

Diversity, relative abundance, new locality records and population structure of Antarctic demersal fishes from the northern Scotia Arc islands and Bouvetøya

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Received: 7 January 2008 / Revised: 26 June 2008 / Accepted: 30 June 2008 / Published online: 18 July 2008
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Abstract A primary objective of the ICEFISH 2004 cruise was to collect and study notothenioid fishes from remote localities in the Atlantic sector of the Southern Ocean. Nearly 1 month was devoted to bottom trawling for fishes on the shelf and upper slope (to 1,000 m) areas around Shag Rocks, South Georgia, South Sandwich Islands and Bouvetøya. The focus was on the latter two locations, because their faunas are more poorly known. Eight species were collected at Shag Rocks with *Patagonotothen guntheri* most abundant; 17 at South Georgia with *Lepidonotothen nudifrons*, *L. larseni* and *Gobionotothen*

gibberifrons most abundant; 13 at the South Sandwich Islands with *L. larseni*, *L. nudifrons* and *G. gibberifrons* most abundant; and 11 at Bouvetøya with *L. larseni*, *Macrourus holotrachys* and *L. squamifrons* most abundant. Ten new locality records were established: Shag Rocks (1), South Georgia (1), South Sandwich Islands (5), South Sandwich Trench at 5,350 m (1) and Bouvetøya (2). Total known demersal fish diversity on the shelf and upper slope at Shag Rocks/South Georgia, South Sandwich Islands and Bouvetøya is 42, 31 and 17 species, respectively. To examine population structure in the four most abundant

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notothenioids at Bouvetøya (*L. larseni*, *L. squamifrons*, *Notothenia coriiceps* and *Chaenocephalus aceratus*), we examined the ND2 portion of mitochondrial DNA. *Chaenocephalus aceratus*, *N. coriiceps* and *L. larseni* exhibited no significant genetic differentiation in comparison with samples from localities in the Scotia Sea and the Antarctic Peninsula. However, *L. squamifrons* showed significant genetic differentiation between the South Shetlands and Bouvetøya populations ($F_{ST} = 0.189$, $P = 0.015$). Thus, these data combined with previous studies of two other notothenioids suggest that five of the six notothenioid species at Bouvetøya are not genetically differentiated from other localities in the Atlantic sector of the Southern Ocean. The location of Bouvetøya within the Antarctic Circumpolar Current and the long (1–2 years) pelagic stages of the notothenioids at Bouvetøya may be at least partly responsible for this genetic homogeneity.

Keywords Notothenioidei · South Sandwich Islands · Dispersal · ND2 mitochondrial DNA

Introduction

Data on fish species diversity, spatial distribution, abundance and genetic structure of populations are important for understanding biogeography, determining community structure and assessing fishery resources for potential human exploitation. The South Sandwich Islands and Bouvetøya, because of their remoteness and difficult trawling conditions are inadequately sampled compared to other islands in the Atlantic sector of the Southern Ocean (Arntz et al. 2005; Arntz 2006). Documenting these faunas is pertinent because, although they are not well known, there are exploratory commercial fisheries developing and expanding in this sector, including around the South Sandwich Islands and Bouvetøya (Rogers et al. 2006; CCAMLR 2007).

The 2-month ICEFISH 2004 cruise aboard the RVIB Nathaniel B. Palmer was designed as an International Collaborative Expedition to collect and study Fish Indigenous to Sub-Antarctic Habitats. Given the relatively extensive knowledge of, and accessibility to, the fish fauna of the High Antarctic, the rationale for the cruise was to collect some of the difficult to obtain and less well studied non-Antarctic and sub-Antarctic fishes, especially notothenioids. We collected fishes using bottom trawls and other sampling gear at locations in the South Atlantic Ocean including the Burdwood Bank and on shelf areas around the Falkland Islands, Shag Rocks, South Georgia, South Sandwich Islands, Bouvetøya, and Tristan da Cunha. We used the fishes in a variety of multidisciplinary projects.

Nearly a month of the cruise was devoted to sampling the shelf areas around the northern Scotia Arc Islands and Bouvetøya. The Scotia Arc is a chain of volcanic islands extending from southernmost South America to the northern Antarctic Peninsula. It is of biogeographic significance because, the fish fauna contains elements from both the Low or West Antarctic Region and the High or East Antarctic Region exemplified by the adjacent Weddell Sea. Since most of the Scotia Arc is situated south of the Antarctic Polar Front and within the Antarctic Circumpolar Current (West Wind Drift), it is also a center of dispersal for Antarctic and sub-Antarctic marine organisms (Andriashev 1965; DeWitt 1971; Arntz et al. 2005). Although Bouvetøya is one of the most isolated oceanic islands, the distributions of several notothenioid species encompass the Scotia Arc islands as well as Bouvetøya. Only two studies have examined the genetic structure of notothenioid populations from the island (Kuhn and Gaffney 2006; Rogers et al. 2006), thus one objective of the cruise was to obtain and analyze mitochondrial DNA samples from additional species and compare population structure between the Scotia Arc Islands and Bouvetøya.

Although the ICEFISH cruise was not designed as a synoptic survey of fish biomass resources in the Atlantic sector of the Southern Ocean, we were able to obtain diversity and relative abundance data for several demersal fish species. More specifically, we sampled shelf areas corresponding to three statistical subareas managed under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR): subareas 48.3 (South Georgia and Shag Rocks), 48.4 (South Sandwich Islands), and subarea 48.6 (Bouvetøya). While there have been recent demersal fish surveys of the Scotia Arc islands at South Georgia (Kock 1992; Marlow et al. 2003; Collins et al. 2007, 2008), the South Shetland Islands (Kock and Jones 2005) and the South Orkney Islands (Jones et al. 2000), there has been limited sampling around the South Sandwich Islands and Bouvetøya. Hence, our emphasis is on these latter islands.

In this paper we: (1) present diversity and relative abundance data for demersal shelf and upper slope fishes from Shag Rocks, South Georgia, the South Sandwich Islands and Bouvetøya; (2) document new locality records using our collections and previously unpublished records and museum specimens; (3) comment on the faunal similarities among the island groups; (4) compare the genetic structure of Bouvetøya populations of four common notothenioid species with those from localities in the Scotia Arc and Antarctic Peninsula and (5) consider the hypothesis that fishes have dispersed to Bouvetøya via the Antarctic Circumpolar Current.

Materials and methods

Collection of specimens

The ICEFISH 2004 cruise aboard the RVIB Nathaniel B. Palmer, a 94-m research icebreaker, began in Punta Arenas, Chile on 17 May 2004 and ended in Cape Town, South Africa on 17 July 2004. During the period 5–30 June 2004, we sampled around the northern Scotia Arc islands including Shag Rocks and South Georgia (Fig. 1a), South Sandwich Islands (Fig. 1b), and Bouvetøya (Fig. 1c). We occupied 36 stations and made 79 gear deployments: 17 stations with 34 deployments at Shag Rocks and South Georgia; 8 stations with 21 deployments at the South Sandwich Islands; and 11 stations with 24 deployments at Bouvetøya (Table 1 and Fig. 1a–c). Station locations for all bottom trawl deployments were based on initial acoustic reconnaissance of the seabed using Simrad EM120 multi-beam and Simrad EK-500 echo sounders and were positioned to provide as wide a geographic range as possible given weather, seabed and ice conditions. We trawled at depths from 45–5,350 m, although the majority of hauls were taken on shelf areas <500 m (Table 1).

Bottom trawls included a 2-m wide steel-frame Blake trawl, 5.48 and 9.14-m otter trawls without ground tackle, and a 7.62-m trawl with small roller gear. All trawl webbing was 32 mm (stretch measured) mesh. We fitted most trawls with a Vemco Minilog that recorded time, temperature, and depth data. Fish traps deployed at several sites were cylindrical 2-cm mesh-covered steel frames measuring 2 m long by 0.8 m in diameter with a collapsible funnel entrance. We occasionally deployed ring nets (Table 1). Due to the roughness of the sea floor and largely unknown fishing conditions, we used the Blake trawl as the primary bottom trawl. Hauls were taken day and night, with a target time for a bottom trawl of 30 min and average tow speed of 2.7 kts.

Processing of specimens during the cruise

The multidisciplinary nature of the ICEFISH cruise, and broad scope of research interests, necessitated two types of fish haul processing: biochemical, molecular and physiological; and ecological and population genetics. In the former, fish were kept alive for in vivo research and were not counted, while in the latter (Table 2) fish were sacrificed shortly after being caught to provide fishery demographic data as well as tissue samples. After a haul was brought on deck, fish were sorted from benthos, identified to species and counted. Total catch weights for all stations and species were not obtained because several gear types were used resulting in mixed gear selectivity and possible avoidance of certain gear types, such as the small-framed

Blake trawl, by fish with rapid or high avoidance response. Furthermore, because of the variety of gear used, our abundance data throughout the paper refer to relative abundance rather than absolute abundance.

Taxonomic nomenclature and disposition of specimens

For taxonomic nomenclature we follow Nelson (2006) for families and Gon and Heemstra (1990) for species. The only exception is for the family Nototheniidae which follows DeWitt et al. (1990) with the additional exception of the *Lepidonotothen squamifrons* group which follows Schneppenheim et al. (1994). We must note, however, that the third author (A.V. Balushkin) has a different view of these taxonomic decisions. In his opinion, *L. squamifrons* and *Notothenia coriiceps* from Bouvetøya, and *Gobionotothen marionensis* from Scotia Arc islands should be considered as *L. kempi*, *N. neglecta*, and *G. angustifrons*, respectively. Thus, *Notothenia neglecta* inhabits the Scotia Arc islands and Bouvetøya, and two species, *L. squamifrons* and *L. kempi*, inhabit the Scotia Arc islands and Bouvetøya (Balushkin 1986, 2000; Voskoboinikova and Balushkin 1987).

In the case of the eel cods, family Muraenolepididae, we follow Balushkin and Prirodina (2006) who corrected the gender of the species names *Muraenolepis marmoratus* and *M. microcephalus* (Chiu and Markle 1990) to *M. marmorata* and *M. microcephala*.

Museum voucher specimens document all new locality records. Although our focus was on demersal shelf and upper slope species, we also established some new records for mesopelagic species collected in the bottom trawls (Table 3) but these are not included in our demersal faunal list (Table 4). Institutional abbreviations in the text and Table 3 follow Leviton et al. (1985), except for SAIAB (South African Institute for Aquatic Biodiversity, formerly J.L.B. Smith Institute of Ichthyology). Frozen tissue samples for population genetics (Table 5) are deposited in the Yale Fish Tissue Collection at the Yale University Peabody Museum where they are documented with voucher specimens.

Tissue sampling and DNA amplification

Muscle tissue samples from four notothenioid species (the channichthyid *Chaenocephalus aceratus* and the nototheniids *L. larseni*, *L. squamifrons* and *N. coriiceps*) were collected during the ICEFISH 2004 cruise and previous cruises, including the Antarctic Marine Living Resources (AMLR) 2001, 2003 and 2006 cruises (Table 5). Tissue samples were stored in 95% ethanol (EtOH) prior to DNA extraction using the tissue protocol specified by QIAGEN's QIAamp[®] DNA Mini Kit (Qiagen Inc., Valencia, CA).

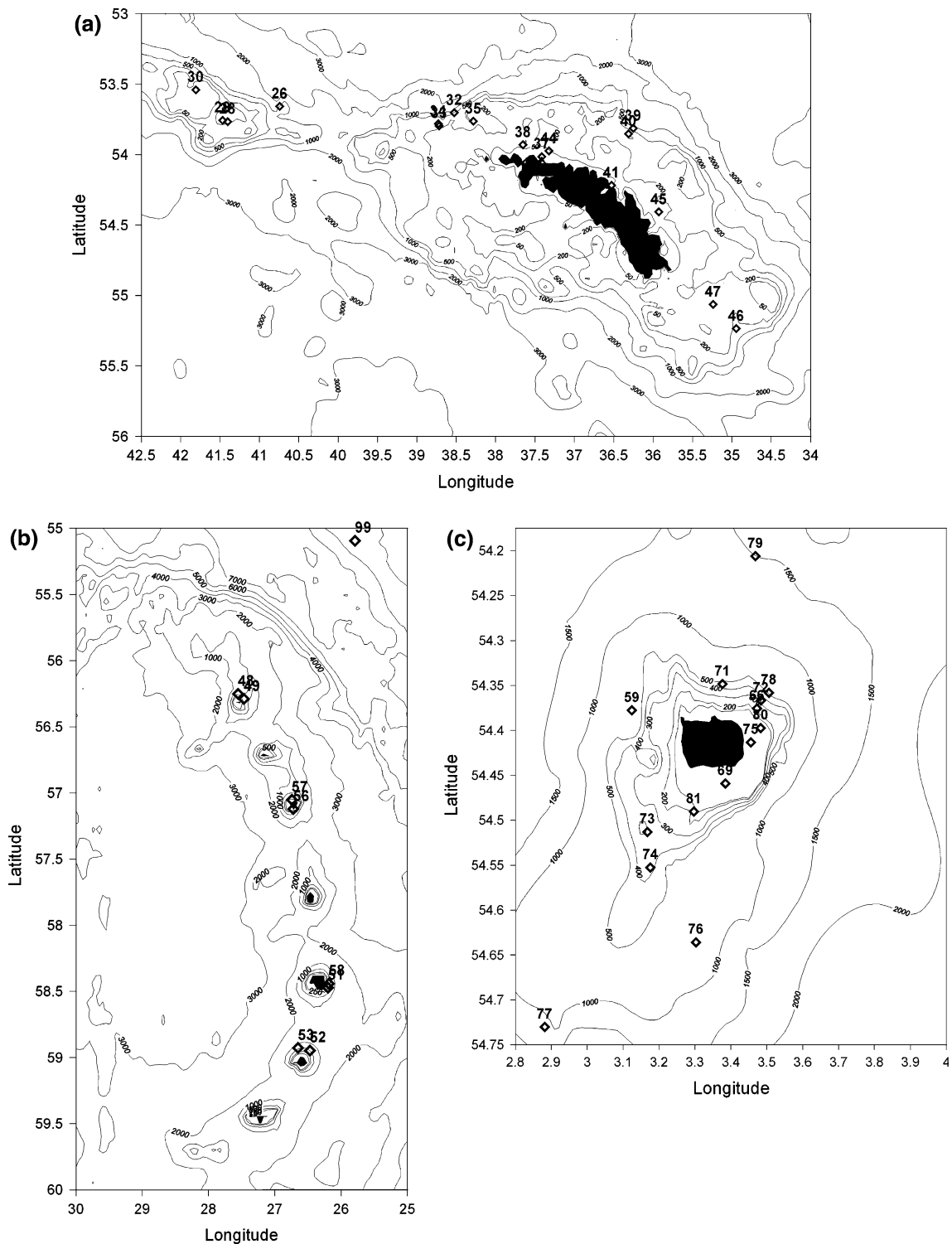


Fig. 1 Location of stations occupied during the ICEFISH 2004 cruise for **a** Shag Rocks and South Georgia, **b** South Sandwich Islands, and **c** Bouvetøya

One mitochondrial locus (NADH dehydrogenase subunit 2 (ND2)) was examined via polymerase chain reaction (PCR) in 25 μ l reactions containing 1 μ l 25 mM MgCl₂, 2.5 μ l 10 \times CoralLoad PCR Buffer (Qiagen Inc., Valencia, CA), 0.5 μ l 10 mM dNTP mix, 0.5 μ l 10 mM forward

primer (5' CTACCTGAAGAGATCAAAC), 0.5 μ l 10 mM reverse primer (5' CGCGTTTAGCTGTAACTAA), 0.3 μ l Taq DNA Polymerase (Invitrogen Co., Carlsbad, CA) and 1.5 μ l DNA template. PCR reactions consisted of an initial denaturation of 2 min at 94 $^{\circ}$ C, followed by

Table 1 Information for 36 stations where fish were collected during the Scotia Arc and Bouvetøya legs of the ICEFISH 2004 cruise

Region	Station	Date	Mid latitude	Mid longitude	Mean depth (m)	Gear deployments ^a
Shag Rocks	26	6/5/2004	53.656°S	40.743°W	410	TR
Shag Rocks	28	6/5/2004	53.765°S	41.404°W	195	BT (2)
Shag Rocks	29	6/5/2004	53.756°S	41.469°W	193	BT, OT ¹ (2)
Shag Rocks	30	6/6/2004	53.539°S	41.809°W	146	BT, OT ¹ (2)
S. Georgia	32	6/6/2004	53.702°S	38.526°W	479	TR
S. Georgia	33	6/8/2004	53.802°S	38.724°W	255	BT, OT ²
S. Georgia	34	6/7/2004	53.781°S	38.731°W	208	BT
S. Georgia	35	6/7/2004	53.756°S	38.287°W	201	BT, OT ¹ (2), OT ² (2)
S. Georgia	37	6/8/2004	54.013°S	37.414°W	78	BT, OT ²
S. Georgia	38	6/8/2004	53.998°S	37.665°W	46	BT, TR, RN
S. Georgia	39	6/9/2004	53.813°S	36.255°W	210	TR
S. Georgia	40	6/9/2004	53.853°S	36.313°W	213	BT
S. Georgia	41	6/10/2004	54.218°S	36.530°W	230	BT (2), TR
S. Georgia	44	6/8/2004	53.972°S	37.326°W	274	BT
S. Georgia	45	6/11/2004	54.406°S	35.930°W	100	BT, RN
S. Georgia	46	6/12/2004	55.234°S	34.946°W	291	OT ³
S. Georgia	47	6/12/2004	55.063°S	35.240°W	116	BT (2)
S. Sandwich	48	6/14/2004	56.254°S	27.590°W	336	BT (2), OT ³ (2), R (2)
S. Sandwich	49	6/14/2004	56.286°S	27.466°W	350	BT (2)
S. Sandwich	51	6/18/2004	58.470°S	26.205°W	200	BT (2)
S. Sandwich	52	6/18/2004	58.946°S	26.463°W	85	BT (2), OT ¹
S. Sandwich	53	6/18/2004	58.926°S	26.653°W	503	BT
S. Sandwich	57	6/16/2004	57.070°S	26.778°W	118	BT (2), OT ² (3)
S. Sandwich	58	6/18/2004	58.441°S	26.188°W	400	BT
S. Sandwich	99	6/15/2004	55.093°S	25.790°W	5,350	OT ³
Bouvetøya	59	6/23/2004	54.378°S	3.124°E	465	BT, OT ³ (2), TR
Bouvetøya	66	6/30/2004	54.378°S	3.496°E	180	OT ² , OT ³
Bouvetøya	71	6/25/2004	54.348°S	3.377°E	200	BT, OT ¹
Bouvetøya	73	6/27/2004	54.513°S	3.168°E	315	OT ² (2), RN (2)
Bouvetøya	75	6/29/2004	54.405°S	3.454°E	45	BT, OT ³ (3), TR
Bouvetøya	76	6/28/2004	54.636°S	3.303°E	648	OT ³
Bouvetøya	77	6/28/2004	54.730°S	2.882°E	956	OT ³
Bouvetøya	78	6/30/2004	54.373°S	3.537°E	446	TR
Bouvetøya	79	6/28/2004	54.235°S	3.599°E	1,572	OT ² , OT ³
Bouvetøya	80	6/29/2004	54.397°S	3.483°E	159	BT
Bouvetøya	81	6/30/2004	54.490°S	3.297°E	169	OT ³

Numbers in parentheses indicate multiple gear deployments

^a Gear codes are: BT = 2-m Blake trawl, OT¹ = 5.48-m otter trawl w/no ground tackle, OT² = 7.62-m bottom trawl w/roller gear, OT³ = 9.14-m otter trawl w/no ground tackle, TR = fish trap, RN = ring net

30 cycles of denaturation at 94°C for 45 s, annealing at 55°C for 1 min and extending at 72°C for 1 min, with a final extension of 5 min at 72°C. PCR products were run on 1% agarose gels to check the success of amplification and were purified for sequencing using the PEG protocol. Cycle sequencing reactions in both directions were run using the ABI BigDye[®] Terminator v3.1 Cycle Sequencing Kit

following the manufacturer's instructions (Applied Biosystems Inc., USA) and were generated by the W.M. Keck Foundation Biotechnology Resource Laboratory at the Yale University Medical School. DNA sequences were edited and aligned using the programs SeqManII (DNASTAR Inc., Madison, WI), Sequencher v. 4.5 (Gene Codes, Ann Arbor, MI) and BioEdit (Hall 1999).

Population structure

Analysis of molecular variance (AMOVA) was applied to mitochondrial data using ARLEQUIN version 3.11 (Excoffier et al. 2005). AMOVA evaluates patterns of molecular variation within and among populations, taking into account the sequence divergence of molecular haplotypes as well as their frequencies. The degree of population subdivision was described by F-statistics (Weir and Cockerham 1984). Nucleotide (π) and haplotype (h) diversities were calculated for mitochondrial sequence data using the program DnaSP v. 4.10.9 (Rozas et al. 2003).

A median-joining network was generated from mitochondrial haplotypes using the program Network v. 4.0.1.7 (<http://www.fluxus-engineering.com>) for each species. Network files were generated from aligned DNA sequence data

Table 2 Species and number of individuals caught by island group during the ICEFISH 2004 cruise (excluding stations 77, 79 and 99 > 650 m deep) but including mesopelagic by-catch species (although these are not counted as components of the shelf and upper slope faunas in the text)

Region	No. (%) in catch	Species	
Shag Rocks	1,488 (95)	<i>Patagonotothen guntheri</i>	
	53 (3)	<i>Champocephalus gunnari</i>	
	22 (1)	<i>Lepidonotothen nudifrons</i>	
	3 (<1)	<i>Lepidonotothen larseni</i>	
	3 (<1)	<i>Muraenolepis microps</i>	
	2 (<1)	<i>Gobionotothen gibberifrons</i>	
	1 (<1)	<i>Artedidraco mirus</i>	
	1 (<1)	<i>Dissostichus eleginoides</i>	
	1,573		
	South Georgia	628 (51)	<i>Lepidonotothen nudifrons</i>
		291 (24)	<i>Lepidonotothen larseni</i>
		137 (11)	<i>Gobionotothen gibberifrons</i>
		43 (4)	<i>Muraenolepis microps</i>
		37 (3)	<i>Artedidraco mirus</i>
		26 (2)	<i>Parachaenichthys georgianus</i>
19 (1)		<i>Pseudochaenichthys georgianus</i>	
15 (1)		<i>Trematomus hansonii</i>	
14 (1)		<i>Gobionotothen marionensis</i>	
11 (<1)		<i>Chaenocephalus aceratus</i>	
6 (<1)		<i>Careproctus georgianus</i>	
6 (<1)		<i>Champocephalus gunnari</i>	
2 (<1)		<i>Notothenia rossii</i>	
2 (<1)		<i>Raja georgiana</i>	
1 (<1)		<i>Notothenia coriiceps</i>	
1 (<1)	<i>Patagonotothen guntheri</i>		
1 (<1)	<i>Trematomus vicarius</i>		
1,240			

Table 2 continued

Region	No. (%) in catch	Species
South Sandwich Islands	3,416 (76)	<i>Lepidonotothen larseni</i>
	535 (12)	<i>Lepidonotothen nudifrons</i>
	394 (9)	<i>Gobionotothen gibberifrons</i>
	51 (1)	<i>Gobionotothen marionensis</i>
	35 (<1)	<i>Muraenolepis marmorata</i>
	31 (<1)	<i>Chaenocephalus aceratus</i>
	8 (<1)	<i>Lepidonotothen squamifrons</i>
	3 (<1)	<i>Macrourus holotrachys</i>
	2 (<1)	<i>Bathyraxa maccaini</i>
	2 (<1)	<i>Electrona carlsbergi</i>
	2 (<1)	<i>Notothenia coriiceps</i>
	1 (<1)	<i>Dissostichus eleginoides</i>
	1 (<1)	<i>Notothenia rossii</i>
	4,481	
	Bouvetøya	1,448 (80)
173 (9)		<i>Macrourus holotrachys</i>
129 (7)		<i>Lepidonotothen squamifrons</i>
29 (2)		<i>Notothenia coriiceps</i>
19 (1)		<i>Chaenocephalus aceratus</i>
10 (<1)		<i>Muraenolepis marmorata</i>
3 (<1)		<i>Champocephalus gunnari</i>
1 (<1)		<i>Electrona spp.</i>
1 (<1)		<i>Mancopsetta maculata</i>
1 (<1)		<i>Melanostigma gelatinosum</i>
1 (<1)		<i>Muraenolepis microps</i>
1,815		

using the program DNA alignment (<http://www.fluxus-engineering.com>). Median-joining networks are commonly used to depict relationships of closely related mitochondrial or nuclear haplotypes, for which traditional phylogenetic approaches yield multiple plausible trees (Bandelt et al. 1999).

Results

Diversity and relative abundance: Shag Rocks and South Georgia

We made 34 gear deployments at 17 stations at depths from 46–479 m (Table 1). Time restrictions prevented sampling to the south of South Georgia (Fig. 1a).

At Shag Rocks we collected eight species. *Patagonotothen guntheri* was most abundant (95%), followed distantly by *C. gunnari* (3%) and *L. nudifrons* (1%) (Table 2), with most *P. guntheri* taken at Station 29. All trawl stations had similar diversity (5–6 species per station). A set of six traps

Table 3 New ICEFISH 2004 locality records for fishes from northern Scotia Arc islands and Bouvetøya

Family and species	Cruise and museum catalog no. or citation
Shag Rocks	
Artedidraconidae	
<i>Artedidraco mirus</i>	ICEFISH 2004; USNM 385872
South Georgia	
Nototheniidae	
<i>Patagonotothen guntheri</i>	ICEFISH 2004; SAIAB 75122
South Sandwich Islands	
Nototheniidae	
<i>Dissostichus eleginoides</i>	ICEFISH 2004; YPM ICH 17045
<i>Pleuragramma antarcticum</i>	Trunov (2001)
Channichthyidae	
<i>Neopagetopsis ionah</i>	ZIN 39426, 39427
Rajidae	
<i>Bathyraja maccaini</i>	ICEFISH 2004; SAIAB 75116
Myctophidae	
<i>Electrona carlsbergi</i>	ICEFISH 2004; SAIAB 74943
Muraenolepididae	
<i>Muraenolepis marmorata</i>	ICEFISH 2004; SAIAB 74964, 75129
Macrouridae	
<i>Macrourus holotrachys</i>	ICEFISH 2004; USNM 382781
South Sandwich Trench	
Macrouridae	
<i>Coryphaenoides filicauda</i>	ICEFISH 2004; SAIAB 75160
Bouvetøya	
Nototheniidae	
<i>Dissostichus eleginoides</i>	Rogers et al. (2006)
<i>Paranotothenia dewitti</i>	ZIN 47167, 47346, 49168; Balushkin (1990)
Bathydraconidae	
<i>Bathydraco antarcticus</i>	<i>Marion Dufresne</i> , MD 24, 1980 MNHN 1986-1009, 1986-1010
Channichthyidae	
<i>Pseudochaenichthys georgianus</i>	Trunov (1999)
Myctophidae	
<i>Electrona carlsbergi</i>	Kirkman et al. (2000)
Muraenolepididae	
<i>Muraenolepis marmorata</i>	<i>Marion Dufresne</i> , MD 24, 1980 MNHN 2005-100; ZIN 54233
<i>M. microps</i>	ICEFISH 2004; SAIAB 75066
<i>M. orangeiensis</i>	<i>Marion Dufresne</i> , MD 24, 1980 MNHN 1986-1001, -1031 and -1032
Macrouridae	
<i>Coryphaenoides filicauda</i>	<i>Marion Dufresne</i> , MD 24, 1980 MNHN 1986-1026
<i>Macrourus holotrachys</i>	<i>Marion Dufresne</i> , MD 24, 1980 MNHN 1986-204, -206, -1018 to -1021 and -1029
Achiropsettidae	
<i>Mancopsetta maculata</i>	ICEFISH 2004; USNM 391433

Previously unpublished museum records and literature records subsequent to Gon and Heemstra (1990) are also provided for fishes from the South Sandwich Islands and Bouvetøya. Mesopelagic records are included here but not in the demersal shelf and upper slope faunal lists in Table 4

Table 4 Summary of presently known demersal fish diversity on the shelf and upper slope (to \approx 1,000 m) of Shag Rocks/South Georgia, the South Sandwich Islands and Bouvetøya, including pelagic notothenioids but excluding the mesopelagic families Myctophidae, Bathylagidae, Gempylidae, Notosuidae and Paralepididae, and the epipelagic Centrolophidae

Family and species	Shag Rocks South Georgia ^a	South Sandwich islands ^b	Bouvetøya ^b
Nototheniidae			
<i>Aethotaxis mitopteryx</i>	X	X	X
<i>Dissostichus eleginoides</i>	X	X	
<i>Gobionotothen gibberifrons</i>	X	X	
<i>G. marionensis</i>	X	X	
<i>Lepidonotothen larseni</i>	X	X	X
<i>L. nudifrons</i>	X	X	
<i>L. squamifrons</i>	X	X	X
<i>Paranotothenia dewitti</i>		X	X
<i>Patagonotothen guntheri</i>	X		
<i>Pleuragramma antarcticum</i>	X	X	
<i>Notothenia coriiceps</i>	X	X	X
<i>N. rossii</i>	X	X	
<i>Trematomus bernacchii</i>	X		
<i>T. hansonii</i>	X	X	
<i>T. vicarius</i>	X		
Harpagiferidae			
<i>Harpagifer antarcticus</i>		X	
<i>Harpagifer</i> sp.	X		
Artedidraconidae			
<i>Artedidracono mirus</i>	X		
Bathydraconidae			
<i>Bathydraco antarcticus</i>		X	X
<i>B. joannae</i>	X		
<i>Parachaenichthys georgianus</i>	X	X	
<i>Psilodraco breviceps</i>	X		
<i>Racovitzia glacialis</i>		X	
Channichthyidae			
<i>Chaenocephalus aceratus</i>	X	X	X
<i>Champocephalus gunnari</i>	X	X	X
<i>Neopagetopsis ionah</i>	X	X	
<i>Pseudochaenichthys georgianus</i>	X	X	X
Rajidae			
<i>Bathyraja maccaini</i>		X	
<i>B. meridionalis</i>	X		
<i>Raja georgiana</i>	X		
Muraenolepididae			
<i>Muraenolepis marmorata</i>		X	X
<i>M. microcephala</i>		X	
<i>M. microps</i>	X	X	X
<i>M. orangiensis</i>			X
Moridae			
<i>Antimora rostrata</i>	X	X	X
<i>Halagyreus johnsonii</i>	X		
<i>Lepidion</i> sp.	X		

Table 4 continued

Family and species	Shag Rocks South Georgia ^a	South Sandwich islands ^b	Bouvetøya ^b
Gadidae			
<i>Micromesistius australis</i>	X		
Macrouridae			
<i>Coelorinchus marinii</i>	X		
<i>Coryphaenoides filicauda</i>		X	X
<i>C. subserrulatus</i>	X		
<i>Macrourus carinatus</i>	X		
<i>M. holotrachys</i>	X	X	X
<i>M. whitsoni</i>	X	X	
Ophidiidae			
<i>Genypterus blacodes</i>	X		
Liparidae			
<i>Careproctus georgianus</i>	X		
<i>Paraliparis antarcticus</i>	X		
<i>P. copei gibbericeps</i>	X		
<i>P. gracilis</i>		X	
<i>P. tetrapteryx</i>	X		
Zoarcidae			
<i>Melanostigma bathium</i>		X	
<i>M. gelatinosum</i>	X		X
<i>Selenio lycus laevifasciatus</i>		X	
Achiropsettidae			
<i>Mancopsetta maculata</i>	X		X
Total species	42	31	17

^a Based on unpublished data provided by Martin A. Collins, British Antarctic Survey. Only one survey was to 1,000 m and depths <75 m may not be fully representative of the fauna. Additional liparids from Stein and Andriashev (1990) and Stein (2006)

^b Based on information in *Fishes of the Southern Ocean* (Gon and Heemstra 1990) and new data in this manuscript

Table 5 Localities and numbers of individuals of Scotia Arc and Bouvetøya notothenioids used for population genetic analysis

Species	South Shetland Islands	South Shetland Islands	South Georgia	South Sandwich Islands	Bouvetøya
<i>Chaenocephalus aceratus</i>	1 ^a	15 ^b	2	1	4
<i>Lepidonotothen squamifrons</i>		9 ^c		1	13
<i>Notothenia coriiceps</i>	1 ^a	9 ^d			11
<i>Lepidonotothen larseni</i>		7 ^e	4	2	10

All samples are from the ICEFISH 2004 cruise except where indicated by footnotes. All material is deposited in the Yale Fish Tissue Collection

^a US Palmer Station, Anvers Island

^b Elephant Island (US AMLR cruises 2001, 2003, 2006)

^c Elephant and Livingston Islands (AMLR 2001, 2003, 2006)

^d Elephant Island (AMLR 2001, 2003, 2006) and King George Island (AMLR 2003)

^e Elephant Island (AMLR 2001, 2003, 2006), King George Island (AMLR 2001) and Nelson Island (AMLR 2001)

deployed at Station 26 with a 15-h soak time yielded no fish. At Station 28 we established a new locality record for the artedidraconid *Artedidraaco mirus* (Table 3), previously known only from South Georgia.

Off South Georgia we collected 17 species (Table 2) and *L. nudifrons* was most abundant at 51%. We also captured a single specimen of *P. guntheri* (an 85 mm SL

juvenile) at Station 35 north of Bird Island, establishing a new locality record for this species (Table 3). Other relatively abundant species species were *L. larseni* (24%), *Gobionotothen gibberifrons* (11%), and the muraenolepidid eelcod *Muraenolepis microps* (4%). The greatest diversity (12 species) was at Station 35, west of South Georgia.

Table 6 Summary of population genetic data for four notothenioid species from the Scotia Arc and Bouvetøya

Species	Sample size (N)	Nucleotide diversity (π) %	Haplotype diversity (h)	Transition/transversion ratio	First position substitutions	Second position substitutions	Third position substitutions	Global AMOVA F_{ST} (P value)
<i>Chaenocephalus aceratus</i>	23	0.064	0.446	1.67	3	2	3	0.278 ($P = 0.064$)
<i>Lepidonotothen squamifrons</i>	23	0.352	0.925	5.00	3	4	11	0.189 ($P = 0.015$)
<i>Notothenia coriiceps</i>	21	0.400	0.862	3.43	8	5	18	0.000 ($P = 0.607$)
<i>Lepidonotothen larseni</i>	23	0.387	0.996	6.75	2	3	26	0.049 ($P = 0.119$)

Significant P values in boldface

Diversity and relative abundance: South Sandwich Islands and South Sandwich Trench

We made 21 gear deployments at eight stations from depths from 85–5,350 m (Table 1). Stations sampled followed the South Sandwich chain from the northernmost island of Zavodovski to Bristol, the second most southerly island (Fig. 1b). Hauls around Bristol Island were conducted almost exclusively in pack ice in the wake of the ship. Increasingly heavy pack ice and fuel considerations prevented the vessel from continuing to the Southern Thule group, the southernmost islands in the chain.

We captured 13 species in the South Sandwich chain (Table 2); the three most abundant were *L. larseni* (76%), *L. nudifrons* (12%) and *G. gibberifrons* (9%). Fish abundance increased to the south, with the greatest numbers of fish collected at Bristol Island, which was also the shallowest station where bottom trawls were taken. Catches at Station 58 off Montague Island, the third most southerly in the chain, were small because the trawl was only on the bottom for 3 min due to rough bottom conditions. The greatest diversity (10 species) was near the more northern Candlemas Island at Station 57. Table 3 summarizes the five new locality records from the ICEFISH cruise as well as two additional records from other sources.

We made one trawl at 5,350 m on the east side of the South Sandwich Trench northeast of Zavodovski Island (Fig. 1b, Station 99) and caught seven specimens of the macrourid *Coryphaenoides filicauda*. This species is wide ranging in the Southern Hemisphere and is known from the vicinity of the Antarctic Polar Front (Iwamoto 1990). This is likely the first record south of the Front (Table 3), although *C. filicauda* has been recorded in the CCAMLR area north of the Front at Crozet and Kerguelen (Duhamel et al. 2005). This record also extends the known depth range of the species by nearly 300 m, from 5,070 to 5,350 m (Iwamoto 1990).

Diversity and relative abundance: Bouvetøya

We made 24 gear deployments at 11 stations at depths from 45 to 956 m. We captured 11 species around Bouvetøya

(Table 2). Catches were dominated by *L. larseni* (80%); *L. nudifrons* was absent. We also captured some *Macrourus holotrachys* (9%), a macrourid, and *L. squamifrons* (7%) (Table 2). Station 66 had the highest abundance, including many *L. larseni*. The greatest diversity (8 species) was west of Bouvetøya at Station 59 (Fig. 1c). One inshore trap deployment in kelp at 45 m east of Bouvetøya (Station 75, Fig. 1c) yielded large individuals of *N. coriiceps* including one, with a total length of 65 cm and weight of 3,383 g the largest recorded for this species (DeWitt et al. 1990). We established two new locality records for the island including the achirosettid *Mancopsetta maculata*, and we include an additional nine records from other sources (Table 3). While there is a record for this species from waters several hundred km southeast of Bouvetøya (Evseenko 1997; Fig. 9), it is for the pelagic stage. Our specimen is an adult.

Population genetics

Here, we present the results of our analysis of the ND2 portion of mtDNA for evidence of population structure in the four most abundant notothenioids at Bouvetøya—*L. larseni*, *L. squamifrons*, *N. coriiceps* and *Chaenocephalus aceratus* (Tables 5, 6; Fig. 2). The latter shows median-joining networks for each of the four species. A brief summary for each species follows.

Chaenocephalus aceratus

Seven mtDNA haplotypes were identified in 23 individuals from five collections of *C. aceratus*. In total, eight variable nucleotide positions were identified. Five of the eight polymorphisms were nonsynonymous and all were observed in single individuals. Analysis of molecular variance (AMOVA) showed no significant global differentiation ($F_{ST} = 0.278$, $P = 0.064$) for the full data set. AMOVA restricted to Bouvetøya, South Georgia and the South Sandwich Islands also showed no significant heterogeneity ($F_{ST} = 0.055$, $P = 0.382$). Additionally, a median-joining network illustrating genealogical relationships among the mitochondrial haplotypes shows little separation between localities (Fig. 2).

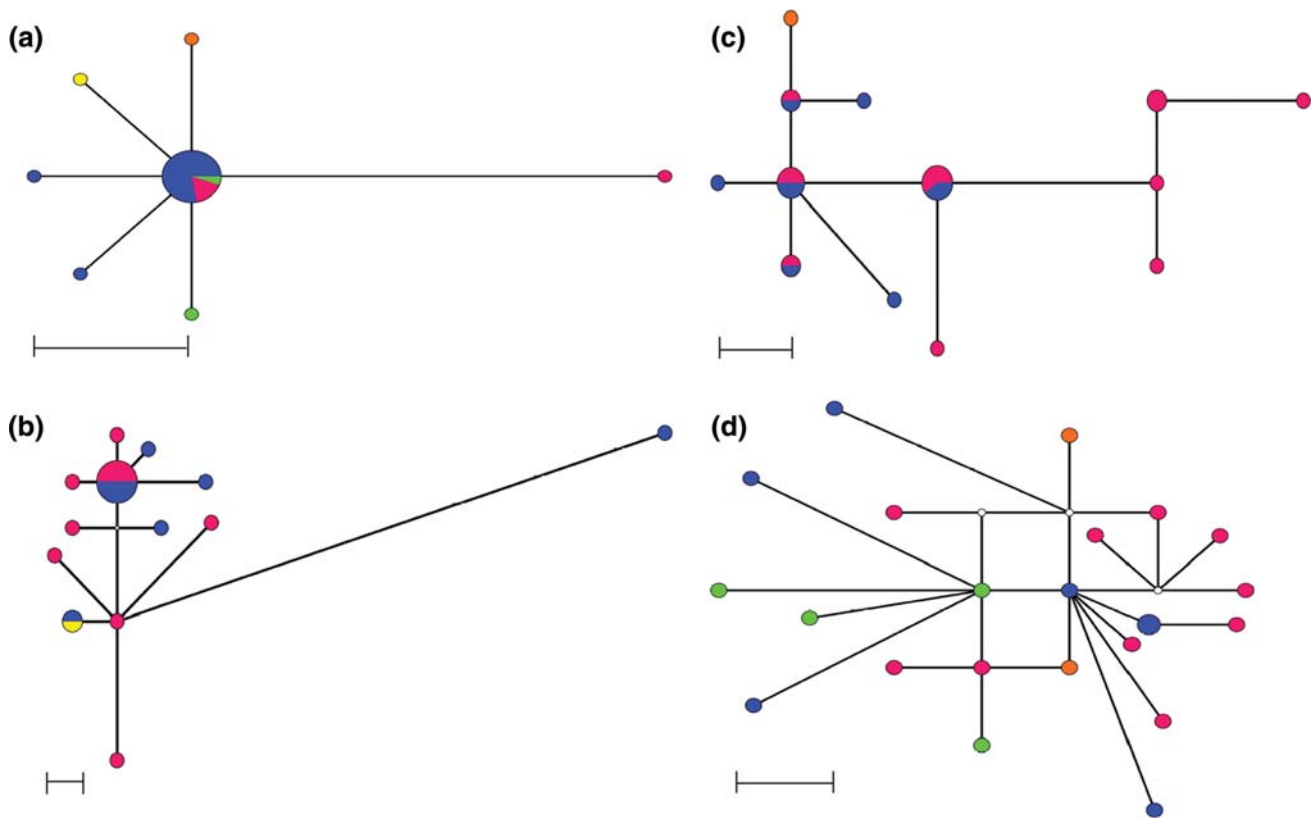


Fig. 2 Median-joining networks for **a** *Chaenocephalus aceratus*, **b** *Notothenia coriiceps*, **c** *Lepidonotothen squamifrons* and **d** *Lepidonotothen larseni* ND2 haplotype data (based on the complete 1,047 base pair sequence). Circle sizes are proportional to the number of individuals possessing the haplotype. Each color represents a different

haplotype locality (orange South Sandwich Islands; yellow Palmer Station, Anvers Island, South Shetland Islands; blue other more northerly South Shetland Islands localities; green South Georgia and pink Bouvetøya). Scale bar represents the length of one mutational step separating haplotypes

Lepidonotothen squamifrons

Thirteen mtDNA haplotypes were identified in 23 individuals from three collections of *L. squamifrons*. In total, 18 variable nucleotide positions were identified, with six of the 18 polymorphisms being nonsynonymous (three of these were observed as singletons). AMOVA showed significant global differentiation ($F_{ST} = 0.189$, $P = 0.015$) for the full data set, with the population from the South Shetlands being genetically differentiated from that of Bouvetøya. A median-joining network of the mitochondrial haplotypes shows some genetic separation between the two localities (Fig. 2).

Notothenia coriiceps

Thirteen mtDNA haplotypes were identified in 21 individuals from three collections of *N. coriiceps*. In total, 31 variable nucleotide positions were identified. Fifteen of the 31 polymorphisms were nonsynonymous and all were observed as singletons. AMOVA showed no significant global differentiation ($F_{ST} = 0.000$, $P = 0.607$) for the full data set. A median-joining network of the mitochondrial

haplotypes shows no genetic separation between localities (Fig. 2).

Lepidonotothen larseni

Twenty-one mtDNA haplotypes were identified in 23 individuals from four collections of *L. larseni*. In total, 31 variable nucleotide positions were identified. Three of the 31 polymorphisms were nonsynonymous and all were observed as singletons. AMOVA showed no significant global differentiation ($F_{ST} = 0.049$, $P = 0.119$) for the full data set. As with *N. coriiceps*, a median-joining network of the mitochondrial haplotypes shows no genetic separation between localities (Fig. 2).

Discussion

Gear selectivity

Because we deployed several types of bottom trawls (mostly with small mouth openings) and had little informa-

tion on mouth area and width while fishing, we could not quantitatively compare fish densities and biomass levels between island groups. However, these gear types did afford opportunities to collect information generally not obtained during surveys using large bottom trawls. Although fish species assemblages on shelf areas around South Georgia have been analyzed extensively using data from trawl surveys, and the region is one of the most heavily fished and best-known areas in the Southern Ocean (Shust 1998), gear types and mesh size used to conduct these surveys do not collect small fishes. The relatively small nets we used sample the bottom more closely and, having smaller mesh, also retain smaller individuals than do larger commercial trawls. The Blake trawl was especially efficient in capturing small fish. Six of our 10 new locality records (Table 3) were collected with the Blake trawl and included small species from the Shag Rocks/South Georgia area such as *Artedidraco mirus*, *P. guntheri* and a small (17 cm TL) *D. eleginoides*.

Comments on new locality records

To provide a more comprehensive list of the fauna, Table 3 includes, in addition to the ICEFISH records, unpublished museum records and records from the literature that were not included in (or were published subsequent to the appearance of) *Fishes of the Southern Ocean* (Gon and Heemstra 1990). Cruise 24 of the RV Marion Dufresne trawled in the vicinity of Bouvetøya in 1980 and established a number of new locality records. These specimens were cataloged into the MNHN and summarized in publications focused on notothenioids (Duhamel et al. 1983) and non-notothenioids (Duhamel 1987). Although both publications are cited in *Fishes of the Southern Ocean* (Gon and Heemstra 1990), not all records were incorporated into the species accounts and distribution maps. Therefore Table 3 contains the records from this cruise omitted from *Fishes of the Southern Ocean*.

Species diversity and new records: Shag Rocks and South Georgia

We collected more *P. guntheri* at Shag Rocks than at any other station to the east. This species also dominates the biomass at this locality (Collins et al. 2007). Before sampling at Shag Rocks, we had found that *P. guntheri* was also the most abundant species on the Burdwood Bank and around the Falkland Islands. Near the southern limit of its range at Shag Rocks, the only region within the Antarctic Polar Front where this species is well established, the population is meristically and morphometrically distinct as *P. guntheri shagensis* (Balushkin and Permitin 1982). Although Balushkin recently recognized this form as

P. shagensis (Balushkin 2000), we prefer to retain the name *P. guntheri* here until there is evidence of the genetic distinctiveness of the Shag Rocks population. The presence and abundance of *P. guntheri* suggests that Shag Rocks may be a region of faunal transition between the Falkland Islands and South Georgia. This species may have initially colonized Shag Rocks from a Falkland Island founder population, transported via oscillations of the Antarctic Polar Front, which in certain years may position between Shag Rocks and South Georgia (Trathan et al. 1997).

Our finding of *L. nudifrons* and *L. larseni* as the numerically dominant species at South Georgia is contrary to data of Collins et al. (2007) who found that these two species were unimportant and *C. gunnari* and *G. gibberifrons* dominated the biomass. Among the factors that may explain this discrepancy is the use, by Collins et al. (2007), of large commercial trawls that may not have collected these smaller species. They also trawled during summer (January–February) whereas, our trawling was conducted in June. Furthermore, the extensive and continuing demersal fish surveys at South Georgia (Collins et al. 2007, 2008) had not previously collected *P. guntheri*, an absence noted by DeWitt et al. (1990). Our specimen from South Georgia (an 85 mm SL juvenile) establishes its presence there for the first time. The fauna of South Georgia is well known, especially of the inshore waters, and it is surprising that this species has not previously been collected. Shag Rocks and South Georgia are only 185 km apart but are separated by a 1,000–1,750 m deep channel. However, *P. guntheri* has pelagic larvae (Efremenko 1984) and currents could transport them to the northwest edge of the South Georgia shelf where our specimen was captured. Our specimen of *P. guntheri* is an example of such expatriation and also evidence of dispersal from Shag Rocks to South Georgia.

Species diversity and new records: South Sandwich Islands

The dominance of *L. larseni* and/or *L. nudifrons* was evident at all island groups east of Shag Rocks. The abundance of *G. gibberifrons* also increased to the east. Although the South Sandwich Islands are located ≈750 km east of South Georgia and are the most isolated archipelago of the Scotia Arc, there were only minor differences in species composition between the two island groups. The three most abundant species were the same (*L. larseni*, *L. nudifrons*, *G. gibberifrons*), but different species like *L. squamifrons* appeared in catches at the South Sandwich Islands. On the other hand, species characteristic of South Georgia such as *Pseudochaenichthys georgianus* and *Parachaenichthys georgianus* were absent in our catches although both are known from the South Sandwich Islands (Iwami and Kock 1990; Gon 1990). *G. marionensis* was the most abundant species found in Targett's (1981) samples, probably

because he trawled in shallow water (15–70 m) where this species is more common; we sampled at 85–503 m. With 10 species, our collections from Candlemas Island were the most diverse in the island group. The total of 13 species we captured (Table 2) represent 42% of the known diversity of 31 species at the South Sandwich Islands (Table 4), and also provided five new locality records (Table 3).

Species diversity and new records: Bouvetøya

Bouvetøya is east of the Scotia Arc, about 2,500 km from South Georgia and 1,800 km from the South Sandwich Islands. With no intervening islands or seamounts between it and South Georgia, Bouvetøya is the prototypical example of an isolated oceanic island. It is a geologically young (≈ 1 my) volcanic hot spot, with a narrow shelf and slope surrounded by water >2,500 m deep. Based on its general faunal similarity to the western Atlantic sector of the Southern Ocean, Bouvetøya is included in the South Georgia Biogeographic Province (Andriashev 1965, 1987; DeWitt 1971). While the fish fauna of Bouvetøya has obvious affinities with that of the Scotia Arc Islands to the west, given the isolation of Bouvetøya it is not surprising that we found differences in species composition from South Georgia and the South Sandwich Islands. *L. larseni* was the most abundant species, similar to the trawling results from the RV *Marion Dufresne* (Duhamel et al. 1983). Consistent with distributions reported in DeWitt et al. (1990), we did not find the most common species of fish from islands west of Bouvetøya, such as *G. gibberifrons* and *G. marionensis*. Absence of the ubiquitous *G. gibberifrons* may be partly because it has a relatively short, one-summer-long pelagic larval stage (Ruzicka 1996), and benthic juveniles (DeWitt et al. 1990; North 2001).

With the exception of Shag Rocks, Bouvetøya had the lowest diversity (11 species) of any of the island groups we sampled. The RV *Marion Dufresne* cruise (Hureau 1986) mentioned above obtained 13 species, including six demersal species from the same depth range as the ICEFISH cruise (Duhamel 1987). *Dissostichus eleginoides* occurs at Bouvetøya (Rogers et al. 2006) and additional fishing should determine whether or not *D. mawsoni* is also present. Our results parallel those of the *Marion Dufresne*, trawling at 20–1,789 m, in that the five most abundant species (Table 2) were identical (Duhamel 1987). Total known fish species diversity (shelf to upper slope) at Bouvetøya is 17 species (Table 4). This low diversity, in comparison to the approximately 42 shelf and upper slope species at South Georgia and 31 species at the South Sandwich Islands (Table 4), probably results from a variety of factors including limited sampling, restricted shallow water, isolation and low success of founder populations arriving from islands of the Scotia Arc to the west. Furthermore, there are likely

substantial differences in relative productivity between islands in the northern Scotia Arc and Bouvetøya, which may influence both abundance and diversity of fish of these communities.

At Bouvetøya there were substantially greater numbers of *L. squamifrons* and *Macrourus holotrachys* than at South Georgia or the South Sandwich Islands. It is likely, however, that the large number of *M. holotrachys* was attributable to a bias introduced by the fact that, ignoring two exceptionally deep stations, five of nine (56%) stations were relatively deep at 200–648 m. The depth range of *M. holotrachys* is 150–1,100 m (Iwamoto 1990). *M. holotrachys* is well represented as by-catch in the longline fishery for *D. eleginoides* at South Georgia (Morley et al. 2004). Our trawls at South Georgia may not have been sufficiently deep to catch this species.

We should note that while we established new locality records for three species of *Muraenolepis* at Bouvetøya (Table 3), the identification and presence of *M. orangeiensis* at Bouvetøya (based on specimens from a RV *Marion Dufresne* cruise) should be regarded as provisional. The species are difficult to identify and some past records may not be correct. Known species in the genus have increased from four (Chiu and Markle 1990) to eight with all subsequent additions by Balushkin and colleagues, most recently a new species from South Georgia (Balushkin and Prirodina 2007). Obviously much remains to be done on the taxonomy and biology of *Muraenolepis*.

Population genetics

Based on mitochondrial DNA, we found that the channichthyid *Chaenocephalus aceratus* and two of the nototheniids (*N. coriiceps* and *L. larseni*) exhibited no significant genetic differentiation among the various Atlantic sector localities. However, *L. squamifrons* showed significant genetic differentiation between the South Shetlands and Bouvetøya populations ($F_{ST} = 0.189$, $P = 0.015$). Thus these data, combined with previous studies of two other notothenioids, suggest that five of the six notothenioid species studied at Bouvetøya are not genetically differentiated from other localities in the Atlantic sector of the Southern Ocean. Although Kuhn and Gaffney (2006) found significant genetic heterogeneity in populations of the channichthyid *C. gunnari* from the South Shetlands and the Scotia Arc ($F_{ST} = 0.303$, $P < 0.00005$), they found no significant mitochondrial or nuclear DNA differentiation in samples from Shag Rocks, South Georgia and Bouvetøya ($F_{ST} = 0.033$, $P = 0.21$). However, because of the small sample size ($N = 3$), additional material will be necessary to confidently evaluate the Bouvetøya population and its relationship to the South Georgia and Shag Rocks populations, which at present appear to be a single stock (Kuhn and Gaffney

2006). In examining populations of *D. eleginoides* from the Falkland Islands, South Georgia and Bouvetøya, Rogers et al. (2006) found significant differentiation between the Falkland Islands population and South Georgia and Bouvetøya; however, they found no significant differentiation between South Georgia and Bouvetøya using mitochondrial DNA ($F_{ST} = 0.000$) (Rogers et al. 2006). In fact, sequence analysis of a portion of 12S rRNA demonstrated that individuals from South Georgia and Bouvetøya shared one mitochondrial haplotype (Rogers et al. 2006).

Currents and dispersal to Bouvetøya

Bouvetøya lies within the eastward flowing Antarctic Circumpolar Current (ACC), a current driven by the world's most forceful westerly winds and extending uninterrupted around the continent (Orsi et al. 1995). This vast system has considerable potential for advection of certain life history stages of notothenioid species. The importance and magnitude of oceanic dispersal has been underestimated (Kinlan and Gaines 2003; de Queiroz 2005) and now with new DNA sequencing methodology and growing databases, there are well-documented examples of dispersal for a variety of organisms in the Southern Ocean (Greve et al. 2005; Sanmartín et al. 2007; Waters 2008).

Many factors determine whether species are good candidates for dispersal to distant localities. Duration of pelagic stages is especially important because longer pelagic life improves chances for successful dispersal (Sponaugle et al. 2002). For example, planktonic larval duration explains >50% of the variation in genetic dispersal estimates for fish and invertebrates that remain planktonic for more than 2 days (Kinlan and Gaines 2003). In the case of notothenioids, the ACC linkage of the peri-Antarctic islands promotes eastward dispersal of pelagic eggs, larvae and juveniles (Kellermann and Kock 1984; Loeb et al. 1993) from the northern Scotia Arc islands to Bouvetøya and beyond. All the nototheniids and channichthyids found at Bouvetøya (Table 4) have pelagic larval stages of long (1–2 years) duration (DeWitt et al. 1990; Kellermann 1991; Kock and Kellermann 1991; Ruzicka 1996; Koubbi et al. 2000; Kock 2005; La Mesa and Ashford 2008). The pelagic eggs, larval and juvenile stages of *N. coriiceps*, for example, have been found drifting northeasterly in the ACC in the Scotia Sea (Kellermann 1991). Furthermore, the achiropsettid *Mancopsetta maculata* also has a prolonged (≈ 1 year) pelagic juvenile stage that does not metamorphose to benthic life until reaching 100 mm SL (Evseenko 1996, 1997). The prolonged pelagic phase in this peri-Antarctic family is unusual among Pleuronectiformes and their evolution has been suggested to be closely associated with the ACC (Evseenko 1996). Although *M. maculata* has a nearly circum-Antarctic distribution in both sub-Antarctic

and Antarctic waters and was previously thought to consist of two subspecies, it is now viewed as a single wide-ranging species (Evseenko 1997).

Another current system, the Weddell Sea Gyre, may also influence the composition of the fish fauna at Bouvetøya and the southernmost South Sandwich Islands. It is a large cyclonic or clockwise rotating cell of recirculating Weddell Sea water located south of the ACC (Orsi et al. 1995) and has been suggested as a dispersal agent for some of the High Antarctic invertebrates of Bouvetøya (Arntz et al. 2006). This may also be the case for some of the notothenioid fish that are more common to the south of Bouvetøya and the South Sandwich Islands than to the west; *Neopagetopsis ionah* found in the South Sandwich Islands may be an example.

Overview and conclusions

The currently known shelf and upper slope fish faunas consist of 42 species at South Georgia, 31 at the South Sandwich Islands and 17 at Bouvetøya (Table 4). This includes 21 new locality records, 10 from ICEFISH collections and another 11 from museum and literature records subsequent to publication of *Fishes of the Southern Ocean* (Gon and Heemstra 1990). The most abundant species differed among the islands with *P. guntheri* dominant at Shag Rocks, *L. nudifrons* at South Georgia and *L. larseni* at the South Sandwich Islands and Bouvetøya. *G. gibberifrons* was also abundant at South Georgia and the South Sandwich Islands. We trawled during the winter with relatively small nets and, as mentioned previously, dominant species are different when trawling is conducted with large trawls in the summer (Collins et al. 2007). Because of their high local abundance these species are ecologically important across much of the Atlantic sector of the Southern Ocean, especially in the diets of piscivorous fish species including targets of fisheries like channichthyids and *D. eleginoides* (Kock 1981, 2005; Kozlov et al. 1988; McKenna 1991; Takahashi and Iwami 1997; Flores et al. 2004; Collins et al. 2007). Because *L. nudifrons* and *G. gibberifrons* are benthic feeders (Targett 1981), they also provide direct trophic linkages between the benthic communities and larger piscivorous fish species, including commercially exploited species.

Bottom trawling around volcanic islands is difficult even when preceded by acoustic reconnaissance of the sea floor, as was the case during the ICEFISH cruise. Further, the light-duty trawls deployed during ICEFISH lacked protective chaffing on the belly and cod end, which at times impaired sampling because they were more easily torn than larger more durable nets. During the entire ICEFISH cruise, we deployed our four types of bottom trawls 106 times,

with 73 of these hauls (69%) successfully catching fish. This light-duty gear was effective in obtaining smaller species, and resulted in six of our ten new locality records.

The faunas of the South Sandwich Islands and Bouvetøya are derived primarily from South Georgia through dispersal via the Antarctic Circumpolar Current and the Low Antarctic genera *Lepidonotothen* and *Notothenia* are the most diverse and abundant nototheniids (DeWitt 1971; Andriashev 1987). The pelagic High Antarctic genera *Aethotaxis* and *Pleuragramma* are present at South Georgia and the South Sandwich Islands but have not yet been found at Bouvetøya. The fauna of Bouvetøya is isolated and impoverished compared to islands to the west (Table 4), and is unusual in lacking endemic fishes. For comparison, the fish fauna of Easter Island, another relatively small, isolated volcanic island slightly younger than Bouvetøya (750,000 years old), has 23% species endemism (Randall 1998). In contrast to the fishes at Bouvetøya, there are many undescribed species among the predominantly benthic brooding invertebrates (Arntz 2006; Arntz et al. 2006) suggesting that Bouvetøya may not conform to predictions of impoverishment based on the MacArthur and Wilson theory of island biogeography (Gutt et al. 2006). The location of Bouvetøya within the ACC and the long pelagic stages of notothenioids at Bouvetøya may ensure sufficient gene flow that fish populations, with the exception of *L. squamifrons*, are genetically homogeneous.

Finally, additional research cruises at the northern periphery of the Southern Ocean are needed because, with few exceptions, fish faunas associated with islands and seamounts here are understudied in contrast to the Antarctic. It is especially important to collect at islands in the Indian and Pacific sectors (Prince Edward and Marion Islands, McDonald and Heard Islands, Macquarie Island, Balleny Islands and Scott Island) and to obtain large samples for population genetic studies that will clarify questions about the validity of species and the composition of the genera *Lepidonotothen*, *Notothenia*, *Gobionotothen*, *Harpagifer* and *Pogonophryne*. Information on the genetic structure of populations will also be useful for better management of commercially important species such as *D. eleginoides*, *D. mawsoni* and *C. gunnari*, all of which are of increasing importance.

Acknowledgments We thank the captain, crew and personnel of Raytheon Polar Services aboard the *RVIB Nathaniel B. Palmer* for their excellent assistance during this long cruise. The ICEFISH cruise was supported by National Science Foundation grant OPP 01–32032 to H. William Detrich (Northeastern University). This is publication number 21 from the ICEFISH Cruise of 2004 (H.W. Detrich, Chief Scientist). For more information on the ICEFISH cruise visit: <http://www.icefish.neu.edu>. J.T. Eastman was supported by National Science Foundation grant ANT 04–36190. We are grateful to Dr. Tom Munroe of the Smithsonian Institution for identifying and facilitating cataloging of flatfishes into the USNM as well as for answering our

questions about this group. Dr. Martin Collins of the British Antarctic Survey kindly provided unpublished data on the number of fish species at South Georgia. K.L. Kuhn and T.J. Near thank Jillian Pennington for her help with the ND2 sequencing. We all thank Sandra K. Parker (Northeastern University) for her meticulous pre-cruise preparation of all logistic issues pertaining to ICEFISH.

References

- Andriashev AP (1965) A general review of the Antarctic fish fauna. In: van Oye P, van Mieghem J (eds) Biogeography and ecology in Antarctica, monographiae biologicae, vol XV. Junk, The Hague, pp 491–550
- Andriashev AP (1987) A general review of the Antarctic bottom fish fauna. In: Kullander SO, Fernholm B (eds) Fifth congress of European ichthyologists, proceedings, Stockholm, 1985. Swedish Museum of Natural History, Stockholm, pp 357–372
- Arntz WE (2006) Bouvet Island: a stepping stone in the Southern Ocean? *Polar Biol* 29:81–82
- Arntz WE, Thatje S, Gerdes D, Gili J-M, Gutt J, Jacob U, Montiel A, Orejas C, Teixidó N (2005) The Antarctic-Magellan connection: macrobenthos ecology on the shelf and upper slope, a progress report. *Sci Mar* 69(Suppl 2):237–269
- Arntz WE, Thatje S, Linse K, Avila C, Ballesteros M, Barnes DKA, Cope T, Christobo FJ, De Broyer C, Gutt J, Isla E, López-González P, Montiel A, Munilla T, Ramos Esplá AA, Raupach M, Rauschert M, Rodríguez E, Teixidó N (2006) Missing link in the Southern Ocean: sampling the marine benthic fauna of remote Bouvet Island. *Polar Biol* 29:83–96
- Balushkin AV (1986) Occurrence of *Lepidonotothen kempi* (Norman) (Nototheniidae) off Bouvet Island (Antarctic Region). *Proc Zool Inst (Leningrad)* 153:76–79 [In Russian]
- Balushkin AV (1990) Review of blue notothenias of the genus *Paranotothenia* Balushkin (Nototheniidae) with description of a new species. *J Ichthyol* 30:132–147
- Balushkin AV (2000) Morphology, classification, and evolution of notothenioid fishes of the Southern Ocean (Notothenioidei, Perciformes). *J Ichthyol* 40(Suppl 1):S74–S109
- Balushkin AV, Permitin YY (1982) Discovery of new subspecies of *Patagonotothen guentheri* (Nototheniidae) off Shag Rocks near South Georgia, Antarctica. *J Ichthyol* 22:13–18
- Balushkin AV, Prirodina VP (2006) A new species of eel cods *Muraenolepis trunovi* sp. nova (Muraenolepididae) from the Lazarev Sea with redescription of lectotypes *Muraenolepis marmorata* Günther, 1880 and *M. microps* (Lönnerberg, 1905). *J Ichthyol* 45:687–693
- Balushkin AV, Prirodina VP (2007) A new species of eel cods *Muraenolepis kuderskii* sp. nova (fam. Muraenolepididae) from South Georgia (the Scotia Sea). *J Ichthyol* 47:683–690
- Bandelt H-J, Forster P, Roehl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol* 16:37–48
- CCAMLR (2007) Statistical bulletin, vol. 19 (1997–2006). CCAMLR, Hobart, Australia
- Chiu TS, Markle DF (1990) Muraenolepididae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp 179–182
- Collins MA, Ross KA, Belchier M, Reid K (2007) Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Mar Biol* 152:135–147
- Collins MA, Shreeve RS, Fielding S, Thurston MH (2008) Distribution, growth, diet and foraging behaviour of the yellow-fin notothen *Patagonotothen guentheri* (Norman) on the Shag Rocks shelf (Southern Ocean). *J Fish Biol* 72:271–286
- de Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol Evol* 20:68–73

- DeWitt HH (1971) Coastal and deep-water benthic fishes of the Antarctic. In: Bushnell VC (ed) Antarctic map folio series, folio 15. American Geographical Society, New York, pp 1–10
- DeWitt HH, Heemstra PC, Gon O (1990) Nototheniidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp 279–331
- Duhamel G (1987) Ichtyofaune des secteurs indien occidental et atlantique oriental de l'océan Austral. Biogéographie, cycles biologiques et dynamique des populations. Thèse de Doctorat d'Etat. Université Paris VI. pp 687. Microfiche SN 87 200 447 Institut d'Ethnologie, pp 512
- Duhamel G, Hureau J-C, Ozouf-Costaz C (1983) Ecological survey of the notothenioid fishes in the Southern Ocean from Bouvet to Kerguelen Islands. Mem Natl Inst Polar Res Tokyo Spec Issue No 27:176–182
- Duhamel G, Gasco N, Davaine P (2005) Poissons des îles Kerguelen et Crozet. Guide régional de l'océan Austral. Patrimoines naturels, tome 63. Muséum national d'Histoire naturelle, Paris
- Efremenko VN (1984) Larvae of the family Nototheniidae from the Scotia Sea. J Ichthyol 24:34–43
- Evseenko SA (1996) Ontogeny and relationships of the flatfishes of the Southern Ocean (Achiropsettidae, Pleuronectoidei). J Ichthyol 36:687–712
- Evseenko SA (1997) Revision of the flounder genus *Mancopsetta* Gill, 1881 (Achiropsettidae, Pleuronectiformes) from the Southern Ocean. J Ichthyol 37:411–430
- Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol Bioinform Online 1:47–50
- Flores H, Kock K-H, Wilhelms S, Jones CD (2004) Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champscephalus gunnari* and *Chaenocephalus aceratus*. Polar Biol 27:119–129
- Gon O (1990) Bathyracidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, pp 364–380
- Gon O, Heemstra PC (eds) (1990) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa
- Greve M, Gremmen NJM, Gaston KJ, Chown SL (2005) Nestedness of Southern Ocean island biotas: ecological perspectives on a biogeographical conundrum. J Biogeogr 32:155–168
- Gutt J, Fricke A, Teixidó N, Potthoff M, Arntz WE (2006) Megaepibenthos at Bouvet Island (South Atlantic): a spatially isolated biodiversity hot spot on a tiny geological spot. Polar Biol 29:97–105
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl Acids Symp Ser 41:95–98
- Hureau J-C (1986) Les rapports des campagnes à la mer à bord du "Marion Dufresne", MD 24 BIOMASSE, MD 25 FIBEX, no 81–01. Territoire des Terres australes et antarctiques Françaises/Muséum national d'Histoire naturelle, Paris, pp 1–101
- Iwami T, Kock K-H (1990) Channichthyidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, pp 381–399
- Iwamoto T (1990) Macrouridae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, pp 192–206
- Jones CD, Kock K-H, Balguerías E (2000) Changes in biomass of eight species of finfish around the South Orkney Islands (Subarea 48.2) from three bottom trawl surveys. CCAMLR Sci 7:53–74
- Kellermann A (1991) Egg and larval drift of the Antarctic fish *Notothenia coriiceps*. Cybium 15:199–210
- Kellermann A, Kock K-H (1984) Postlarval and juvenile notothenioids (Pisces, Perciformes) in the Southern Scotia Sea and Northern Weddell Sea during FIBEX 1981. Meeresforschung 30:82–93
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020
- Kirkman SP, Wilson W, Klages NTW, Bester MN, Isaksen K (2000) Diet and estimated food consumption of Antarctic fur seals at Bouvetøya during summer. Polar Biol 23:745–752
- Kock K-H (1981) Fischereibiologische Untersuchungen an drei antarktischen Fischarten: *Champscephalus gunnari* Lönnberg 1905, *Chaenocephalus aceratus* (Lönnberg, 1906) und *Pseudochannichthys georgianus* Norman, 1937 (Notothenioidei, Channichthyidae). Mitt Inst Seefisch Hamburg 32:1–226
- Kock K-H (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge
- Kock K-H (2005) Antarctic icefishes (Channichthyidae): a unique family of fishes: a review, Part I. Polar Biol 28:862–895
- Kock K-H, Jones CD (2005) Fish stocks in the Southern Scotia Arc Region—a review and prospects for future research. Rev Fish Sci 13:75–108
- Kock K-H, Kellermann A (1991) Reproduction in Antarctic notothenioid fish. Antarct Sci 3:125–150
- Koubbi P, Duhamel G, Herbert C (2000) Role of bay, fjord and seamount on the early life history of *Lepidonotothen squamifrons* from the Kerguelen Islands. Polar Biol 23:459–465
- Kozlov AN, Pinskaya IA, Podrazhanskaya SG, Tarverdiyeva M (1988) Feeding of glassfishes in different regions of the Atlantic sector of Antarctica. J Ichthyol 28:137–145
- Kuhn KL, Gaffney PM (2006) Preliminary assessment of population structure in the mackerel icefish (*Champscephalus gunnari*). Polar Biol 29:927–935
- La Mesa M, Ashford J (2008) Age and early life history of juvenile Scotia Sea icefish, *Chaenocephalus aceratus*, from Elephant Island and the South Shetland Islands. Polar Biol 31:221–228
- Leviton AE, Gibbs RH Jr, Heal E, Dawson CE (1985) Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832
- Loeb V, Kellermann AK, Koubbi P, North AW, White MG (1993) Antarctic larval fish assemblages: a review. Bull Mar Sci 53:416–449
- Marlow TR, Agnew DJ, Purves MG (2003) Movement and growth of tagged *Dissostichus eleginoides* around South Georgia and Shag Rocks. CCAMLR Sci 10:101–111
- McKenna JE Jr (1991) Trophic relationships within the Antarctic demersal fish community of South Georgia Island. Fish Bull US 89:643–654
- Morley SA, Mulvey T, Dickson J, Belchier M (2004) The biology of the bigeye grenadier at South Georgia. J Fish Biol 64:1514–1529
- Nelson JS (2006) Fishes of the world, 4th edn. Wiley, Hoboken
- North AW (2001) Early life history strategies of notothenioids at South Georgia. J Fish Biol 58:496–505
- Orsi AH, Whitworth TIII, Nowlin WD Jr (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep Sea Res I 42:641–673
- Randall JE (1998) Zoogeography of shore fishes of the Indo-Pacific region. Zool Stud 37:227–268
- Rogers AD, Morley S, Fitzcharles E, Jarvis K, Belchier M (2006) Genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) populations on the Patagonian Shelf and Atlantic and western Indian Ocean Sectors of the Southern Ocean. Mar Biol 149:915–924
- Rozas J, Sánchez-DelBarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496–2497
- Ruzicka JJ (1996) Comparison of the two alternative early life-history strategies of the Antarctic fishes *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Mar Ecol Prog Ser 133:29–41

- Sanmartín I, Wanntorp L, Winkworth RC (2007) West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. *J Biogeogr* 34:398–416
- Schneppenheim R, Kock K-H, Duhamel G, Janssen G (1994) On the taxonomy of the *Lepidotothen squamifrons* group (Pisces, Perciformes, Notothenioidei). *Arch Fish Mar Res* 42:137–148
- Shust KV (1998) Fishes and fish resources of the Antarctic. VNIRO, Moscow. ISBN 5-85382-179-2
- Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bull Mar Sci* 70(Suppl):341–375
- Stein DL (2006) New and rare species of snailfishes (Scorpaeniformes: Liparidae) collected during the ICEFISH cruise of 2004. *Polar Biol* 29:705–712
- Stein DL, Andriashev AP (1990) Liparididae. In: Gon O, Heemstra PC (eds) *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa, pp 231–255
- Takahashi M, Iwami T (1997) The summer diet of demersal fish at the South Shetland Islands. *Antarct Sci* 9:407–413
- Targett TE (1981) Trophic ecology and structure of coastal Antarctic fish communities. *Mar Ecol Prog Ser* 4:243–263
- Trathan PN, Brandon MA, Murphy EJ (1997) Characterization of the Antarctic Polar Frontal Zone to the north of South Georgia in summer 1994. *J Geophys Res* 102:10483–10497
- Trunov IA (1999) New data on species of fish from Subantarctic and Antarctic waters of the Atlantic Ocean. *J Ichthyol* 39:488–497
- Trunov IA (2001) Occurrence of *Pleuragramma antarcticum* (Nototheniidae) off South Georgia Island and the South Sandwich Islands (Antarctica). *J Ichthyol* 41:549–550
- Voskoboinikova OS, Balushkin AV (1987) On the taxonomical status of the *Gobionotothen angustifrons sandwichensis* (Nybelin, 1947) (Nototheniidae). *Proc Zool Inst (Leningrad)* 162:100–107 [In Russian]
- Waters JM (2008) Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *J Biogeogr* 35:417–427
- Weir B, Cockerham C (1984) Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370