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Bathymetric distributions of notothenioid fishes

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Abstract There has been no comprehensive study of the bathymetry of notothenioid fishes. Therefore, I analyzed minimum and maximum depths and depth ranges for 128 of 142 species that collectively range from 0 to ≈ 3000 m. Means (and medians) for maximum depths are 176 m (75 m) for non-Antarctic, 511 m (360 m) for sub-Antarctic, and 963 m (899 m) for Antarctic species; medians are significantly different. Means (and medians) for depth ranges for the three groups are 140 (55 m), 470 (345 m), and 727 m (714 m), respectively, with significantly different medians. The mean maximum depths for the Cryonotothenioidea are: Nototheniidae—525 m, Harpagiferidae—88 m, Artedidraconidae—906 m, Bathydraconidae—1165 m, and Channichthyidae—910 m. If five species of *Bathydraco*, with a mean of 2098 m are excluded, the mean for the Bathydraconidae is 741 m. With the exceptions of the harpagiferids and *Bathydraco*, there is overlap of the 95% confidence intervals for the means of other families. Thirteen Antarctic and sub-Antarctic species with maximum depths and/or depth ranges ≥ 1500 m are especially deep-living: four nototheniids, four species of *Bathydraco*, three species of *Pogonophryne*, and two channichthyids. The most common depth range is 0–50 m for non-Antarctic, 200–400 m for sub-Antarctic and 600–800 m for Antarctic species. Three species have depth ranges >2000 m. Species diversity peaks at 50 m for non-Antarctic, 100 m for sub-Antarctic, and 500 m for Antarctic species. Notothenioids are not eurybathic compared with older deep-sea taxa but are eurybathic relative to marine percomorphs.

Keywords Antarctic · Sub-Antarctic · Non-Antarctic · Mean maximum depth · Depth range · Eurybathy

Introduction

Notothenioid fishes have long been associated with Gondwana, initially appearing in the western Weddellian Paleobiogeographic Province centered on southern South America. Their subsequent diversification was linked to the fragmentation of Gondwana and to the isolation of Antarctica where they evolved in situ in the waters around the continent (Near et al. 2015). Today the relict notothenioid *Percophis brasiliensis*, with a depth range of 5–75 m, inhabits the waters of southeastern South America, likely similar to the shallow coastal depths occupied by the ancestral notothenioid. During the past 25 million years (Ma), and especially during that last 10 Ma (Near et al. 2012), the Antarctic continental shelf and slope have hosted irregular bursts of diversification that have propelled the Cryonotothenioidea (formerly the Antarctic clade) to a level of morphological and ecological diversity that encompasses inshore to slope depths and most energetically feasible niches on the substrate and in the water column (Eastman 1993, 2005; Near et al. 2012, 2015). Recently multiple lines of evidence and approaches have bolstered the rationale for concluding that notothenioids, or components thereof, are exemplars of adaptive radiation (Janko et al. 2011; Matschiner et al. 2011, 2015; Rutschmann et al. 2011; Lautrédou et al. 2012; Lecointre et al. 2013; Wilson et al. 2013; Colombo et al. 2015).

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The bathymetric distribution of notothenioids has received less attention than morphological, physiological and ecological aspects of the radiation. Nybelin (1947) first compiled the depth ranges of notothenioids and designated some species as eurybathic. Andriashev (1965, 1987) also noted that many notothenioids have what he considered wide depth ranges of 500–700 m, while DeWitt (1971) expanded the taxonomic coverage of notothenioid depth ranges and recognized that many near shore species also have ranges encompassing outer shelf and even upper slope depths. Both Andriashev and DeWitt concluded that maximum species diversity on the Antarctic shelf is greatest at 300–600 m versus 100–200 m elsewhere in the world. DeWitt (1971; Fig. 2), however, specifically noted that maximum species diversity was at 250–350 m on the West Antarctica shelf versus 500–550 m in East Antarctica. The current state of our knowledge, as compiled in *Fishes of the Southern Ocean* (Gon and Heemstra 1990), indicates that, as a group, Antarctic notothenioids are found from shallow inshore waters to slope depths of 1500–2000 m, with a few species reaching 2000–3000 m.

Eighty-six percent of the Southern Ocean seafloor is >1000 m deep (Griffiths et al. 2014). The deep-sea is usually demarcated by depths ≥1000 m (Angel 1997) and deep sea-fishes have mean maximum depths of occurrence at or below this depth (Priede and Froese 2013). Although their classification is influenced by ongoing phylogenetic realignments, many deep-sea demersal species are members of phylogenetically older clades such as anguilliforms, gadiforms, and alepocephaliforms, although there has also been expansion into this habitat by members of some percomorph clades (Haedrich 1997; Merrett and Haedrich 1997; Weitzman 1997; Priede and Froese 2013). For example liparids, the deepest-living fishes with one species known from 8145 m (Linley et al. 2016), are now included in a percomorph clade with zoarcids, cottoids, serranids, and notothenioids, on the basis of a phylogeny with a bootstrap score of 100% inferred from a nuclear gene supermatrix for acanthomorphs (Near et al. 2013).

Although *Fishes of the Southern Ocean* (Gon and Heemstra 1990) provides the most recent summary of notothenioid depth ranges, it does not include the non-Antarctic species. Moreover, in the 26 years since its publication, there has been considerable research trawling, as well as commercial longlining, that has extended on to the slope and into the deep-sea. The number of notothenioid species has increased by 18%, from 120 to 142. There is no summary or general discussion of the bathymetry of notothenioids. Therefore, this paper will provide updated minimum and maximum depths of occurrence and depth ranges for all Antarctic, sub-Antarctic, and non-Antarctic notothenioid species, and will address these questions: (1) are the shallowest- and deepest-living notothenioids confined to particular taxa; (2) is the record for the deepest-living notothenioid valid; and (3) are notothenioids eurybathyic.

Materials and methods

Nomenclature and taxonomic coverage

The taxonomy for notothenioids generally follows relationships identified by recent molecular phylogenetic analyses. These revisions have *Percophis brasiliensis* as the phylogenetically basal notothenioid (Near et al. 2015), and amalgamate the genera *Cryothenia* and *Pagothenia* into *Trematomus*, and *Paranotothenia* into *Notothenia* (Sanchez et al. 2007; Dettai et al. 2012; Near et al. 2015). The polyphyly in the genus *Artedidraco* (Lecointre et al. 2011) has yet to be resolved so the status quo is retained. Although I employ the new rank-free clade names from Near et al. (2015), I also retain some traditional family names to facilitate clarity of discussion of the bathymetric data while acknowledging that the relationships implied by these names are no longer tenable. The sequencing of taxa in Table 1 and the figures follows the phylogeny in Near et al. (2012, 2015).

I recognize 142 species of notothenioids based on the list in Eastman and Eakin (2000) with updates current to April, 2017. The list purposefully does not reflect the recent synonymization of *Bovichtus oculus* with *B. psychrolutes* (Balushkin 2016). All 142 species are included in Table 1 with collection depths and ranges, but the maximum depth and depth range analyses and figures include only 128 species. I excluded these 14 species (asterisks in Table 1) because their descriptions are based on a single specimen and/or a single depth or a limited depth range: *Trematomus amphitreta*, *Pogonophryne albipinna, P. bellingshausenensis*, *P. cerebropogon*, *P. dewitti*, *P. fusca, P. maculiventrata*, *P. pallida*, *P. pavlovi*, *P. platypogon*, *P. sarmentifera* and *P. stewarti*. I also excluded *Artedidraco longibarbatus* because the two known specimens were captured close to each other and the depth range is minimal (372–396 m). Although now recognized as a valid species (La Mesa et al. 2002; Dornburg et al. 2016a), I excluded *Cryodraco atkinsoni* because it is sympatric with *C. antarcticus* in East Antarctica, and therefore, its collection depths had not previously been distinguished from the latter species. Several species of *Pogonophryne* have been placed in synonymy since 1990. The depths of occurrence of these species were amalgamated with those of the valid species (Eakin and Eastman, unpublished information). Finally, *Lepidonotothen nudifrons* has been convincingly shown to consist of two cryptic species (Dornburg et al. 2016b), but this is not reflected in Table 1.

Table 1 Minimum and maximum depths of occurrence and depth ranges (maximum depth minus minimum depth) for 142 species of notothenioids, 31 non-Antarctic (n-A), 33 sub-Antarctic (s-A), and 64 Antarctic (A), arranged in approximate phylogenetic sequence based on Near et al. (2012, 2015)

Species	Habitat	Depth (m)			References
		Min	Max	Range	
Notothenioidei					
Percophidae					
1. *Percophis brasiliensis*	n-A	5	75	70	Militelli and Macchi (2001), Barretto et al. (2011) and Avigliano et al. (2015)
Notothenioidea					
Bovichtidae					
2. *Bovichtus angustifrons*	n-A	0	30	30	Hardy (1988) and Bray (2011)
3. *B. chilensis*	n-A	0	50	50	Sielfeld and Vargas (1999)
4. *B. diacanthus*	n-A	0	20	20	Andrew et al. (1995)
5. *B. oculus*	n-A	847	902	55	Hardy (1988) and Stewart (2015a)
6. *B. psychrolutes*	n-A	0	620	620	Hardy (1988), Stewart (2015a) and Balushkin (2016)
7. *B. variegatus*	n-A	0	40	40	Stewart (2015a)
8. *B. veneris*	n-A	0	30	30	Duhamel (1989) and Duhamel pers. com. (2017)
9. *Cottoperca trigloides*	n-A	5	310	305	Sielfeld and Vargas (1999); Laptikhovsky and Arkhipkin (2003) and Arkhipkin et al. (2015)
10. *Halaphritis platycephala*	n-A	5	13	8	Last et al. (2002)
Pseudaphritioidea					
11. *Pseudaphritis urvillii*	n-A	0	4	4	Raadik (2008)
Eleginopsioidea					
12. *Eleginops maclovinus*	n-A	0	250	250	Brickle et al. (2005a, b)
Cryonotothenioidea					
Nototheniidae					
13. *Aethotaxis mitopteryx*	A	400	1500	1100	Kunzmann and Zimmermann (1992) and Trunov (1999)
14. *Dissostichus eleginoides*	s-A	0	2144	2144	Collins et al. (2010), Petrov (2011), Duhamel et al. (2005), Péron et al. (2016) and Duhamel pers. com. (2016)
15. *D. mawsoni*	A	12	2210	2198	DeWitt et al. (1990), Fuiman et al. (2002), Petrov (2011a, b) and Hanchet et al. (2015)
16. *Pleuragramma antarctica*	A	0	1000	1000	DeWitt et al. (1990), Gerasimchuk (1986) and Robison (2003)
17. *Gvozdarus svetovidovi*	A	295	556	261	DeWitt et al. (1990) and Shandikov and Kratkiy (1990)
18. *Trematomus amphitreta**	A	0	20	20	Cziko and Cheng (2006)
19. *T. bernacchii*	A	0	700	700	DeWitt et al. (1990)
20. *T. borchgrevinki*	A	0	72	72	DeWitt et al. (1990)
21. *T. brachysoma*	A	0	90	90	DeWitt et al. (1990)
22. *T. eulepidotus*	A	70	823	753	DeWitt et al. (1990), Causse et al. (2011) and Causse pers. com. (2016)
23. *T. hansoni*	A	5	550	545	DeWitt et al. (1990)
24. *T. lepidorhinus*	A	99	1658	1559	DeWitt et al. (1990), Gutt and Ekau (1996), Eastman and Hubold (1999) and Hanchet et al. (2013)
25. *T. loennbergii*	A	65	1243	1178	DeWitt et al. (1990), Gutt and Ekau (1996) and Eastman and Hubold (1999)
26. *T. newnesi*	A	0	400	400	DeWitt et al. (1990)
27. *T. nicolai*	A	0	460	460	DeWitt et al. (1990) and Kuhn et al. (2009)
28. *T. peninsulae*	A	50	400	350	Daniels (1981)

Table 1 continued

Species	Habitat	Depth (m)			References
		Min	Max	Range	
29. *T. pennellii*	A	0	732	732	DeWitt et al. (1990)
30. *T. scotti*	A	20	793	773	DeWitt et al. (1990)
31. *T. tokarevi*	A	196	791	595	DeWitt et al. (1990), Causse et al. (2011) and Causse pers. com. (2016)
32. *T. vicarius*	s-A	20	240	220	DeWitt et al. (1990)
33. *L. larseni*	s-A	30	550	520	DeWitt et al. (1990)
34. *L. mizops*	s-A	20	510	490	DeWitt et al. (1990) and Duhamel et al. (2005)
35. *L. nudifrons*	s-A	5	350	345	DeWitt et al. (1990)
36. *L. squamifrons*	A	5	900	895	DeWitt et al. (1990)
37. *Patagonotothen brevicauda*	n-A	5	173	168	DeWitt (1966) and Sielfeld and Vargas (1999)
38. *P. canina*	n-A	14	102	88	DeWitt (1966)
39. *P. cornucola*	n-A	0	40	40	DeWitt (1966), Pequeño (1986) and Hüne and Vega (2016)
40. *P. elegans*	n-A	10	256	246	DeWitt (1966)
41. *P. guntheri*	s-A	111	470	359	Collins et al. (2008)
42. *P. jordani*	n-A	18	94	76	DeWitt (1966)
43. *P. kreffti*	n-A	155	210	55	Balushkin and Stehmann (1993)
44. *P. longipes*	n-A	10	434	424	DeWitt (1966) and Murillo and Oyarzún (2002)
45. *P. ramsayi*	n-A	50	450	400	Hart (1946) and Arkhipkin et al. (2013)
46. *P. sima*	n-A	0	16	16	DeWitt (1966) and Gosztonyi and Lopez-Arbarello (2000)
47. *P. squamiceps*	n-A	0	16	16	DeWitt (1966)
48. *P. tessellata*	n-A	0	141	141	DeWitt (1966) and Hüne and Vega (1966)
49. *P. trigramma*	n-A	0	12	12	Sielfeld and Vargas (1999)
50. *P. thompsoni*	n-A	0	50	50	Sielfeld and Vargas (1999)
51. *P. wiltoni*	n-A	0	35	35	Sielfeld and Vargas (1999)
52. *Gobionotothen acuta*	s-A	0	390	390	DeWitt et al. (1990) and Duhamel et al. (2005)
53. *G. barsukovi*	s-A	100	300	200	Balushkin (1991, 2014)
54. *G. gibberifrons*	s-A	5	750	745	DeWitt et al. (1990)
55. *G. marionensis*	s-A	0	240	240	DeWitt et al. (1990) and Duhamel et al. (2005)
56. *Notothenia angustata*	n-A	0	100	100	Paulin and Roberts (1992) and Stewart (2015b)
57. *N. coriiceps*	s-A	0	550	550	DeWitt et al. (1990)
58. *N. cyanobrancha*	s-A	0	102	102	DeWitt et al. (1990), Duhamel et al. (2005) and Duhamel pers. com. (2017)
59. *N. dewitti*	A	0	470	470	Balushkin (1990)
60. *N. magellanica*	s-A	0	440	440	DeWitt et al. (1990) and Stewart (2015b)
61. *N. microlepidota*	n-A	0	650	650	Paulin et al. (1989) and Stewart (2015b)
62. *N. rossii*	s-A	0	550	550	DeWitt et al. (1990)
Harpagiferidae					
63. *Harpagifer andriashevi*	s-A	80	320	240	Prirodina (2000)
64. *H. antarcticus*	s-A	0	5	5	Hureau (1990), Hüne et al. (2015) and Aghmich et al. (2016)
65. *H. bispinis*	n-A	0	50	50	Hureau (1990), Peréz et al. (2003), Hüne et al. (2015) and Hüne and Vega (2016)
66. *H. crozetensis*	s-A	0	5	5	Prirodina (2004)
67. *H. georgianus*	s-A	40	100	60	Hureau (1990) and Williams (1988)
68. *H. kerguelensis*	s-A	0	5	5	Hureau (1990), Prirodina (2002) and Duhamel et al. (2005)
69. *H. macquariensis*	s-A	0	6	6	Prirodina (2000)

Table 1 continued

Species	Habitat	Depth (m)			References
		Min	Max	Range	
70. *H. nybelini*	s-A	64	76	12	Prirodina (2002)
71. *H. permitini*	s-A	65	80	15	Neyelov and Prirodina (2006)
72. *H. palliolatus*	n-A	0	50	50	Hureau (1990)
73. *H. spinosus*	s-A	140	275	135	Prirodina (2002) and Duhamel et al. (2005)
Artedidraconidae					
74. *Artedidraco glareobarbatus*	A	84	130	46	Eastman and Eakin (1999) and La Mesa et al. (2006)
75. *A. longibarbatus**	A	372	396	24	Eakin et al. (2015)
76. *A. loennbergi*	A	105	878	773	Eakin (1990), La Mesa et al. (2006), Causse et al. (2011) and Causse pers. com. (2016)
77. *A. mirus*	s-A	18	320	302	Eakin (1990)
78. *A. orianae*	A	82	801	719	Eakin (1990)
79. *A. shackletoni*	A	56	460	404	Eakin (1990)
80. *A. skottsbergi*	A	5	666	661	Eakin (1990)
81. *Dolloidraco longedorsalis*	A	99	1243	1144	Eakin (1990) and Gutt and Ekau (1996)
82. *Histiodraco velifer*	A	210	910	700	Eakin (1990) and Eastman and Hubold (1999)
83. *Pogonophryne albipinna**	A	1565	1674	109	Eakin (1990)
84. *P. barsukovi*	A	195	1120	925	Eakin (1990)
85. *P. bellingshausenensis**	A	1947	1947	0	Eakin et al. (2008)
86. *P. brevibarbata*	A	726	1568	842	Balushkin et al. (2010)
87. *P. cerebropogon**	A	300	300	0	Eakin and Eastman (1998)
88. *P. dewitti**	A	884	915	31	Eakin (1990)
89. *P. eakini*	A	80	247	167	Balushkin (1999)
90. *P. favosa*	A	219	330	111	Balushkin and Korolkova (2013)
91. *P. fusca**	A	466	493	27	Balushkin and Eakin (1998)
92. *P. immaculata*	A	1195	2542	1347	Eakin (1990) and Eakin et al. (2009)
93. *P. lanceobarbata*	A	233	667	434	Eakin (1990)
94. *P. macropogon*	A	570	836	266	Eakin (1990)
95. *P. maculiventrata**	A	360	360	0	Spodareva and Balushkin (2014)
96. *P. marmorata*	A	140	1405	1265	Eakin (1990)
97. *P. mentella*	A	210	540	330	Gosse (1966) and Andriashev (1967)
98. *P. neyelovi*	A	700	1390	690	Shandikov and Eakin (2013)
99. *P. orangiensis*	A	420	670	250	Eakin and Balushkin (1998) and Eakin and Eastman, unpublished data
100. *P. pallida**	A	1131	1505	374	Balushkin and Spodareva (2015)
101. *P. pavlovi**	A	1422	1623	201	Balushkin (2013)
102. *P. permitini*	A	430	1120	690	Eakin (1990)
103. *P. platypogon**	A	360	360	0	Eakin (1990)
104. *P. sarmentifera**	A	1036	1157	121	Balushkin and Spodareva (2013a)
105. *P. scotti*	A	100	1180	1080	Eakin (1990)
106. *P. skorai*	A	360	490	130	Balushkin and Spodareva (2013b)
107. *P. stewarti**	A	1696	1738	42	Eakin et al. (2009)
108. *P. squamibarbata*	A	651	1116	465	Eakin and Balushkin (2000), Eakin and Eastman unpublished data
109. *P. tronio*	A	726	1568	842	Shandikov et al. (2013)
110. *P. ventrimaculata*	A	247	460	213	Eakin (1990)
Bathydraconidae					
111. *Gerlachea australis*	A	200	952	752	Gon (1990), Causse et al. (2011) and Causse pers. com. (2016)

Table 1 continued

Species	Habitat	Depth (m)			References
		Min	Max	Range	
112. *Cygnodraco mawsoni*	A	85	475	390	Gon ([1990](#)) and Ekau (1990)
113. *Parachaenichthys charcoti*	s-A	5	480	475	Gon ([1990](#)) and Balushkin and Voskoboinikova ([2011](#))
114. *P. georgianus*	s-A	5	350	345	Gon ([1990](#)); Balushkin and Voskoboinikova ([2011](#))
115. *Racovitzia glacialis*	A	219	867	648	Gon ([1990](#)), Causse et al. ([2011](#)) and Causse pers. com. (2016)
116. *Prionodraco evansii*	A	70	910	840	Gon ([1990](#)); Eastman and Hubold (1999)
117. *Vomeridens infuscipinnis*	A	445	902	457	Gon ([1990](#)), Balushkin and Voskoboinikova ([2011](#)) and Kuhn et al. (2011)
118. *Akarotaxis nudiceps*	A	371	1191	820	Gon ([1990](#)) and Eastman and Hubold (1999)
119. *Bathydraco antarcticus*	s-A	340	2400	2060	Gon ([1990](#))
120. *B. joannae*	s-A	230	1800	1570	Gon ([1990](#)) and Balushkin and Voskoboinikova ([2011](#))
121. *B. macrolepis*	A	450	2100	1650	Gon ([1990](#))
122. *B. marri*	A	300	1250	950	Gon ([1990](#))
123. *B. scotiae*	A	2100	2941	841	Gon ([1990](#))
124. *Gymnodraco acuticeps*	A	0	1000	1000	Gon ([1990](#)), Balushkin and Voskoboinikova ([2011](#)) and Hanchet et al. (2013)
125. *Psilodraco breviceps*	s-A	60	360	300	Gon ([1990](#)) and Balushkin and Voskoboinikova ([2011](#))
126. *Acanthodraco dewitti*	A	253	667	411	Skóra (1995), Vacchi et al. (2001) and Balushkin and Voskoboinikova ([2011](#))
Channichthyidae					
127. *Dacodraco hunteri*	A	300	926	626	Iwami and Kock (1990) and Hanchet et al. (2013)
128. *Champsocephalus esox*	n-A	0	250	240	Iwami and Kock (1990) and Sielfeld and Vargas (1999)
129. *C. gunnari*	s-A	0	700	700	Iwami and Kock (1990)
130. *Pagetopsis macropterus*	A	5	752	747	Iwami and Kock (1990) and Hanchet et al. (2013)
131. *P. maculatus*	A	200	910	710	Iwami and Kock (1990) and Eastman and Hubold (1999)
132. *Neopagetopsis ionah*	A	20	1587	1567	Iwami and Kock (1990) and Hanchet et al. (2013)
133. *Pseudochaenichthys georgianus*	s-A	0	475	475	Iwami and Kock (1990)
134. *Chaenodraco wilsoni*	A	50	800	750	Iwami and Kock (1990), Kock ([2005](#)) and Hanchet et al. (2013)
135. *Chionodraco hamatus*	A	4	972	968	Iwami and Kock (1990), Kock ([2005](#)), Causse et al. ([2011](#)) and Causse pers. com. (2016)
136. *C. myersi*	A	99	926	827	Iwami and Kock (1990), Gutt and Ekau (1996) and Hanchet et al. (2013)
137. *C. rastrospinosus*	A	200	1000	800	Iwami and Kock (1990) and Kock ([2005](#))
138. *Chaenocephalus aceratus*	s-A	5	770	765	Iwami and Kock (1990) and Kock ([2005](#))
139. *Channichthys rhinoceratus*	s-A	5	750	745	Iwami and Kock (1990); Kock ([2005](#)) and Duhamel et al. ([2005](#))
140. *Chionobathyscus dewitti*	A	358	2025	1667	Iwami and Kock (1990), Eastman et al. ([2013](#)) and Hanchet et al. (2013)
141. *Cryodraco antarcticus*	A	300	800	500	Iwami and Kock (1990) and Kock and Jones (2002)
142. *C. atkinsoni**	A	300	800	500	Iwami and Kock (1990)

Rank-free clade names are from Near et al. ([2015](#)) but traditional family names (some paraphyletic) are retained for clarity in the discussion. Asterisks (*) indicate 14 Antarctic species excluded from the analysis because of insufficient data. References (in Online Resource 1) include the original as the basis, and subsequent updates or confirmations

Sources and evaluation of bathymetric data

I obtained maximum and minimum depths of occurrence and depth ranges (maximum depth minus minimum depth) from the literature. I used the chapters on notothenioids in *Fishes of the Southern Ocean* (Gon and Heemstra 1990) as the initial source for Antarctic and sub-Antarctic species and DeWitt's (1966) doctoral dissertation as the source for non-Antarctic nototheniids. The papers of Nast et al. (1988) and Tiedtke and Kock (1989) were the basis for the depth ranges for many of the West Antarctic species in the DeWitt et al. (1990) chapter on the Nototheniidae in *Fishes of the Southern Ocean*. These data were then updated from the recent literature including descriptions of new species, regional field guides, and articles on ecology, including feeding, reproduction, and biogeography. For example, a recent volume on the Bathydraconidae by Balushkin and Voskoboinikova (2011) contains seven new depth records based on specimens in Russian collections. I also made judgment calls in excluding records not supported by a specimen or a reference, or that seemed biologically unrealistic as in the reports of *Dissostichus eleginoides* from 3850 m (Miller 1993, p. 124) and of *Lepidonotothen squamifrons* from 2033 m (Petrov 2011a; Petrov pers. comm. 2016). In the latter case, the *L. squamifrons* were hooked directly as bycatch on a toothfish longline resulting in an unlikely doubling of the depth range of this well-studied species. Nor did I use www.fishbase.org as a source of depth records as I found the notothenioid data to be incomplete, unreliable, or outdated. I did draw on personal communications from experts.

It is likely that all notothenioids have pelagic larvae (Loeb et al. 1993) that inhabit surface waters and that experience ontogenetic shifts in habitat depth. Well-known examples include species of nototheniids (Duhamel 1981; Burchett 1983; Ślósarczyk 1983) and channichthyids (Kompowski 1980; Kock 2005) that, while benthic as adults, have juvenile stages that live and feed in shallow waters. In some channichthyids, this pelagic phase may persist for several years (Kock 2005), and these depths are included in Table 1. Even some of the deepest-living species, such as *Dissostichus mawsoni*, have been documented as present in the upper reaches of the water column as adults feeding at a depth of 12 m (Fuiman et al. 2002). Depth records given here therefore reflect all life history stages, and reporting the shallow depths of life history stages does not artificially inflate the depth ranges; it is an integral aspect of notothenioid biology and has been noted as such in the previous definitive literature (Norman 1938; Nybelin 1947; Gon and Heemstra 1990).

Literature records for some species of the genera *Bovichtus, Harpagifer,* and *Patagonotothen* refer to these fishes as "intertidal" or living in "tide pools." In these instances I assigned depth ranges of 0–5 m if no specific depths were provided. A minimum depth of 0 m is applicable to intertidal species because at King George Island Aghmich et al. (2016), for example, found *Harpagifer antarcticus* "on the underside of stones" in tide pools at low tide. The same is true for *H. kerguelensis* and *Notothenia cyanobrancha* at Kerguelen and Crozet (Duhamel et al. 2005; Duhamel pers. com. 2017). *Harpagifer bispinus* and *Patagonotothen cornucola* also exemplify intertidal notothenioids, and are the dominant species in the intertidal of some areas of southern South America (Hüne and Vega 2016). I also note that juveniles of other Antarctic notothenioids that are not intertidal as adults, for example *Trematomus borchgrevinki* and channichthyids, have been found in shallow pools in the intertidal of Adelaide Island (Griffiths and Waller 2016, pp. 1151, 1153). This further validates 0 m as a documented minimum depth for some notothenioids.

Long benthic trawling times with non-closing nets invite skepticism about the validity of some depth records. However, most tow times on the Antarctic shelf and slope are over limited bathymetric ranges and last only 20–30 min. I excluded data from benthic trawls that resulted in extraordinarily deep records for typically shallow-living species, for example 517 m for *Trematomus borchgrevinki* and 608 m for *T. brachysoma* (Matallanas and Olaso 2007). These records were obtained with non-closing trawls and the actual depth of capture is unknown (Matallanas, pers. com. 2015). I also excluded records where the specimens collected were not individually identified, but rather lumped into a species complex, e.g., *Trematomus lepidorhinus/T. loennbergii* (Causse et al. 2011). In sampling at depths of 150–2065 m in the Dumont d'Urville Sea, Causse et al. (2011, p. 275) also observed *Pleuragramma antarctica* "at different levels in the water column" and also "close to the bottom". However, in the absence of more precise statements about its maximum depth of occurrence I used a record documenting 1000 m. Finally, I did not consider records based on the stomach contents of predators, especially those from commercially caught longline specimens of *Dissostichus mawsoni*. For example, a *Gymnodraco acuticeps* in stomach of a *Chionobathyscus dewitti* that was in the stomach of a *D. mawsoni* from 1158 m (Petrov 2011b).

Statistical computation and graphing were performed using GraphPad Prism version 7.0b (GraphPad Software, La Jolla California USA, www.graphpad.com). In Table 2, I provide margins of error for means, specifically the 95% confidence intervals, rather than the standard deviations because the data are not non-normally distributed and because the parameter of interest is the behavior of the mean (Greenacre 2016).

Table 2 Minimum and maximum depths of occurrence and depth ranges including means, with 95% confidence intervals (CI), and medians for maximum depth and depth range for 128 notothenioid species arranged by family and summarized by habitat

Taxa	Species (*n*)	Depth (m)				Depth range (m)			
		Min	Max	Mean (95% CI)	Median	Min	Max	Mean (95% CI)	Median
Phylogenetically basal	12	0	902	195 (12–378)	45	4	620	124 (7–240)	45
Nototheniidae	49	0	2210	525 (379–670)	440	12	2198	489 (348–629)	400
Harpagiferidae	11	0	320	88 (15–162)	50	5	240	53 (7–102)	15
Artedidraconidae	25	5	2542	906 (684–1129)	863	46	1347	583 (425–742)	661
Bathydraconidae	16	5	2941	1165 (758–1573)	931	300	2060	845 (571–1118)	786
Without 5 spp. of *Bathydraco*	11	0	1191	741 (548–934)	867	345	1000	586 (427–744)	475
5 spp. of *Bathydraco*	5	230	2941	2098 (1311–2886)	2100	841	2060	1414 (781–2048)	1570
Channichthyidae	15	0	2025	910 (677–1142)	800	250	1667	806 (601–1012)	747
All non-Antarctic spp.	31	0	902	176 (95–258)	75[a]	4	650	140 (76–204)	55[b]
All sub-Antarctic spp.	33	0	2400	511 (310–712)	360[a]	5	2144	470 (283–657)	345[b]
All Antarctic spp.	64	0	2941	963 (824–1102)	889[a]	5	2198	727 (621–834)	714[b]
All notothenioid spp.	128	0	2941	656 (552–760)	525	4	2198	519 (436–610)	429

[a,b] Kruskal–Wallis tests of medians for maximum depths ($H = 59$, $p < 0.0001$) and for depth ranges ($H = 49$, $p < 0.0001$) of non-Antarctic, sub-Antarctic and Antarctic notothenioids are significantly different

Results

Table 1 provides the maximum and minimum depths of occurrence and depth ranges of all notothenioids. Table 2 summarizes depths by family and habitat, and provides means and medians for maximum depths and depth ranges. The boxplots in Fig. 1 show the data for both maximum depths (Fig. 1a) and depth ranges (Fig. 1b) by habitat and indicate that the data for all species have a positive skew, with means greater than medians. Only the data for depth ranges of Antarctic species are somewhat less skewed. Five of 6 D'Agostino–Pearson omnibus tests for normality ($H2 = 19$–28) had significance levels of $p < 0.0001$, while that for depth range of Antarctic species was ($H2 = 12$) with $p = 0.0024$.

Maximum depths

As shown in Table 2, Kruskal–Wallis tests indicate that medians for maximum depths are significantly different ($H = 59$, $p < 0.0001$) among non-Antarctic (75 m), sub-Antarctic (360 m), and Antarctic species (889 m). The bar graph in Fig. 2 shows the 95% confidence intervals for the mean maximum depths of five the families of the Cryonotothenioidea. The primarily intertidal and inshore harpagiferids have a significantly shallower mean maximum depth than the other families that live considerably deeper, but overlap of the confidence intervals for these four families indicates that their mean maximum depths are not significantly different from one another. However, when species of the genus *Bathydraco* are considered separately from the other bathydraconids, the mean

maximum depth for *Bathydraco* is significantly greater than those of all of the non-bathydraconid families. With *Bathydraco* excluded, the mean and median for the remaining bathydraconids decrease (Table 2), and channichthyids and artedidraconids become the deepest-living families with mean maximum depths of 910 and 906 m.

Scatterplots display maximum depths for all 128 species on arithmetic (Fig. 3) and logarithmic (Online Resource 2, Fig. S1) depth axes and provide an intuitive representation of the distribution of notothenioids in the water column. Counts based on Fig. 3 reveal that 80% (102/128) of all notothenioids have maximum depths of <1000 m, 15% (19/128) are at 1000–2000 m, and 5% (7/128) are at 2000–2941 m. If a maximum depth of ≥1500 m is used to distinguish deeper-living notothenioids, thereby eliminating most outer shelf species with ranges extending onto the upper slope, 3 sub-Antarctic and 10 Antarctic species, or 10% (13/128) as labeled in Fig. 3, fall into this category—four nototheniids, four bathydraconids of the genus *Bathydraco*, three artedidraconids of the genus *Pogonophryne*, and two channichthyids.

As for the shallower living notothenioids, 61% (19/31) non-Antarctic species have maximum depths of ≤100 m, and 39% (12/31) live at 101–902 m. This is more easily visualized on a logarithmic depth axis that provides greater separation at shallower depths (Online Resource 2, Fig. S1). The 11 non-Antarctic taxa with the shallowest (≤40 m) maximum depths are *Pseudaphritis*, *Halaphritis*, species of *Bovichtus* and species of the nototheniid genus *Patagonotothen*. Seven of 33 (21%) sub-Antarctic species have maximum depths ≤100 m, and all seven of are members of the genus *Harpagifer*. Four of the seven live at
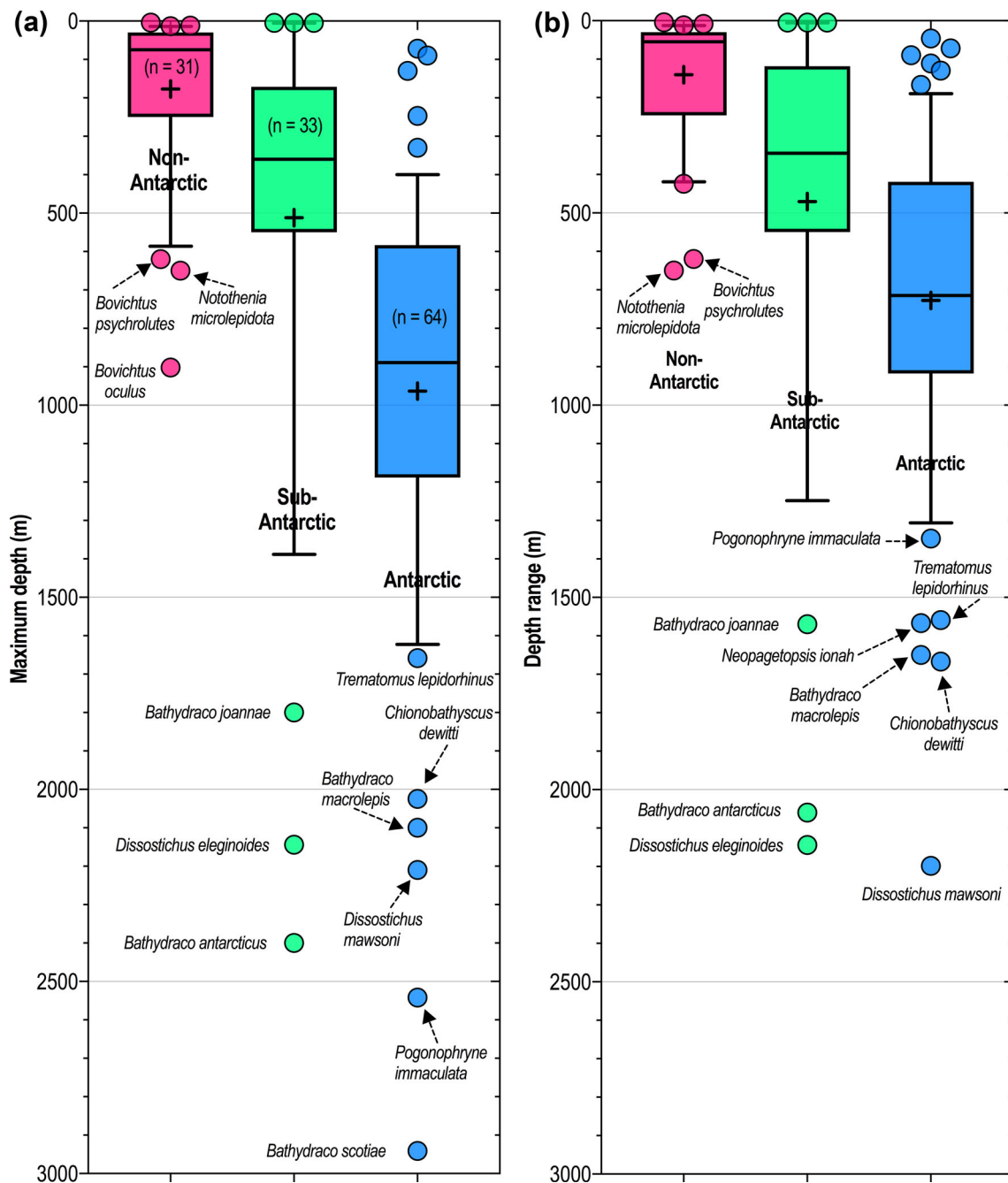
Fig. 1 *Boxplots* summarizing maximum depths (**a**) and depth ranges (**b**) for 128 species of non-Antarctic, sub-Antarctic and Antarctic notothenioids. *Horizontal line* in *box* indicates median, *cross* is mean,

upper and *lower* hinges of *box* are 25th and 75th percentiles, *upper* and *lower* extremes of *whiskers* are 10th and 90th percentiles, *dots* show outliers at <10th and >90th percentiles

<6 m. Only two Antarctic species have maximum depths <100 m, the nototheniids *Trematomus borchgrevinki* and *T. brachysoma*.

Depth ranges

The median depth ranges (Table 2) for non-Antarctic (55 m), sub-Antarctic (345 m) and Antarctic (714 m) species are significantly different ($H = 49$, $p < 0.0001$).

The value for the median depth range for the Bathydraconidae decreases by about 40% when species of *Bathydraco* are excluded, and the mean for the family becomes the second lowest among the families of the Cryonotothenioidea. The scatterplots for depth ranges on arithmetic and logarithmic axes are available in Online Resource 2, Figs. S2–S3.

Figure 4a is a histogram of depth ranges for non-Antarctic species. The most common depth range is
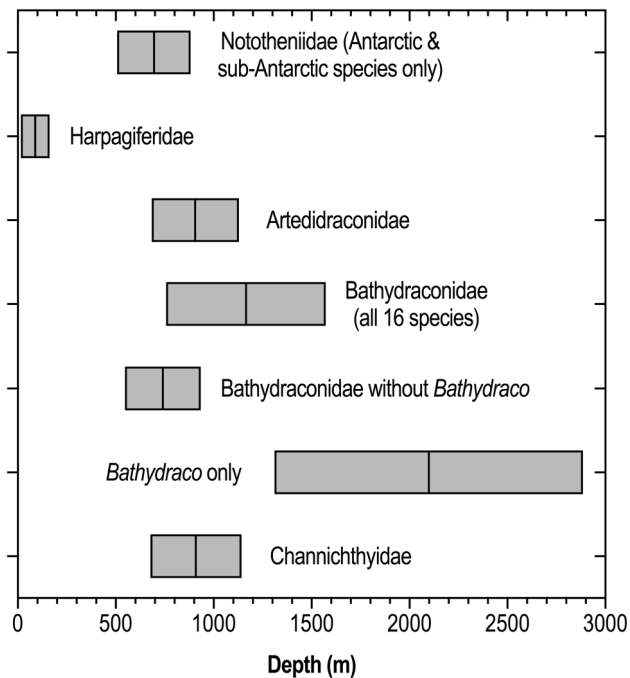
Fig. 2 Bar graph of the 95% confidence intervals for the mean maximum depths of the five families of the Cryonotothenioidea. The Bathydraconidae is shown with and without inclusion of the deep-living genus *Bathydraco*. *Vertical line* indicates mean

0–50 m, seen in 11 of 31 species (35%), and 20 of 31 species (65%) have a depth range of 0–100 m. In sub-Antarctic species (Fig. 4b), 200–400 m is the most common depth range as seen in 10 of 33 species (30%), and the greatest ranges (>2000 m) are those of *Dissostichus eleginoides* and *Bathydraco antarcticus*. Antarctic species (Fig. 4c) have more expansive depth ranges, with 600–800 m the most common, as seen in 16 of 64 species (25%). Among Antarctic species, 40 of 64 (63%) have ranges <800 m, while 24 of 64 (37%) have ranges >800 m. Considering the 64 Antarctic and 33 sub-Antarctic species together, only three of 97 species (3%), *Dissostichus mawsoni, D. eleginoides,* and *Bathydraco antarcticus*, have depth ranges >2000 m. They are also the most distant outliers among the >90th percentile dots in depth range boxplot (Fig. 1b).

Number of species versus depth

Figure 5 shows that species diversity for non-Antarctic notothenioids peaks at depths 50 m, then falls off by about 50% and continues to decline to a few species at 500–1000 m. The plot line for sub-Antarctic species peaks at 100 m with a range of maximum diversity at 100–300 m, and then falls steeply to 900 m where the number levels off at 2–3 species that persist to depths of 2400 m. Antarctic species diversity peaks at 500 m, with

the 300–600 m increment encompassing the range of maximum diversity. After peaking, the plot line falls off to a minor shoulder at 1200 m, and another at 2000–2100 m, before leveling off at 1–2 species.

Discussion

Perspective on shelf and slope habitats and depths

Historical

The Antarctic ice sheet first reached the coastline at the Eocene–Oligocene boundary at 34–33 Ma (Galeotti et al. 2016). Later during the early Miocene (23–16 Ma), it was dynamic, advancing, and retreating over <100,000 year time scales and possibly reaching volumes similar to that of the current East Antarctic Ice Sheet (Pekar and DeConto 2006). Conditions similar to the contemporary polar environment first appeared about 14 Ma during the major cooling of the Middle Miocene Climate Transition (Knorr and Lohmann 2014). Since then, the Antarctic shelf has been an exceptionally dynamic and disturbed habitat. For example, the West Antarctic ice sheet advanced and retreated 38 times in the past 5 Ma (Naish et al. 2009). As recently as the Last Glacial Maximum about 10,000 years ago, the ice sheet reached the outer continental shelf in all areas of West Antarctica and some in East Antarctica (Anderson et al. 2002, 2014), and was grounded at depths up to 1000–1200 m (Huybrechts 2002). Thus, it is likely that Antarctic ice sheets and their associated ice bergs have periodically caused regional annihilation of habitats and forced the existing fauna toward the shelf edge and into deeper waters (Barnes and Conlan 2007; Thatje et al. 2008; Barnes and Souster 2011; Allcock and Strugnell 2012; Barnes et al. 2016). In the case of benthic notothenioids, these disturbances probably drove them into refugia such as upper to mid-slope depths beyond the ice sheet edge, unglaciated sections of the shelf or shelf break, or even to the most southern sub-Antarctic islands and the south island of New Zealand. Based on population genetic signatures, it has been suggested that habitat destruction by Pleistocene advances of the ice sheet had a differential effect on various notothenioid life history types and, as would be expected, more profoundly influenced benthic than pelagic species (Janko et al. 2007; Kašparová et al. 2015). Historically, however, disturbance created by advances and retreats of the ice sheet also generates ecological opportunities and conditions for speciation. The capacity to occupy upper- and mid-slope depths probably enhanced the ability of notothenioids to persist and to diversify during these Late Miocene and Early Pliocene periods of ice sheet movement and habitat disruption.
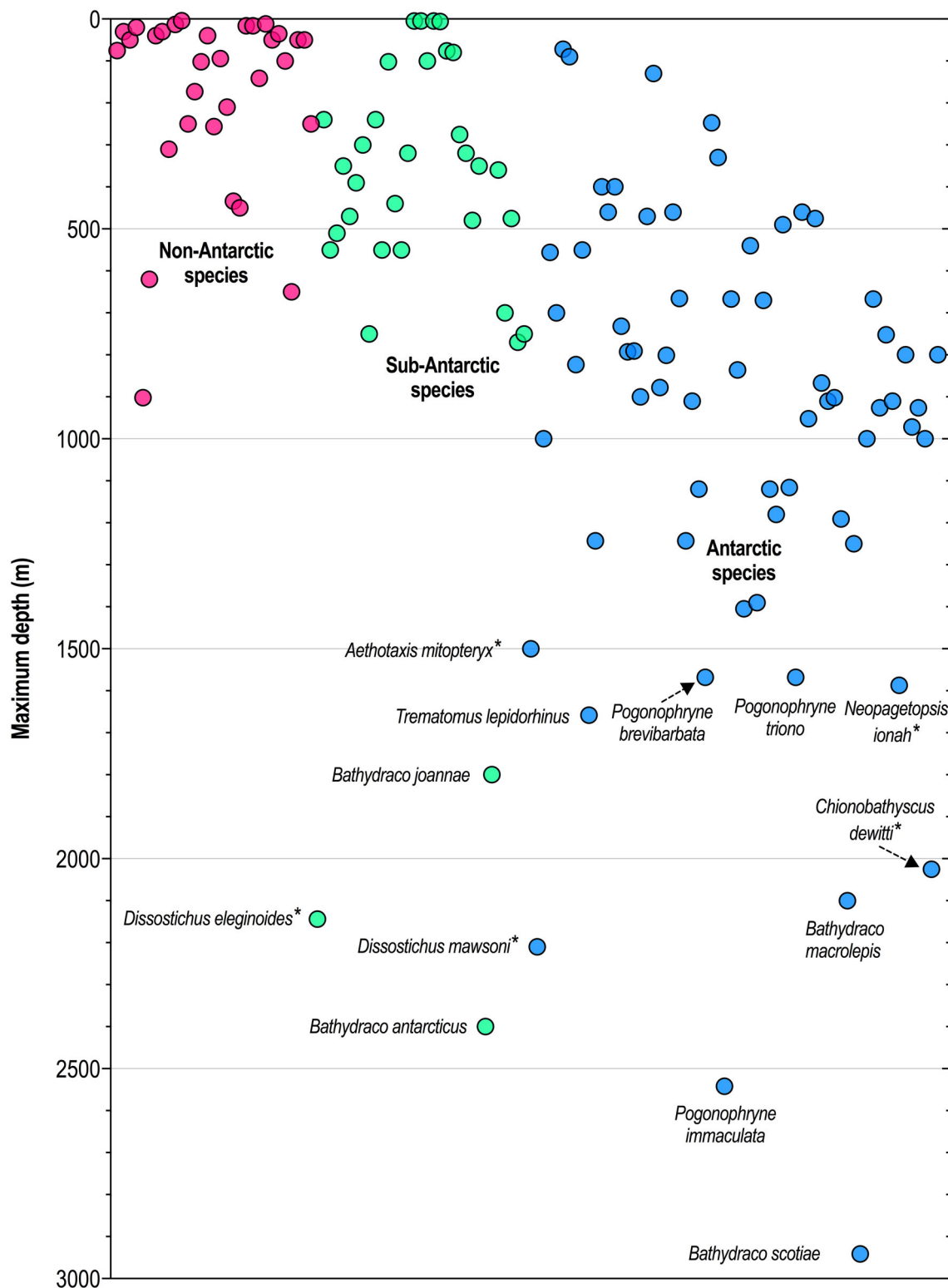
Fig. 3 *Scatterplot* showing the maximum depths of occurrence for 128 species of non-Antarctic, sub-Antarctic, and Antarctic notothenioids. The position of dots relative to the horizontal axis is representative of the species approximate phylogenetic sequence in Table 1. Thirteen sub-Antarctic and Antarctic species with maximum depths ≥1500 m are identified and *asterisks* indicate five species with neutral or near neutral buoyancy
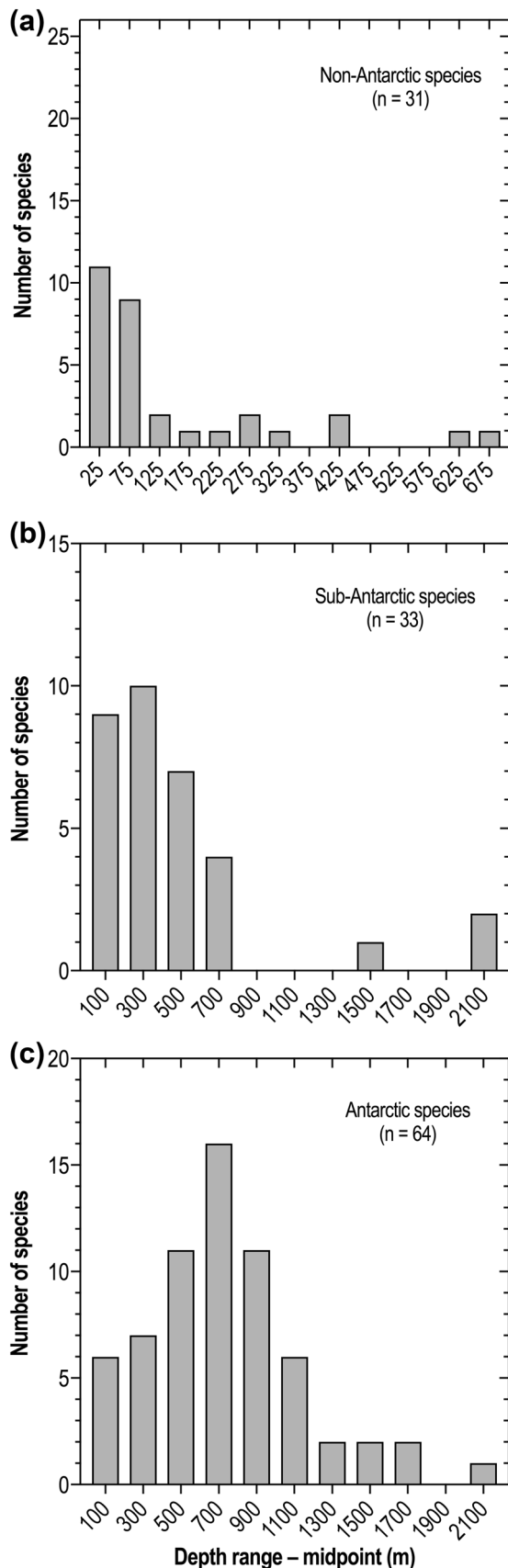
(a) Non-Antarctic species (n = 31)

(b) Sub-Antarctic species (n = 33)

(c) Antarctic species (n = 64)

◀ **Fig. 4** Frequency distribution of depth ranges for 31 species of non-Antarctic (**a**), 33 species of sub-Antarctic (**b**), and 64 species of Antarctic (**c**) notothenioids. Increments for depth range bins are 50 m (**a**) and 200 m (**b**, **c**), with each bin centered on the midpoint of the increment
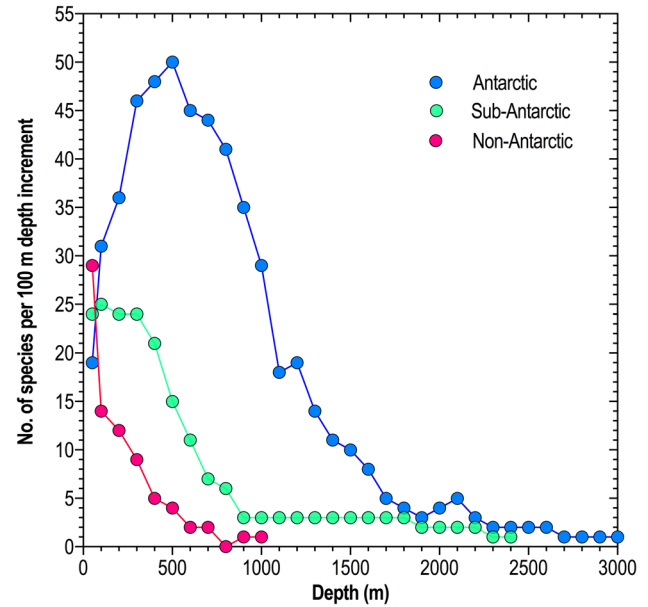
Fig. 5 Plots of species diversity across 100 m depth increments for 31 species of non-Antarctic, 33 species of sub-Antarctic, and 64 species of Antarctic notothenioids. Numbers for diversity were obtained by recording presence of each species within each 100 m increment in its depth range, and these were then summed for all species in each depth bin to provide the value on the *y*-axis. *First dot* on the left (without a corresponding *tick* mark in the *x*-axis) represents the number of species found at 0–50 m. Subsequent *dots* and *tick* marks represent counts that include the total number of species found at depths 51–100, 101–200 m, etc

Using a dataset composed of a time-calibrated molecular phylogeny as well as paleoclimatic, antifreeze, and buoyancy data, Near et al. (2012) found that divergence times of major species-rich notothenioid radiations coincided with periods of cold and disruption during the past 10 Ma, specifically 9.1 Ma for *Trematomus*, 6.3 for Channichthyidae, and 3.0 for Artedidraconidae. These radiations account for 48% (68/142) of modern notothenioid species diversity. Within the Artedidraconidae, the 28 species of *Pogonophryne* are an example of an even more recent benthic radiation at depths of ≈ 100–2500 m (Eakin et al. 2009).

Modern

The relict species *Percophis brasiliensis* occupies relatively shallow inshore waters, as do most of the other

phylogenetically basal non-Antarctic notothenioids. Antarctic and sub-Antarctic notothenioids, on the other hand, have undergone life history and depth-related diversification on the Antarctic shelf and slope that, in spite of the absence of a swim bladder, has allowed them to fill a pelagic and semipelagic niches as well as niches on and near the substrate from shallow, including tide pools in the case of *Harpagifer*, to mid-slope depths (Eastman 1993, 2005; Klingenberg and Ekau 1996). There are aspects of this that are unusual from a bathymetric perspective, especially as related to non-notothenioid taxa. Notothenioids are represented over the 0–3000 m depth spectrum, rather that being replaced at slope depths by a phylogenetically and taxonomically distinct fauna as in deep waters elsewhere (Haedrich 1996). This does not mean that macrourids (Iwamoto 1990), morids (Chiu and Markle 1990), liparids (Stein and Andriashev 1990; Andriashev 2003), and zoarcids (Anderson 1990) are unimportant elements of the Antarctic slope fauna, but simply that notothenioids are sympatric with them. Furthermore in deep-sea faunas elsewhere, the pelagic and demersal species are usually distinct and unrelated (Haedrich 1996), unlike the variety of life history types in the notothenioid radiation, including pelagic taxa like *Dissostichus*.

The modern notothenioid fauna inhabits an Antarctic Region where about 90% of the habitat is deeper than 1000 m (Griffiths 2010). Sub-Antarctic shelves, like those around South Georgia, have an average depth of 200 m (Gregory et al. 2017). In waters south of 65°–70°S, including the broad shelves of the Ross and Weddell seas, the mean depth is ≈500 m and the shelf break is at ≈800 m (Smith et al. 2007). Isostatic down warping and glacial erosion have deepened high latitude Antarctic shelves to hundreds of meters beyond those in temperate regions (Anderson 1999), although this is less prominent in Subantarctic areas where the ice load is less. The tongues of outlet glaciers have also gouged innershelf depressions close to the coast where the water can be as deep as 1200 m (Andriashev 1977). In addition, inshore habitats for fishes are more limited than in other marine localities, especially in the permanent pack ice zone of East Antarctica, where the ice foot and anchor ice to a depth of 33 m constrain shallow habitats in the intertidal and subtidal (Dayton et al. 1969), although these habitats are available during summer in most areas of the seasonal pack ice zone of West Antarctica and in the sub-Antarctic islands. Given the conditions described above and that the High Antarctic also lacks coral and rocky reefs, sites of great fish diversity in temperate and tropical oceans, it is not surprising that maximum Antarctic notothenioid species diversity is shifted to greater depths, peaking at 500 m with a range 300–600 m versus a peak at 100 m and range if 100–300 in

sub-Antarctic species (Fig. 5). Andriashev (1965, 1987, p. 361) first recognized and referred to this phenomenon as "glacial submergence." The plot for Antarctic species in my Fig. 5 has the same peak and range as the plot in Andriashev's (1987, Fig. 2), although he used only East Antarctic species, whereas I have included all Antarctic notothenioids. It is also possible that non-notothenioids were also included in Andriashev's graphs as both his 1965 and 1987 papers were reviews of the entire Antarctic fish fauna. DeWitt (1971, Fig. 2) also graphed notothenioid and non-notothenioid species together but separated West and East Antarctic species. The range of maximum diversity for the former was 200–350 m and 350–550 m for the latter.

Are the shallowest and deepest-living notothenioids confined to particular taxa?

Shallow-living species

Figure 6 shows depth ranges for 128 species arranged in phylogenetic sequence. Given the short bars near the lower left of the graph, it is clear that most of the phylogenetically basal genera (*Percophis*, *Bovichtus*, *Halaphritis* and *Pseudaphritis*) are found in water <100 m deep. Within this group, the noteworthy exceptions are *Bovichtus psychrolutes* and *B. oculus* that reach maximum depths of 620 m and 902 m, respectively. The shallow-living species in the Cryonotothenioidea are species of the nototheniid genus *Patagonotothen* (all non-Antarctic with one exception) and of the Harpagiferidae, a primarily intertidal/inshore group with a sub-Antarctic island distribution. The Antarctic genus *Trematomus* is also of interest with respect to habitation of both shallow and deep waters. *Trematomus* has a circum-Antarctic distribution in both the seasonal and permanent pack ice zones, and recent collecting in water 5–25 m deep at James Ross Island (Jurajda et al. 2016) has substantiated previous reports documenting the presence of adults of several species in waters only a few meters deep. However most of the 15 species of *Trematomus* live at 400–700 m, although *T. loennbergii* (65–1243 m) and *T. lepidorhinus* (99–1658 m) have more extensive depth ranges and demonstrate the habitat breadth of this 9.1 Ma old radiation (Near et al. 2012).

Deep-living species

When evaluated by family, fishes are considered to be "deep-sea" if they have mean maximum depths of occurrence ≥1000 m (Priede and Froese 2013). Among actinopterygians there are 31 families containing about 2500 species that meet this criterion, including synaphobranchids, alepocephalids, macrourids, ophidiids, liparids and zoarcids (Priede and Froese 2013). Only the
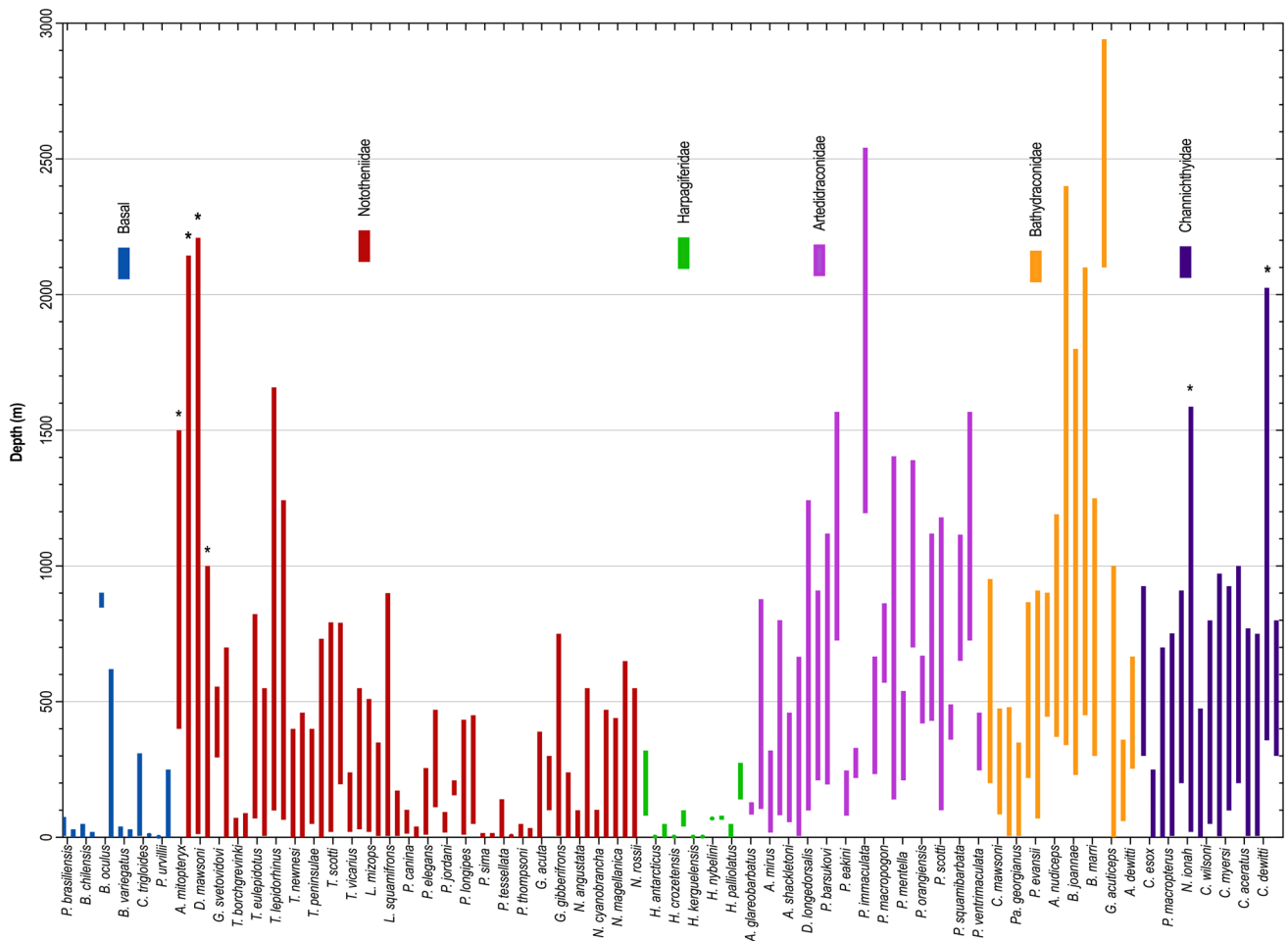
Fig. 6 Bar graph of depth ranges for 128 notothenioid species arranged in phylogenetic sequence. There is a *bar* for each species but only 64 species are named along the axis; missing names can be interpolated from the identical sequence of names in Table 1 (excluding names with an *asterisk*). *Colors* demarcate the grouped basal clades and traditional five families of the Cryonotothenioidea (Antarctic clade). *Asterisks* indicate the *six* species with neutral or near neutral buoyancy

notothenioid family Bathydraconidae has, at 1165 m, a mean maximum depth ≥1000 m (Table 2, Fig. 2). However, this is attributable to the deep-dwelling species of the genus *Bathydraco* and, when these are not included, the mean falls to 741 m. Considered separately species of the genus *Bathydraco*, with a mean maximum depth of 2098 m, could be considered "deep-sea." *Bathydraco scotiae* is interesting in that, although it lives at greater depths (2100–2941 m) than any other notothenioid, its depth range is only 841 m. It is not known whether this is attributable to inadequate sampling or to physiological specialization that restricts it to greater depths. Or this may reflect what is seen in some other oceans where individual deeper-living species of a eurybathic family do not have broader bathymetric ranges than those that live shallower (Pearcy et al. 1982). However at lower taxonomic levels, as in the deep-sea macrourid genus *Coryphaenoides*, abyssal species have broader depth ranges than non-abyssal species (Gaither et al. 2016). Finally, reduction in species diversity

at ≥3000 m is not unique to notothenioids and is also seen, for example, in phylogenetically diverse deep-sea benthic fishes from the northeastern Pacific Ocean (Pearcy et al. 1982).

If a maximum depth (Fig. 3) and/or depth range (Fig. S2) of ≥1500 m is used to designate "deep-living" notothenioids, 13 species of the Cryonotothenioidea fall in this category and, based on the distribution of the longest bars in Fig. 6, they are not confined to a particular taxon. The species are: the nototheniids *Aethotaxis mitopteryx*, *Dissostichus eleginoides*, *D. mawsoni* and *Trematomus lepidorhinus;* the artedidraconids *Pogonophryne brevibarbata*, *P. triono* and *P. immaculata;* the bathydraconids *Bathydraco joannae*, *B. macrolepis*, *B. antarcticus* and *B. scotiae;* and the channichthyids *Neopagetopsis ionah* and *Chionobathyscus dewitti.* Thus habitation of depths ≥1500 m is seen in species from all families of the Cryonotothenioidea, with the exception of the Harpagiferidae.

Because 11 of the 28 species of the artedidraconid genus *Pogonophryne* (asterisks in Table 1) were excluded due to insufficient data, this discussion may underestimate the significance of *Pogonophryne* as a taxon with deep-living species. Of the 11 excluded species, five have maximum depths ≥1500 m. Additional sampling will certainly expand known bathymetric ranges and reveal more deep-living species of *Pogonophryne*, as suggested by the photograph of an unidentified species of *Pogonophryne* at 2127 m on the slope of Marguerite Bay (Eastman et al. 2013, Fig. 1k). Previously the only documented maximum depth ≥2000 m for a species of *Pogonophryne* is that for *P. immaculata* at 2542 m (Eakin 1990). Another indication of the deep-living proclivities of species of *Pogonophryne* is that, among all notothenioids, only *P. immaculata* (1195 m) and the bathydraconid *Bathydraco scotiae* (2100 m) have minimum depths of occurrence >1000 m (Fig. 6).

It is also of interest that the maximum depth (Fig. 3, asterisks) and depth range graphs (Figs. S2, asterisks) reveal that among the species living at depths ≥1500 m, 5 of 13 and 4 of 8, respectively, are at or near neutral buoyancy based on data in Near et al. (2012, Table S5). The two species of *Dissostichus*, both neutrally buoyant as adults, exemplify habitation of the 0–2100 m interval of the water column during the course of their life cycle which involves pelagic larvae, benthic subadults on the shelf, and adults that range throughout the water column over the shelf and slope (Collins et al. 2010; Hanchet et al. 2015). Many deep-sea fishes that are predominantly slope inhabitants as adults spend their growth phases in shallower water where there is greater availability of high quality prey (Drazen and Haedrich 2012). This is reflected in the life cycle of *D. mawsoni*; benthic subadults inhabit the more productive shelf waters and feed on another nototheniid, the energy-rich *Pleuragramma antarctica*, enabling them to accumulate the lipid deposits necessary for neutral buoyancy (Eastman 1988). Upon reaching a total length of ≈100 cm, neutral buoyancy potentially allows *D. mawsoni* to range through the water column (Near et al. 2003).

Is the record for the deepest-living notothenioid valid?

Bathydraco scotiae deserves comment given its status as the deepest-living notothenioid with a maximum reported depth of 2950 m (Gon 1990). This is about 400–500 m deeper than records of most other specimens of this species, as well as those for *B. antarcticus* at 2400 m. The source for the *B. scotiae* record is a bar graph plotting depth ranges for species of *Bathydraco* contained in a review of the genus by DeWitt (1985, p. 298, Fig. 3). In the

graph, depth ranges for each species are rounded off to the nearest 50 m. However, DeWitt (1985) does not specifically mention *B. scotiae* or a 2950 m depth when stating, "*Bathydraco* comprises fishes from rather deep water, the range being approximately 500–2600 m." The graph is also the source of the record in Gon (1990), but there is no mention in either DeWitt or Gon of a specimen or specimens collected at this depth.

Are there museum specimens that document the 2900+ m depth records for *Bathydraco scotiae*? The answer is affirmative, and the specimens are in the ichthyological collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California. One specimen, catalog number 10,526.002, was collected north of the Weddell Sea at 63°3′0″S, 49°11′0″W with a 1.5 m Blake Trawl on 03 March 1963 at Station 529 during a cruise of the USNS *Eltanin*. The trawl was on the substrate for 60 min, and both the minimum and maximum depths of collection were 2941 m. DeWitt (1985, p. 298) does list this specimen as one examined for his account of *B. scotiae*, but without the depth of collection or the LACM catalog number. There is also a second lot of two specimens (LACM 11462.003) collected in 1968 from the Ross Sea at a depth of 2907 m. My conclusion is that records of *B. scotiae* from depths of 2900+ m are well documented and valid and that the precise depth of collection is 2941 m.

Are sub-Antarctic and Antarctic notothenioids eurybathic?

The most common depth range for notothenioids in general is 600–800 m, as seen in 25% of Antarctic species (Fig. 4c). Whether or not this is eurybathic is relative and depends on the comparison being made—whether to actinopterygians in general or only to other percomorphs. As a group notothenioids are not eurybathic when compared with phylogenetically older actinopterygian deep-sea groups or even with younger "deep-sea invasive" (Priede and Froese 2013) groups. For example, depth ranges of 1000 m or 2000 m are common in deep-sea demersal species of macrourids, liparids and zoarcids from various oceans (Pearcy et al. 1982; Merrett and Haedrich 1997). Within the macrourid genus *Coryphaenoides*, depth ranges of 1000 or 2000 m are frequent and a few species have a range of 3000+ m (Gaither et al. 2016). However, two sub-Antarctic notothenioids and one Antarctic species with depth ranges of 2144, 2198 and 2060 m—*Dissostichus eleginoides, D. mawsoni,* and *Bathydraco antarcticus*—are extreme outliers (Figs. 1b,4b, c; S2) and probably could be considered eurybathic.

Unfortunately there are few examples of depth radiations in percomorphs that can be used for comparison with

notothenioids. Radiations of marine percomorphs have taken place in shallow waters and involved taxa such as scarids (parrotfishes) and serranids of the genus *Hypoplectrus* (hamlets) that are associated with coral reefs and therefore usually found at maximum depths of only 50–100 m (Streelman et al. 2002; Puebla et al. 2008). Probably the best example for comparison with notothenioids is the northeastern Pacific Ocean scorpaenid genus *Sebastes* (rockfishes) that are now included in a percomorph clade with notothenioids (Near et al. 2103). *Sebastes* in the northeastern Pacific has diverged along a depth gradient, a feature that defines the radiation, although as a group these 66 species range from the intertidal to maximum depth of only 600 m (Ingram 2011). The depth ranges of individual species are on the order of a few hundred meters or less (Love et al. 2002). As a group, then, notothenioids would be considered eurybathic in comparison to this radiation of *Sebastes*.

Concluding remarks

From their ancestral Gondwanan coastal habitat, notothenioids diverged from shallow waters to those nearly 3000 m deep as they became adapted to a variety of habitats around the Antarctic continent over the last ≈ 25 Ma. In a historical context, the notothenioid radiation should probably be viewed as occurring under reduced competition from a taxonomically diverse fish fauna which, based on the late Early Eocene fossil record from the La Meseta Formation of Seymour Island dated at 49–51 Ma (Ivany et al. 2008), was largely eliminated during the oceanographic, thermal, and trophic changes that accompanied the post-Eocene isolation of Antarctica (Eastman 2005). Oligocene, Miocene, and Pliocene exposures are limited in Antarctica and have not yielded any fish fossils, but there probably was a transitional or intermediate fauna between the La Meseta and modern faunas. It might have consisted, at least in part, of a mixture of persisting Eocene elements like gadiforms (Schwarzhans et al. 2017) and newly emerging notothenioids. If more of the abundant species of La Meseta gadiforms (Schwarzhans et al. 2017) had survived into the Neogene, they might have provided competition for and impinged on the diversification of notothenioids into outer shelf and upper slope habitats.

During adaptation to Antarctic conditions, notothenioids may have benefited from the energetic savings associated with the absence of a swim bladder. However, the ability of some species to reduce density and to attain neutral buoyancy has not been compromised. Pedomorphic changes reduced skeletal density, and accumulated lipid conferred neutral or near neutral buoyancy and allowed the exploitation of large reaches of the water column. For example, of the six species in this study with neutral or near neutral buoyancy, five have maximum depths ≥ 1500 m and four have depth ranges of 1500–2200 m. Notothenioids also have the coincidental advantage that adaptations associated with life under Antarctic conditions, especially low temperature and reduced light and productivity, are similar to those necessary for life in the deep-sea, and these may have contributed to their ability to inhabit greater depths. Conversely, notothenioids depart from deep-sea fishes (Marshall 1971, 1979) in that their habitation of depths >1000 m has been unaccompanied, as far as our knowledge extends, by any extraordinary brain and sense organ specializations at the morphological level (Eastman and Lannoo 2003a, b, 2011). All species studied to date have a typical array of olfactory, visual, gustatory and mechanosensory systems and present no examples of sensory hypertrophy. They also lack the distinctive trophic and reproductive specializations that characterize some deep-sea fishes (Marshall 1971, 1979). Notothenioids, however, are younger and are living at depths a few thousand meters less than many phylogenetically older deep-sea fishes, and they would not be expected to be as specialized.

Twenty-seven percent (26 of 97 species) of Antarctic and sub-Antarctic notothenioids have maximum depths ≥ 1000 m, but nothing is known about their physiological adaptation to hydrostatic pressure. As mentioned previously, some of the metabolic and locomotor adaptations associated with life under Antarctic conditions are similar to those necessary for habitation of the deep-sea; however, adaptation to hydrostatic pressure is another matter and requires the stabilization of proteins (Somero 1992). It is possible that adaptation to hydrostatic pressure co-occurs with the eurybathy (Somero 1992, p. 573–574) many Antarctic notothenioids experience during their life history, but this does not explain its physiological basis. Another consideration is that freezing resistance adaptations in notothenioids, such as elevated levels of the organic osmolyte trimethylamine oxide (Raymond and DeVries 1998), may also have the capability to stabilize proteins and thus to serve as piezolytes (Yancey and Siebenaller 1999, 2015). Whatever the means involved in their tolerance of hydrostatic pressure and other aspects of life in the deep-sea, the wide spectrum of depths inhabited by notothenioids is another example of the amazing adaptive potential of the percomorph subclade of the spiny-rayed (acanthomorph) fishes that compose nearly one-half of all fish diversity (Alfaro et al. 2009; Near et al. 2013).

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