis longimana</i>	483	180	148.7	6.57*
<i>Gonatus antarcticus</i>	278	109	85.6	6.39*
<i>Psychroteuthis glacialis</i>	272	92	83.8	0.81
<i>Filippovia knipovitchi</i>	149	69	45.9	11.65**
<i>Alluroteuthis antarcticus</i>	129	60	39.7	10.35**
<i>Histioteuthis B</i>	67	36	20.6	11.45**
<i>Chiroteuthis sp.</i>	60	27	18.5	3.93*
<i>Chiroteuthis veranyi</i>	35	18	10.8	4.84*
<i>Batoteuthis skolops</i>	31	13	9.5	1.25
<i>Mastigoteuthis psychrophila</i>	27	13	8.3	2.64
<i>Taonius sp.</i>	22	13	6.8	5.72*
Fish				
<i>Protomyctophum choriodon</i>	61	24	18.8	1.45
<i>Champsocephalus gunnari</i>	59	20	18.2	0.18
<i>Electrona antarctica</i>	57	13	17.6	1.18
<i>Magnisudis prionosa</i>	33	11	10.2	0.07
<i>Patagonotothen guntheri</i>	23	6	7.1	0.17
Black-browed albatross				
<i>Galiteuthis glacialis</i>	430	11	11.8	0.05

Expected co-occurrence based on overall incidence of lamprey of 0.3079 in diet samples (287 of total $n=932$) of grey-headed albatrosses, and 0.0274 in diet samples (25 of total $n=912$) of black-browed albatrosses. * $P < 0.05$, ** $P < 0.01$

Table 5 Values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (mean \pm SD, with range in parentheses if available) in lamprey and selected fish and cetaceans sampled in the Southern Ocean

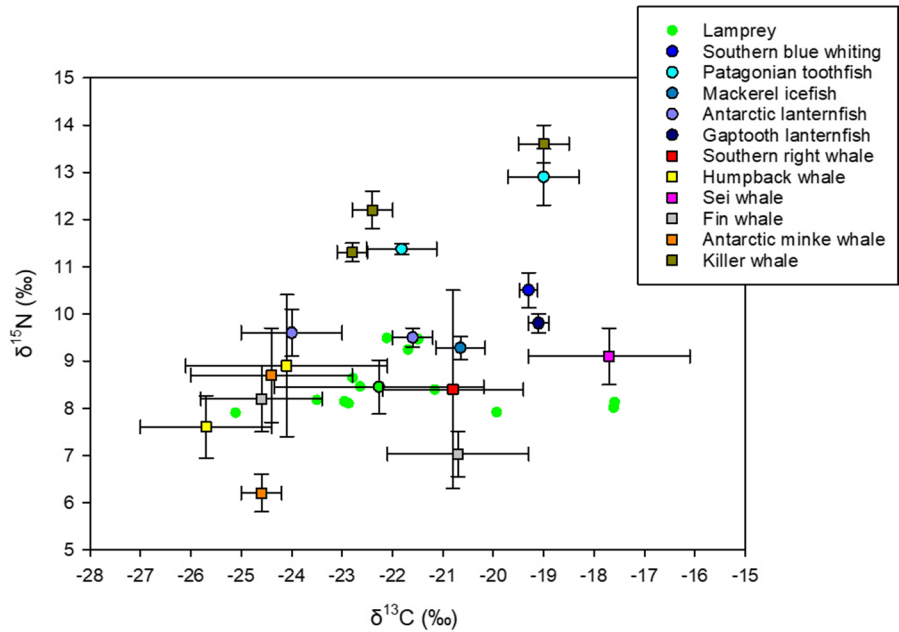
Species	Sampling location	Year	Tissue	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
Geotriidae							
<i>Geotria macrotoma</i>	South Georgia ¹	2002	Muscle	11	-22.27 ± 2.08 (-25.11 to -17.60)	8.45 ± 0.57 (7.90 to 9.49)	Anderson et al. (2009)
Gadidae							
Southern blue whiting <i>Micromesistius australis</i>	Falkland Islands	2010	Muscle	14	-19.3 ± 0.18	10.5 ± 0.37	Quillfeldt et al. (2015)
Notothenoidei							
Patagonian toothfish	Kerguelen	2006	Muscle	15	-19.0 ± 0.7	12.9 ± 0.6	Cherel et al. (2008)
<i>Dissostichus eleginoides</i>	South Georgia ¹	2002	Muscle	3	-21.82 ± 0.7 (-22.59 to -21.21)	11.37 ± 0.11 (11.3–11.5)	Anderson et al. (2009)
Mackerel icefish <i>Champscephalus gunnari</i>	South Georgia ¹	2002	Muscle	16	-20.65 ± 0.49 (-21.27 to -19.68)	9.28 ± 0.25 (8.93 to 9.71)	Anderson et al. (2009)
Myctophidae							
Gaptooth lanternfish <i>Protomyctophum choriodon</i>	Scotia Sea	2008	Muscle	20	-19.1 ± 0.2	9.8 ± 0.2	Stowasser et al. (2012)
Antarctic lanternfish	Scotia Sea	2008	Muscle	20	-24.0 ± 1.0	9.6 ± 0.5	Stowasser et al. (2012)
<i>Electrona antarctica</i>	Kerguelen	2005	Muscle	12	-21.6 ± 0.4	9.5 ± 0.2	Cherel et al. (2008)
Cetacea							
Southern right whale <i>Eubalaena australis</i>	Pen. Valdés	2003–2006	Skin	196	-20.8 ± 1.4 (-23.9 to -17.2)	8.4 ± 2.1 (6.0 to 15.0)	Valenzuela et al. (2018)
Humpback whale	Antarctic Pen	2013–2016	Skin	67	-24.1 ± 2.0	8.9 ± 1.5	Seyboth et al. (2018)
<i>Megaptera novaeangliae</i>	Gabon	2000–2005	Skin	43	-25.7 ± 1.3 (-28.5 to -21.8)	7.6 ± 0.66 (6.9 to 8.6)	Montanari et al. (2020)
Sei whale <i>Balaenoptera borealis</i>	South Georgia	n/a	Baleen ²	3	-17.7 ± 1.6 (-21.1 to -14.3)	9.1 ± 0.6 (7.7 to 10.2)	Buss et al. (2022)
Fin whale	Antarctic Pen	2013–2016	Skin	23	-24.6 ± 1.2	8.2 ± 0.7	Seyboth et al. (2018)
<i>Balaenoptera physalus</i>	South Georgia	n/a	Baleen ²	3	-20.7 ± 1.4 (-23.1 to -17.4)	7.0 ± 0.5 (5.9–7.9)	Buss et al. (2022)
Antarctic minke whale	Antarctic Pen	2016	Skin	16	-24.4 ± 1.6	8.7 ± 1.0	Seyboth et al. (2018)
<i>Balaenoptera bonaerensis</i>	Southern Ocean	2000–2006	Muscle	10	-24.6 ± 0.4 (-25.1 to -23.9)	6.2 ± 0.4 (5.7 to 7.2)	Endo et al. (2012)
Killer whale	Crozet	2011–2012	Skin	18	-19.0 ± 0.5	13.6 ± 0.4	Tixier et al. (2019)
Type B1	Antarctic Pen	2009–2013	Skin	11	-22.4 ± 0.4	12.2 ± 0.4	Durban et al. (2017)
Type B2	Antarctic Pen	2009–2013	Skin	8	-22.8 ± 0.3	11.3 ± 0.2	Durban et al. (2017)

Table 5 (continued)

Species	Sampling location	Year	Tissue	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Reference
<i>Orcinus orca</i>							

Values are means \pm SD. *N*=number of individuals. ¹ Obtained from albatross diet samples. ² Repeated sequential sampling providing a year-round diet signal

Fig. 4 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) in lamprey (individual values and mean \pm SD) and selected fish and cetaceans (mean \pm SD) sampled in the Southern Ocean. See Table 5 for data and references



Although pouched lamprey are eaten in continental shelf waters by some abundant commercial fish species and by yellow-eyed penguins *Megadyptes antipodes* (Miller et al. 2021), based on our thorough review of the literature, lamprey hardly feature in the diet of pelagic seabirds other than the grey-headed albatross (Table 6). However, this is only at South Georgia as lamprey are not reported in the diet of the breeding populations of grey-headed albatrosses at the Prince Edward, Campbell, Kerguelen or Diego Ramírez Islands (Arata et al. 2004; Hunter and Klages 1989; Chérel et al. 2002; Waugh et al. 1999; Richoux et al. 2010). Hence as far as we are aware the APFZ appears to be the only known hotspot in abundance of an anadromous lamprey in oceanic waters.

Identification of lamprey hosts

Based on the very limited information available at the time, Potter et al. (1979) suggested that the lamprey hosts might be Patagonian toothfish or southern blue

whiting. However, those two species, as well as killer whale and lanternfish can now be ruled out, given the range of $\delta^{13}\text{C}$ values is much wider and the $\delta^{15}\text{N}$ values are lower in lamprey muscle (Fig. 4), contrary to the expected trophic enrichment of predator compared with prey. In addition, there is scant evidence that the distribution of the southern blue whiting stock on the Patagonian Shelf extends to the APFZ or South Georgia (cf. Niklitschek et al. 2010). Apart from a single southern blue whiting caught in Cumberland Bay, South Georgia in 2004 (Martin Collins *pers. comm.*), the only records south of the APFZ are from >60 years ago (Merrett 1963). Southern blue whiting has never been recorded in the diet of any predators at South Georgia, including grey-headed albatrosses, despite extensive sampling (see references above); only one southern blue whiting was found in the stomachs of ~800 juvenile Patagonian toothfish caught at Shag Rocks and South Georgia which had consumed 1000 s of individuals of 25 other fish species (Collins et al. 2007). Patagonian

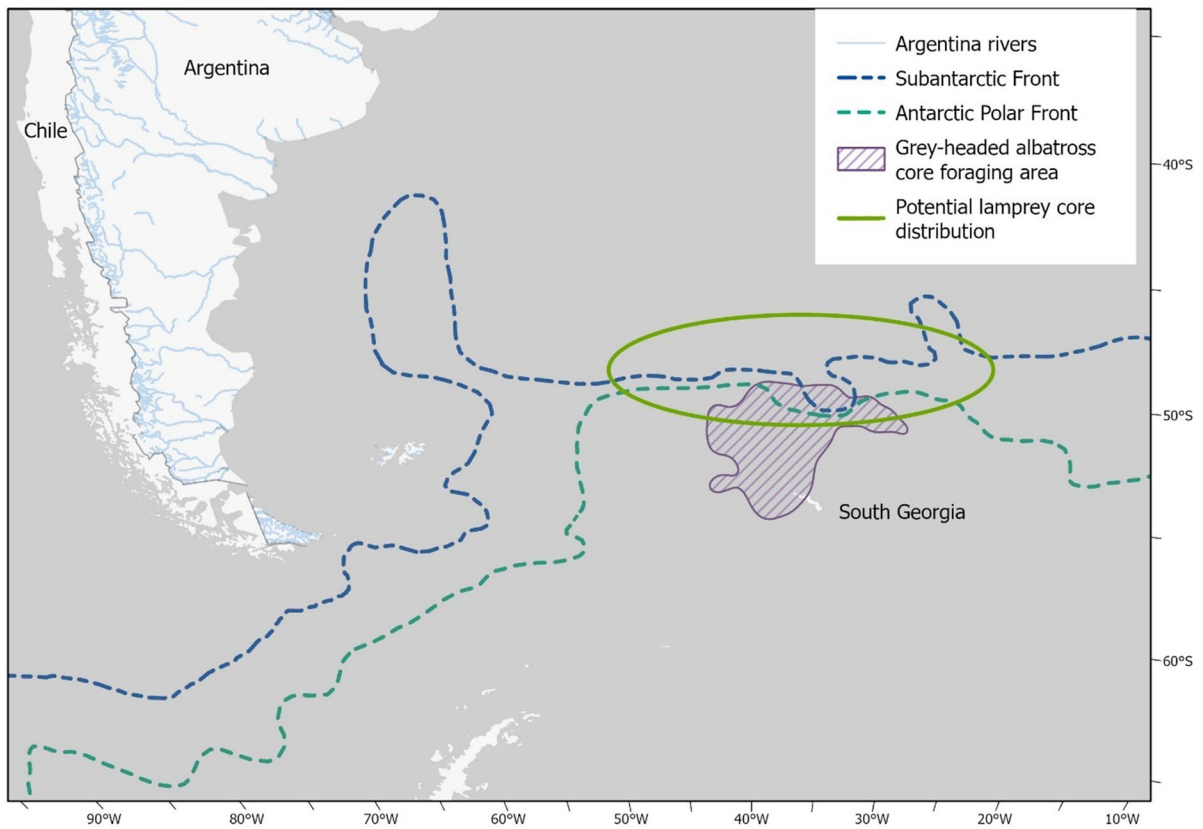


Fig. 5 Potential core distribution of Patagonian lamprey in their marine phase based on incidence in the diet of marine predators

toothfish caught by longliners in the South Georgia fishery never have lamprey attached, nor any tell-tale scars, and nor do mackerel icefish which, moreover, are at the northernmost extent of their distribution at South Georgia and do not occur in the APFZ (Morley et al. 2014; Mark Belchier and Martin Collins pers. comm.). Myctophids are abundant in the northern Scotia Sea and APFZ, but have not been caught with attached lamprey or scars, and the majority are too small to be suitable hosts; *Gymnoscopelus bolini* at 15.7–23.1 cm is the only species with a mean body length > 15 cm (Collins et al. 2008). Nor did lamprey co-occur more than expected with any myctophid, nototheniid or other fish in the diet of the albatrosses that might provide circumstantial evidence of a likely host. Lamprey did co-occur more often than expected with eight species of squid, but squid have never been recorded as hosts from analysis of DNA or morphological remains in guts of any lamprey species (Clemens et al. 2019; Shink et al. 2019; Silva et al. 2014).

As such, it is much more likely that the lamprey co-occurrence with squid reflects overlapping distribution and biogeography.

Although we are unable to identify any teleost fish that is likely to be a host, the isotopic comparison points to several baleen whale species as candidate hosts. That would also explain why the range of $\delta^{13}\text{C}$ values in the lamprey muscle was so wide even though all individuals were likely caught by albatrosses in the APFZ, as it is consistent with feeding on different hosts with isotopic signatures indicative of marine distributions from the Antarctic to the subtropics (Phillips et al. 2009; Stowasser et al. 2012). Of course, it should be recognised that the stable isotope ratios in the lamprey were from a single sampling year, and there is variation among species, stock, sex, age class and season in values for baleen whales (Seyboth et al. 2018; Valenzuela et al. 2018; Montanari et al. 2020). Stable isotope ratios in general are affected by temperature, concentrations of CO_2 ,

Table 6 Lamprey in the diet of pelagic seabirds. Values are mean \pm SD, with range in parentheses if available. There are also single records of pouched lamprey in the diet of Antipodean albatross *Diomedea antipodensis* (Imber 1992) and black petrel *Procellaria parkinsoni* (Imber 1976), and of Pacific lam-

prey *Entosphenus tridentatus* and Arctic lamprey *Lethenteron camtschaticum* in the diet of short-tailed albatross *Phoebastria albatrus* and short-tailed shearwater *Ardenna tenuirostris*, respectively (Walker et al. 2015; Ogi et al. 1980)

Seabird species	Site	Years	Lamprey % occurrence	Years	Lamprey % mass	References
Grey-headed albatross <i>Thalassarche chrysostoma</i>	Bird Island, South Georgia	1959–1961, 1975–1976, 1986, 1994, 1996–2022	27.7 \pm 16.6 (0–60.0)	1975–1976, 1986, 1994, 1996–2022	3.02 \pm 3.20 (0–10.7)	This study
Black-browed albatross <i>Thalassarche melanophris</i>	Bird Island, South Georgia	1959–1961, 1975–1976, 1986, 1994, 1996–2022	2.8 \pm 2.6 (0–10)	1975–1976, 1986, 1994, 1996–2022	0.33 \pm 0.63 (0–2.4)	This study
Buller's albatross <i>Thalassarche bulleri</i>	The Snares, New Zealand	1996–1997	2	1996–1997	1	James and Stahl (2000)
Buller's albatross <i>Thalassarche bulleri</i>	Solander Island, New Zealand	1997	2	1997	<0.5%	James and Stahl (2000)

O₂ and nutrients and light intensity, hence there is extensive spatio-temporal variation in baselines, and in predators by tissue-specific isotopic fractionation and turnover rates, as well as age, sex, breeding and nutritional status etc. (Stowasser et al. 2012; Shipley and Matich 2020). Values from other studies reported here are from whales sampled at calving grounds north of the APF, or in the Antarctic or subantarctic during the summer. The isotopic composition of whales is likely to be particularly variable because they are very mobile, and there is a seasonal switch from warm-water to cold-water prey. For example, in the southern right whale, the diet and hence trophic level changes during migration from mostly copepods north of 40°S, to mostly euphausiids south of 50°S (Tormosov et al. 1998), which is also apparent from stable isotope ratios in baleen plates (Best and Schell 1996).

Only part of the body of a whale is visible during surfacing, and so lamprey will frequently go unnoticed. Lamprey were deemed responsible for the scars on fin whales *Balaenoptera physalus*, humpback whales *Megaptera novaeangliae*, sei whales *Balaenoptera borealis* and sperm whales *Physeter macrocephalus*, and harbour porpoise *Phocoena phocoena* because of tooth marks that corresponded to lamprey

dentition (Pike 1951; Van Utrecht 1959). Newer evidence for whales as hosts includes photographs showing live sea lamprey attached to western North Atlantic right whales *Eubalaena glacialis*, minke whales *Balaenoptera acutorostrata* and killer whales *Orcinus orca*, confirming that lamprey can cause the oval scars seen routinely on whales in the north Atlantic and Pacific oceans that previously were often ascribed to bites from cookie-cutter sharks *Isistius brasiliensis* (Samarra et al. 2012; Nichols and Hamilton 2004; Nichols and Tscherter 2011). Patagonian lamprey may therefore be responsible for the numerous old or healing scars recorded on fin, sei and blue whales *Balaenoptera musculus*, and to a lesser extent humpback and sperm whales caught during the whaling era at South Georgia; these scars were noted to have been inflicted in temperate and tropical, rather than Antarctic waters, but the cause was unknown (Mackintosh and Wheeler 1929; Matthews 1938a, c, b).

There are no observations of albatrosses picking lamprey or other parasites off whales. Grey-headed and black-browed albatrosses are poor divers and the majority of their prey are ingested in daylight (Bentley et al. 2021; Catry et al. 2004; Phalan et al. 2007). Fishing effort is low in the foraging areas of grey-headed or black-browed albatrosses in chick-rearing

(Clay et al. 2019), so the lamprey were not caught in fisheries and discarded. Also, unlike some tropical seabirds which benefit from fish driven to the surface by deep-diving tuna, the diet of grey-headed albatrosses during chick-rearing only includes prey species that the birds could have caught by themselves (Mills et al. 2020a, b). Together, these lines of evidence indicate that the lamprey caught by the albatrosses are free-swimming, and were very abundant within a few metres of the water surface probably during the day. In contrast, catches of Pacific lamprey *Entosphenus tridentatus* in the open ocean are at greater depths (Clemens et al. 2019). As the lamprey are caught by albatrosses in the APFZ, we surmise that they detach from southerly-migrating baleen whales when they reach this thermal boundary between warmer subantarctic waters and cold Antarctic water. Based on the ratio of fresh vs. healing scars on whales taken off northwest Vancouver Island, Pike (1951) concluded that lamprey attacks occurred during the northward, spring migration of the whales i.e., while they were still in warm waters. This circumstantial evidence from both hemispheres suggests that lamprey have a poor tolerance for very cold waters, and might explain why they are sluggish enough to be caught by grey-headed albatrosses in surface waters, as swimming speed and duration in lamprey are closely correlated with temperature (Moser et al. 2015)..

Many of the same whale species on which Pike (1951) noted lamprey scars also occur in the Southern Ocean. Humpback whales start migrating south from calving grounds off South America in late October to late December, taking 40 to 60 days to reach the eastern Scotia Sea, South Georgia and the South Sandwich Islands, and the central-south Atlantic (Zerbini et al. 2006; Engel and Martin 2009). Similarly, a substantial proportion of southern right whales migrate by December from waters off Argentina and Brazil south to South Georgia and the Scotia Sea (Valenzuela et al. 2018), and sei whales and immature male and female blue and fin whales arrive in Antarctic waters from February onwards (Mackintosh and Wheeler 1929; Matthews 1938b; Širović et al. 2009). Movements of Antarctic minke whales are poorly known, but most are thought to be in mid latitude breeding grounds, including off northeastern Brazil during the austral winter, and those must also migrate south to Antarctica in the early summer (Perrin et al.

2018). The incidence of lamprey in the albatross diets in the austral spring and early summer is unknown, as studies are based on sampling of stomach contents during the chick-rearing period, just as they are elsewhere (McInnes et al. 2016). However, the timing of the whale migrations coincides with the within-season change in percentage occurrence of lamprey in diets of both grey-headed and black-browed albatrosses (similar in February and March but dropping by ~50% in April).

Long-term changes in lamprey consumption and availability

As samples were only available for one or two years per decade prior to 1994, and there was considerable annual variability thereafter, long-term trends in the importance of lamprey until the mid 1990s are uncertain. There was, however, a clear decrease in both percentage occurrence and percentage mass of lamprey from 2012 onwards to values in grey-headed albatrosses that were less than one third and one fiftieth, and in black-browed albatrosses were less than one half and one fifteenth, respectively, of those in previous decades. Our estimates of the consumption by chicks in 1975–1976 are higher than the totals of 119 tonnes and 15 tonnes for grey-headed and black-browed albatrosses estimated by Prince (1980), because the breeding populations were under-counted at the time (Poncet et al. 2006). Accounting for adult and chick requirements, the values for grey-headed albatrosses in 1975–1976 and 1986 are similar (538 and 516 t, respectively), and much higher than in black-browed albatrosses (77 and 31 t, respectively).

Taking account of declining albatross population sizes and annual breeding success, total lamprey consumption by grey-headed albatrosses was highly variable from 1994 to 2011, and mostly low, but with a few years when it reached around half the peak of those earlier years. Thereafter, levels of lamprey consumption by both albatross species have been extremely low. The reason for the dramatic decline in consumption of lamprey in the last decade is unknown. Although the relative reliance of grey-headed albatrosses on different regions within their overall foraging range changes to some extent from year to year, there is no evidence for a broad-scale shift in distribution over the same time period (Phillips et al. 2004; Xavier et al. 2013; Scales et al.

2016). Nor are the albatrosses likely to have changed prey preference per se, as lamprey are lipid-rich and consequently of higher calorific value than other prey taxa, including notothenioids, myctophids, squid and Antarctic krill (Clarke and Prince 1980). Lamprey would not have been misidentified or missed, as the fish and their jaws are easily distinguished, and the same researcher processed diet samples in the field in 2008, 2009, 2010, 2018 and 2019, i.e., including years of high and low incidence. There is extensive evidence from other studies that changes in importance of particular prey items in the diet of generalist seabirds are indicative of fluctuations in prey biomass and availability in foraging areas, as assessed independently from fisheries landings and scientific surveys (Green et al. 2015; Thayer and Sydeman 2007; Montevecchi and Myers 1995). As such, we infer that the lamprey must either have greatly decreased in abundance, or their distribution has changed. The latter would presumably have to reflect a decline in abundance or major shift in distribution of their hosts; assuming those are baleen whales, the former at least is highly unlikely. Following the whaling moratorium that came into force in 1987, and the declaration of the entire Southern Ocean as a whale sanctuary in 1994, populations of most baleen whales are likely to be increasing (Thomas et al. 2016). That is indeed the case for several populations in the southwest Atlantic, including humpback, blue and southern right whales (Zerbini et al. 2019; Calderan et al. 2020; Crespo et al. 2019), and even though the trend is unknown for Antarctic minke whale, the population remains huge (Thomas et al. 2016). A change in distribution is slightly more plausible, as whale migration patterns can vary annually (Thiele et al. 2004; Matthews 1938b), and there is isotopic evidence for a decadal shift from South Georgia to subtropical waters by southern right whales that calve off southwest Africa (van den Berg et al. 2021). However, it seems highly unlikely that this would occur in so many whale populations to have such a huge effect on lamprey distribution, given the range of alternative hosts and the continued high abundance in Antarctic waters of hundreds of thousands of baleen whales that are north–south migrants (Murphy et al. 2021). In a previous study of all diet components, there was no correlation between percentage wet mass or percentage occurrence of lamprey in the albatross diets and remotely sensed near-surface chlorophyll a,

suggesting that environmental changes are not driving the trend in lamprey availability (Mills et al. 2020). Moreover, it is highly improbable that environmental conditions at the APFZ would have deteriorated so much that lamprey now avoid this region when it is still the main foraging area of grey-headed albatrosses. Therefore it seems much more likely that Patagonian lamprey have experienced a steep decline in abundance.

Implications for lamprey conservation

Worldwide declines in lamprey have resulted from degradation of habitats in rivers and estuaries as a consequence of climatic or anthropogenic changes, including watercourse mismanagement, new dams that block access to breeding areas, sewage or other pollution, overfishing or introduction of alien predators (Barletta and Lima 2019; Clemens et al. 2019; Lucas et al. 2021). Research in New Zealand and Australia suggests that loss of habitat through construction of dams is a key factor leading to major declines in pouched lamprey populations (Barletta and Lima 2019; Clemens et al. 2019; Lucas et al. 2021; Riva-Rossi et al. 2020). Known threats to the Patagonian lamprey include recent and planned construction of two hydro-electric dams, channelization of waterways, water abstraction and impacts of agriculture (Barletta and Lima 2019; Clemens et al. 2019; Lucas et al. 2021; Riva-Rossi et al. 2020). In addition, there is contamination of fish with mercury (and other metals) in the Río de La Plata estuary (Barletta and Lima 2019), and although concentrations of mercury in lamprey that we collected in 2001/2002 were lower than in most notothenioid fish, those of another toxic metal, cadmium, were high (Anderson et al. 2009, 2010). Moreover, mercury concentrations in grey-headed albatrosses have increased considerably in recent decades, indicating increased contamination of the pelagic food web in the APFZ (Mills et al. 2020a, b). However, further work would be required to determine if levels of toxic metals or persistent organic pollutants are contributing to the long-term decline in Patagonian lamprey.

Given a steep decline is highly likely, there is clearly a pressing need to improve knowledge of the biology, ecology, migration, hosts etc. of the Patagonian lamprey, which is certainly feasible

with more investment in research as exemplified for pouched lamprey in New Zealand (Lucas et al. 2021; Miller et al. 2021). The pouched lamprey is currently listed as Data Deficient by IUCN. Although sampling by grey-headed albatrosses rather than nets is an unconventional means of assessing fish abundance, the data presented here provide a compelling case for the Patagonian lamprey to be listed by IUCN at least as Near threatened, if not a higher category, given the decadal decline in abundance in what was formerly a core area. As lamprey are rich in lipid and energy, the decline also has implications for foraging success and hence chick growth in grey-headed albatrosses at South Georgia, where the population has been in steep decline since the 1980s because of generally low adult survival and breeding success (Pardo et al. 2017). The decline also has repercussions in Argentinian river systems as lamprey that return to spawn provide marine nutrients that enrich terrestrial ecosystems (Nislow and Kynard 2009).

Acknowledgements We would like to thank all the field assistants at Bird Island who collected and analysed diet samples from albatrosses over the years. Diet sampling was approved by the British Antarctic Survey Animal Welfare and Ethics Committee and carried out with permission of the Government of South Georgia and the South Sandwich Islands. AKM would like to thank Neil Gemmill for his supervision and support, as well as the Gemmill Lab members and the Genetic Analysis Services team (Joanne Gillum and Patricia Fuentes-Cross). The project benefited from discussions or comments on the manuscript from Mark Belchier, Paul Brickle, Danny Buss, Martin Collins, Jen Jackson, Carla Riva-Rossi and José Xavier, and helpful comments from the handling editor and three reviewers. This work represents a contribution to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by the Natural Environment Research Council. AKM was funded by a University of Otago Doctoral Scholarship, a National Institutes of Health Minority Health International Research Training Programme run through the University of California Santa Cruz, and a Fisheries Society of the British Isles (FSBI) Small Research Grant.

Data availability DNA sequences are available from the Aotearoa Genomic Data Repository at: <https://data.agdr.org.nz/discovery/TAONGA-AGDR00020>. Data are available as Supporting Information Tables S2 to S8.

Declarations

Conflict of interest The authors declare no conflict of interest.

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