ORIGINAL PAPER

Degree of herbivory and intestinal morphology in nine notothenioid fishes from the western Antarctic Peninsula

Eugenia Moreira[1,2,3] · Manuel Novillo[3,4] · Joseph T. Eastman[5] · Esteban Barrera-Oro[1,3,4]

Abstract

Although many notothenioid fishes are primarily carnivorous, some species consistently feed on macroalgae and are therefore omnivorous. Among fish, the degree of herbivory is usually reflected in the morphology of the gastrointestinal system especially intestine length. We examined a large number of juvenile and adult specimens of nine sympatric notothenioid species collected sequentially over eight summer seasons at Potter Cove, South Shetland Islands. We provide relative intestine lengths (RIL), distinct proportions of algae and animal prey in the diets (W%), and numbers of pyloric caeca for all species. The sister species *Notothenia coriiceps* (NOC) and *N. rossii* (NOR) evidenced significantly different intestinal growth over ontogeny and ate distinctly different proportions of algae and animal prey. We establish a ranking of the degree of herbivory for the fish species in the local ecosystem, and this was found to be related to their distinct feeding types and strategies. There is a correspondence between intestine length/RILs and degree of herbivory in six of the nine species analysed but no clear association between the number of pyloric caeca and degree of omnivory or carnivory. Compared to other teleosts, our results, and those in the literature, indicate modest divergence in notothenioids that include a phylogenetic decrease in the number of pyloric caeca, from 6 to 7 in most nototheniids to 2–3 in channichthyids, and a 1.8-fold difference in average relative intestine lengths which are most frequently 50–70% of body length and never exceed body length. This is consistent with the unspecialized gastrointestinal morphology that reflects the dietary and ecological plasticity of many notothenioids, exemplified by the high degree of omnivory in species such as NOC and NOR.

Keywords Notothenioidei · Relative intestine lengths · Trophic ecology · Potter cove · South Shetland Islands

Introduction

Antarctic notothenioid fishes dominate species diversity, abundance and biomass in the coastal waters of the Southern Ocean surrounding Antarctica (Eastman 2005). Although they lack a swim bladder, virtually all species utilize pelagic food resources, and krill feeding among primarily demersal notothenioids is especially common (Nyeblin 1947; Foster and Montgomery 1993; Kock 2005; Kock et al. 2012). However, notothenioids also forage in a variety of other habitats (Targett 1981; Daniels 1982; McKenna 1991; Gröhsler 1994), and consume an array of taxa including algae, zooplankton and, in addition to krill, other nekton such as copepods, hyperiid amphipods, squid and fish (Barrera-Oro 2002).

The morphology of the alimentary canal in fishes, especially of the stomach, pyloric caeca and intestine, frequently reflects the composition of the diet. For example, compared to carnivores, herbivorous fish generally

✉ Eugenia Moreira
 eugeniamoreira@yahoo.com.ar

1 Instituto Antártico Argentino, Av. 25 de Mayo, 1143 San Martín, Prov. de Buenos Aires, Argentina

2 Laboratorio de Biología Funcional Y Biotecnología (BIOLAB) - UNCPBA-CICBA - INBIOTEC-CONICET. Facultad de Agronomía, UNCPBA, Av. República de Italia 780, Azul, 7300 Buenos Aires, Argentina

3 Consejo Nacional de Investigaciones Científicas Y Técnicas (CONICET), Godoy Cruz, 2290 Buenos Aires, Argentina

4 División Ictiología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" MACN-CONICET, Angel Gallardo, 470, CABA, Argentina

5 Department of Biomedical Sciences, Ohio University, Athens, OH 45701, USA

have longer intestines, presumably because plant cell walls require more prolonged processing given the absence of both intrinsic cellulase and symbiotic cellulase-producing microorganisms in most fish (Clements and Raubenheimer 2006; Wilson and Castro 2011). Corallivorous fishes also have relatively longer intestines because of their detrital load of calcium carbonate (Elliott and Bellwood 2003). Pyloric caeca increase surface area for digestion and absorption and, although there is considerable interspecific variation in size and number, there is no unequivocal association with diet other than that they are more likely to be absent in herbivores than in carnivores and omnivores (Wilson and Castro 2011).

The extensive literature on the diets of Antarctic notothenioids indicates that while most species are carnivorous, some consistently feed on macroalgae and are therefore omnivorous (Kock 1992, Barrera-Oro 2002 and references therein). The nototheniid *Notothenia coriiceps*, for example, selectively consumes macroalgae in the waters of the western Antarctic Peninsula (Barrera-Oro and Casaux 1990; Iken et al. 1997; Casaux et al. 2003; Casaux and Barrera-Oro 2013), although the extent to which macroalgal cell walls are digested and assimilated is unclear (Zamzow et al. 2011).

The anatomy and histology of the alimentary canal has been documented for many notothenioid species (Ojeda 1986; Korovina 1986; Korovina and Prirodina 1986; Korovina et al. 1986, 1991a, b; 2004; Eastman and DeVries 1997; Voronina and Balushkin 1998; Voronina 1999; Voronina and Neelov 2001). Other than inter- and intraspecific variation in the number of pyloric caeca, the pigmentation pattern of the gut wall, and the relative length of the intestine, unique or specialized morphology has not been discovered. Furthermore, only a small number of juveniles ($n < 10$) have been examined in this context (Ojeda 1986); hence, ontogenetic changes in the structure and function of the notothenioid digestive system are largely unscrutinised (Eastman and DeVries 1997).

Given that there has been little effort in determining whether there is a relationship between alimentary canal morphology and diet in notothenioids during ontogeny, especially in species that consume macroalgae, we address this topic here by employing a unique data set—almost 1400 similarly sized specimens of juvenile and adult notothenioids, representing nine sympatric species, that were collected sequentially over eight summer seasons at Potter Cove, South Shetland Islands. More specifically, we will provide: (1) relative intestine lengths and numbers of pyloric caeca; (2) dietary proportions of algae and animal prey, in some cases for first time in an ontogenetic series; and (3) a ranking of the degree of herbivory for the notothenioid species in the local ecosystem. We discuss our findings in the context of trophic ecology and the food web of the coastal Antarctic marine ecosystem.

Materials and methods

Sampling and measurements of fish

A total of 1397 specimens of *Notothenia rossii* ($n = 401$), *N. coriiceps* (247), *Lepidonotothen nudifrons* (252), *Trematomus newnesi* (217), *T. bernacchii* (76), *Harpagifer antarcticus* (157), *Parachaenichthys charcoti* (14), *Chaenocephalus aceratus* (29) and *Gobionotothen gibberifrons* (4) were collected at Potter Cove, King George Island/Isla 25 de Mayo, near Argentine scientific station "Carlini" (62°14′ S and 58°40′ W) during austral summer (December to March) from 2008 to 2018. Medium-large size fish were caught with trammel nets (length 25 m, width 1.5 m, inner mesh 2.5 cm outer mesh 12 cm) set for 16–24 h on rocky bottoms with macroalgae beds at 20–70 m depth (average 45 m) in the outer portion of the cove. Small-size fish were caught with a bottom trawl (square mouth 1 m², length 2 m and mesh 4 mm) towed at day and night for 15–30 min at 4–30 m depths (average, 12 m) in the inner cove (Fig. 1). For a detailed description of the fishing procedure, as well as of the biotic components and abiotic features of Potter Cove, refer to Barrera-Oro et al. (2019). Fish nomenclature follows Gon and Heemstra (1990).

All fish measurements were performed on fresh specimens. Total length (TL), standard length (SL) and total weight (TW) of the fish were recorded. After dissection sex and gonad stage were determined according to Kock and Kellerman (1991). The entire alimentary canal from proximal oesophagus to distal rectum (anus) was removed and the number of pyloric caeca was recorded. Intestine length (IL) was measured in a straight line from the base of the pyloric caeca to the anus (Ojeda 1986).

Analysis of intestine length and diet

Relative intestine length (RIL) was expressed as the percentage of standard length applying the relationship RIL = IL/SL × 100. Shapiro–Wilk's and Levene's tests were calculated to verify normality of distribution and equality of variances, respectively. Based on these tests, a non-parametric Kruskal–Wallis comparison for multiple independent samples was performed followed by multiple comparisons to determine p values (Sokal and Rohlf 1981). The level of significance was established as $p \leq 0.05$. Coefficient of variation was calculated for the number of pyloric caeca as CV % = (SD/X) × 100, where SD is the standard deviation and X is the mean. Statistica V.7.0 software was used to perform the statistical analysis.

Dietary data were expressed as percentage by weight (W%) of (a) algae and (b) total animal prey found in fish
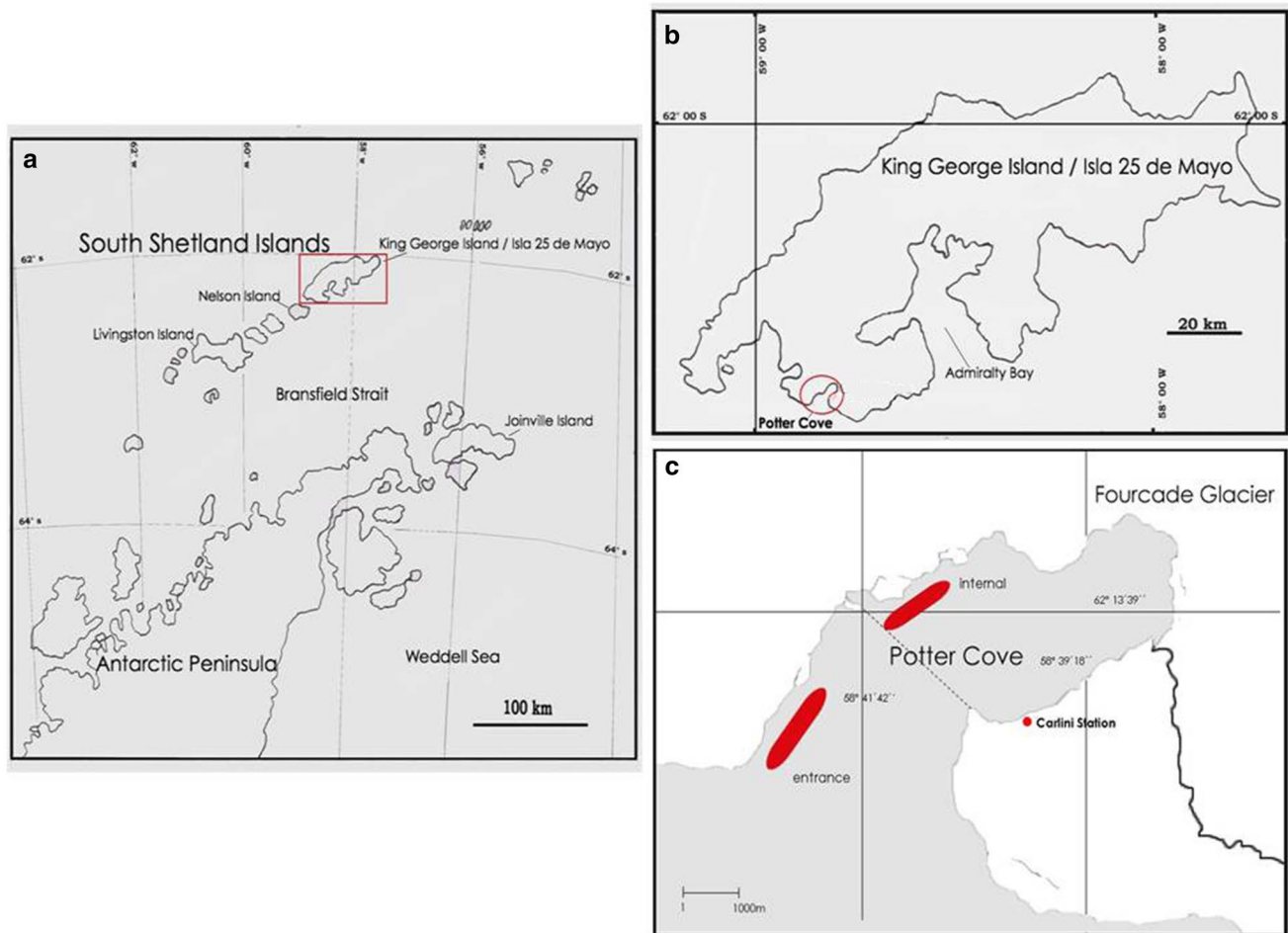
Fig. 1 General view of the South Shetland Islands and Antarctic Peninsula (**a**) with enlargements of King George Island/Isla 25 de Mayo (**b**) and Potter Cove (**c**). Shaded zones in (**c**) denotes the sampling areas

stomachs. Minor components of these calculations were estimated from data of previous studies at Potter Cove.

To evaluate ontogenetic changes in intestine length and diet of *N. rossii* and *N. coriiceps* we used complementary data, meaning that the ranges in lengths of specimens from two different summer seasons consisted of only small specimens in the first season and primarily medium to large size specimens in the second season. Both seasons were characterized by a scarcity of lkrill (see Juares 2013; Barrera-Oro et al. 2019). Diet variability was evaluated using a Chi-square test. The analyses were conducted in the open-source language R 2.9.2 (R Development Core Team 2009) at a significance level of $p \leq 0.05$.

Results

Table 1 provides summary statistics and Fig. 2 shows violin plots of relative intestine lengths in the notothenioids in this study. As expected, when relative intestine lengths are plotted against standard lengths (not shown), all species show positive trends in RILs over ontogeny. Based on the distinct separation between median and mean values in the low 50 s and high 60 s in Table 1, *Trematomus newnesi, Harpagifer antarcticus* and *Lepidonotothen nudifrons* have relatively shorter intestines than *Parachaenichthys*

Table 1 Summary statistics for relative intestine lengths of 1369 specimens representing nine notothenioid species sequenced on the basis of increasing size of median

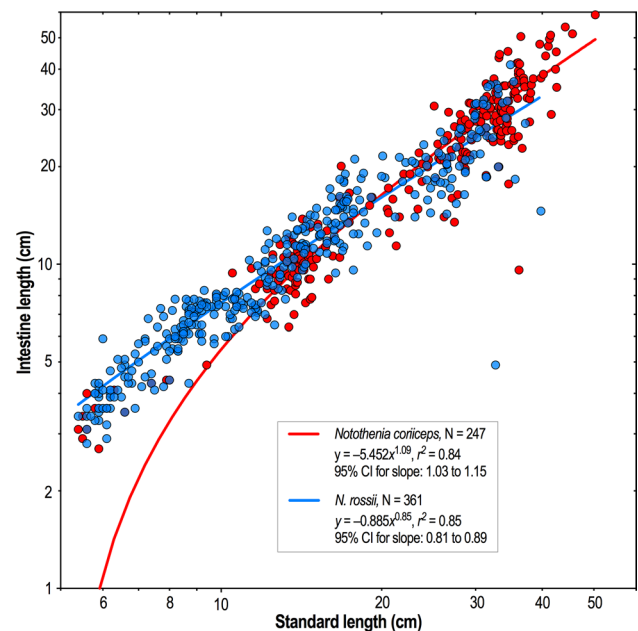| Fish species	N	Length range SL (cm)	Relative intestine length (%)				Percentiles	
			Min	Max	Mean (SD)	Median[a]	(25th)	(75th)
Trematomus newnesi	206	4.4–20.2	8.4	105.7	51.32 (12.27)	51.21	43.93	57.35
Harpagifer antarcticus	151	2.4–9.2	32.4	76.7	52.67 (8.42)	52.56	46.43	58.18
Lepidonotothen nudifrons	248	3.1–19.8	18.5	71.3	52.83 (9.74)	54.22	46.27	60.70
Parachaenichthys charcoti	14	26.7–46.6	57.4	92.9	70.37 (10.85)	69.81	60.76	74.97
Trematomus bernacchii	75	14.6–29.7	13.5	102.4	68.68 (14.46)	70.69	61.59	76.15
Notothenia rossii	396	5.4–39.8	15.0	126.8	77.90 (15.14)	76.76	67.53	88.87
Chaenocephalus aceratus	28	35.7–61.6	49.2	127.2	78.32 (15.49)	78.27	68.71	86.13
Notothenia coriiceps	247	5.4–50.3	26.5	153.9	82.59 (19.09)	80.38	69.53	94.20
Gobionotothen gibberifrons	4	23.6–29.3	80.9	93.2	87.77 (5.45)	88.49	82.20	92.62

[a]Kruskal–Wallis test ($H_8 = 749$, $p < 0.0001$) indicates that medians vary among species (*G. gibbberifrons* excluded)
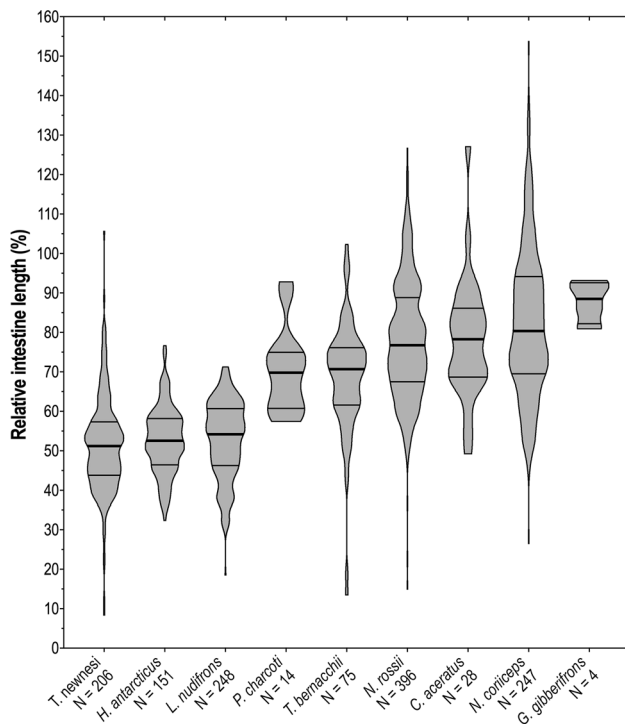
Fig. 2 Violin plot of relative intestine length in nine notothenioids from Potter Cove. Thick horizontal lines are medians, thin lines are 25th and 75th percentiles

Fig. 3 Ontogeny of intestinal growth in *Notothenia rossii* and *N. coriiceps*

charcoti, T. bernacchii, Notothenia rossii, Chaenocephalus aceratus, N. coriiceps and *Gobionotothen gibberifrons.*

Kruskal–Wallis tests indicate that the interspecific RIL medians are significantly different ($H_8 = 749$; $p < 0.0001$) (*G. gibberifrons* was excluded due to the low *n*). RIL values were significantly smaller (medians $< 54.5\%$) for *H. antarcticus, L. nudifrons* and *T. newnesi* than for the remaining species (*Posteriori test*; $p < 0.01$ for all comparisons).

Notothenia coriiceps and *N. rossii* have higher RILs (medians $> 76.5\%$) than *T. bernacchii* (median 70%) (*Posteriori comparison test*; $p < 0.05$).

Figure 3 provides the allometric equations and plots for intestinal growth in *N. rossii* and *N. coriiceps*. Growth in intestinal length exhibits slightly positive allometry in *N. coriiceps* but is negatively allometric in *N. rossii*. The slopes of the lines are significantly different: *N. coriiceps* ($F = 1286$; $df = 1, 245$; $p < 0.0001$) and *N. rossii* ($F = 1983$; $df = 1, 359$; $p < 0.0001$). The plot for *N. coriiceps* is nonlinear because our sample of this species contained few specimens < 11 cm SL; however, the plot becomes linear at

Table 2 Proportion of consumption of algae and prey during ontogeny in the omnivorous species *Notothenia rossii* and *N. coriiceps* at Potter Cove

| Fish species | Season | | Diet (wt%) | | |
	(Dec to Mar)	Stage (*N*, range in SL)	Algae	Prey	Chi-square test
Notothenia coriiceps	2008–2009	Juv. (17, 79–168 mm)	49.79	50.21	χ^2 test = 3.277
	2015–2016	Juv. and Adults (118, 186–484 mm)	37.10	62.90	$df = 1$, $p = 0.070$
Notothenia rossii	2008–2009	Juv. (104, 72–190 mm)	46.38	53.62	χ^2 test = 6.697
	2015–2016	Juv. and Pre-Adults (103, 191–343 mm)	28.66	71.34	$df = 1$, **$p = 0.0096$**

Bold value indicate significant result

12–13 cm and intestinal growth begins outpacing that of *N. rossii* at about 20 cm SL, the size when the diet is shifting and *N. coriiceps* begin retaining significantly more algae in their diet than *N. rossii* as shown in Table 2.

Algae represented an important food item for *N. rossii* and *N. coriiceps* in the two seasons analysed (W% = 28.66–49.79). However, variability in composition of the diet, specifically the proportion of algae consumed between the two size groups examined was significant for *N. rossii* ($\chi^2 = 6.69$, $df = 1$, $p = 0.0096$) but not for *N. coriiceps* ($\chi^2 = 3.277$, $df = 1$, $p = 0.070$) (Table 2).

Our analysis shows a correspondence between intestine length/RILs and degree of herbivory diet (Table 3) for six of the notothenioids analysed: there is an association between higher RILs (mean 78–83%) and higher degrees of herbivory (W% of algae = 24–30) in the benthos feeders *N. coriiceps* and *N. rossii*. This association may also be valid for *T. bernacchii* (RIL mean 69%), because, although we have no diet data for this species at Potter Cove,

instances of herbivory have been consistently reported for this species (Moreno 1980; Kiest 1993; among others). On the other hand, lower RILs (mean 52–53%) were characteristic of the predominantly carnivorous *H. antarcticus*, *T. newnesi* and *L. nudifrons* (W% of algae < 1.5). Conversely, no correspondence was found between a high RIL (87.8%) and low herbivory (algae W% = 5.4) in the detritivorous *G. gibberifrons*, and between the high RILs (mean 70–78%) and no algae consumption in the exclusively carnivorous *P. charcoti* and *C.aceratus*.

Table 4 and Fig. 4 summarize data of the number of pyloric caeca in the notothenioids of this study. There is no clear association between the number of pyloric caeca and the diet type—omnivory or carnivory. The average number of caeca was 6–7, with medians ranging from 2.0 to 7.0. *Chaenocephalus aceratus* was the only species with no intraspecific variation (CV% = 0). *Parachaenichthys charcoti* and *G. gibberifrons* had higher coefficients of variation (CV% = 13.3%), whereas that of *H. antarcticus*

Table 3 Parameters relative to intestine length and degree of herbivory in nine notothenioid species at Potter Cove, arranged according to feeding type Cove, arranged according to feeding type

| Fish species | Diet (W%) | | | RIL | | Feeding mode* | Degree of herbivory |
	N	Algae	Prey	N	(mean ± SD)		
Notothenia coriiceps[a]	355	23.9	76.1	247	82.6 ± 19.1	Benthos feeders-benthic, epibenthic	High
Harpagifer antarcticus[b]	273	1.4	98.6	151	52.7 ± 8.4	"	Low
Lepidonotothen nudifrons[c]	77	0.7	99.3	248	52.8 ± 9.7	"	Low
Gobionotothen gibberifron[d]	4	5.4	94.6	4	87.8 ± 5.4	"	Low
Notothenia rossii[e]	524	29.7	70.3	396	77.9 ± 15.1	Benthos & plankton feeders-benthic, benthopelagic	High
Trematomus newnesi[f]	497	1.0	99.0	207	51.5 ± 12.4	"	Low
Trematomus bernacchii[g]	–	–	–	75	68.7 ± 14.5	"	–
Parachaenichthys charcoti[h]	14	0	100	14	70.4 ± 10.9	"	Null
Chaenocephalus aceratus[i]	28	0	100	28	78.3 ± 15.5	"	Null

Seasonal diet data: [a]1988-1989 (Barrera-Oro and Casaux 1990), 2008–2012, 2015–2016 (Barrera-Oro et al. 2019); [b]1992 (Casaux 1998), 2009–2012; [c]2008–2011; [d]2016–2018; [e]2005–2006 (Barrera-Oro and Winter 2008), 2008–2012, 2015–2016 (Barrera-Oro et al. 2019); [f]2004–2006 (Barrera-Oro and Piacentino 2007), 2008–2012; [g]No data available; [h]2008–2012, 2016–2018; [i]2008–2012, 2016–2018

*Barrera-Oro (2002) and compilation therein

Table 4 Summary statistics for number of pyloric caeca in 1382 specimens representing nine notothenioid species sequenced on the basis of increasing size of median

Fish species	N	Number of pyloric caeca				Percentiles	
		Min	Max	Mean (SD)	Median[a]	(25th)	(75th)
Chaenocephalus aceratus	29	2	2	2.00 (0.00)	2.00	2.00	2.00
Parachaenichthys charcoti	14	2	4	3.00 (0.39)	3.00	3.00	3.00
Harpagifer antarcticus	156	3	4	3.01 (3.00)	3.00	3.00	3.00
Gobionotothen gibberifrons	4	3	4	3.75 (0.50)	4.00	3.25	4.00
Lepidonotothen nudifrons	244	4	7	5.89 (0.63)	6.00	6.00	6.00
Notothenia rossii	398	5	8	5.91 (0.57)	6.00	6.00	6.00
Notothenia coriiceps	247	3	7	5.96 (0.55)	6.00	6.00	6.00
Trematomus newnesi	214	3	8	6.69 (0.65)	7.00	6.00	7.00
Trematomus bernacchii	76	6	9	6.93 (0.72)	7.00	6.00	7.00

[a]Kruskal–Wallis test ($H_8 = 814$, $p < 0.0001$) indicates that medians vary among species (*G. gibberifrons* excluded)
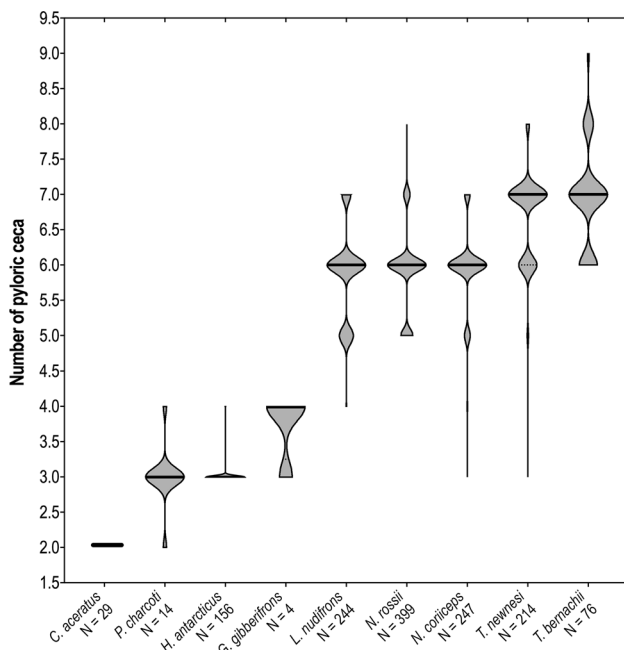
Fig. 4 Violin plot of number of pyloric caeca in nine notothenioids from Potter Cove. Thick horizontal lines are medians, thin lines are 25th and 75th percentiles

was lower (CV % = 3.3). In the other species, the variation was 1–4 caeca.

Discussion

The basic feeding strategies in fishes are herbivory, omnivory and carnivory, and omnivores with a tendency for carnivory are the most numerous group (Bakke et al. 2011). Most notothenioids are opportunistic carnivores and consume what is immediately available in the vicinity including motile benthic and pelagic invertebrates, especially krill, and fishes. Four carnivorous species are more specialized as either zooplanktivores (*Pleuragramma antarctica* and *Aethotaxis mitopteryx*) or piscivores (*Dissostichus* spp.). There are no herbivores but *Notothenia coriiceps* and *N. rossii* are omnivorous with diets that include macroalgae. With the exception of fishes associated with coral reefs, herbivores are rare among marine fishes, and the number of herbivorous and omnivorous species declines with increasing latitude (Harmelin-Vivien 2002). In a review of marine herbivorous fishes, Clements et al. (2009) highlighted the *Notothenia* spp. as examples of species that, while not strictly herbivorous, do selectively consume algae as part of their diet (Barrera-Oro and Casaux 1990; Iken et al. 1997; Barrera-Oro 2002; Casaux et al. 2003). Selective in this context means that they avoid consuming species of macroalgae that are chemically defended and have been shown experimentally to be unpalatable to species such as *N. coriiceps* (Amsler et al. 2005).

The importance of algae in the diet of the notothenioids at Potter Cove was in general agreement with literature information for the same species in other areas of the western Antarctic Peninsula (compiled in Barrera-Oro 2002, pp. 296–297/Tables II and III). Although our data set of notothenioids from Potter Cove is large and has been obtained over a sampling period of many years, it does not contain a wide size range—from small to large specimens—in a single season for any of the sampled fish species. To carry out the comparative ontogenetic dietary analysis between the two mainly omnivorous species—*N. coriiceps* and *N. rossii*—we used, from the total data set, complementary data of two non-consecutive summer seasons, which included all life history stages available inshore from early juveniles of both species to large adults of *N. coriiceps* and large juveniles and pre-adults of *N. rossii* (Table 2). These two seasons

were similar in the scarcity of krill in the cove, as reported in Juares (2013) and in Barrera-Oro et al. (2019). There is inter-annual variability in the occurrence of krill in waters of the entire western Antarctic Peninsula (Atkinson et al. 2008; Siegel and Watkins 2016). The presence of krill as a resource has a great influence in the diet analysis of predators. Therefore in the present study of the proportions of algae and prey consumed, we have avoided combining data from sampling seasons that may have had dissimilarities in the availability of krill. Our results from the diet analysis over ontogeny show that in both species, the consumption of algae decreases with growth, and in the case of *N. rossii* this change was significant (Table 2). This ontogenetic shift in the diet towards a greater ingestion of animal prey is associated with the increased capacity of the fish species to capture progressively larger prey of greater energetic value (Kock 1992; Barrera-Oro 2002; Marina et al. 2018). These two sympatric species are ideal for this comparison because sample sizes are large, the body sizes reached in inshore waters are similarly medium-large and they are also sister species (Near et al. 2018), hence the effects of phylogenetic distance are minimalized. The chi-square test was significant for *N. rossii* probably because the species is benthopelagic, with a higher capacity to migrate within the water column to feed on pelagic prey. The test was not significant for *N. coriiceps*, a more benthic–epibenthic species that lives within macroalgae beds and feeds on algae and their associated fauna during its entire life cycle (Moreira et al. 2014; Barrera-Oro et al. 2019). The greater buoyancy of *N. rossii* (%$B = 3.82$%) over *N. coriiceps* (%$B = 4.34$%), which was reported for fish of Potter Cove, is consistent with its lower density and more active swimming, migratory and feeding behaviour compared to *N. coriiceps* (Eastman et al. 2011).

The dietary composition of fish species can fluctuate seasonally owing to a variety of factors such as prey availability along depth gradients, seasonal variability and the different mechanical capacities of fish to ingest food during their ontogeny. While seasonal diet variability in *N. rossii* may be strongly influenced by ontogenetic changes, this variability in *N. coriiceps* is mainly linked to food availability. The comparative dominance of algae consumption between both species fluctuated throughout the entire sampling period (this is not shown in Table 3): *N. rossii* was more herbivorous than *N. coriiceps* in summer seasons 1985–1986 (Casaux et al. 1990) and 2009–2010 (present study), whereas *N. coriiceps* was more herbivorous than *N. rossii* in summer seasons 2008–2009, 2010–2011, 2011–2012 (present study) and in 2015–2016 (Barrera-Oro et al. 2019). Therefore, although the algal consumption of *N. rossii* expressed in mean W% for the total period estimated for a local inshore site such as Potter Cove was slightly higher than that of *N. coriiceps*, we suggest that, within the general context of the trophic ecology of the Antarctic notothenioids, both species

can be considered as highly herbivorous to a similar degree (Table 3). In contrast, in the other fish species analysed, the degree of herbivory was low—*Gobionotothen gibberifrons*, *Harpagifer antarcticus*, *Trematomus newnesi* and *Lepidonotothen nudifrons*- or null—*Parachaenichthys charcoti* and *Chaenocephalus aceratus*.

The pyloric caeca are amazingly unspecialized in their gross morphology among the notothenioids we studied. In our samples of notothenioids from Potter Cove we found no clear association between the number of pyloric caeca and degree of omnivory or carnivory. Pyloric caeca are present in about 60% of actinopterygian species and, as diverticula of the intestine, they serve to increase mucosal surface area for both digestion and absorption. They vary in size and in number from zero to thousands (Wilson and Castro 2011). In most perciform species, there is no ontogenetic variation in the number of pyloric caeca as it is fixed at an early stage of larval life (Hossain and Dutta 1988).

As far as intestinal length is concerned, we did detect a correlation between intestine length/RILs and degree of herbivory in six of the nine species analysed. Our results and those of others indicate modest divergence that includes a phylogenetic decrease in the number of pyloric caeca, with 6–7 in most nototheniids, 3–4 in harpagiferids, 3–4 in artedidraconids, 3–4 in bathydraconids and 2–3 in channichthyids (Ojeda 1986; Eastman and DeVries 1997; Voronina and Neelov 2001), and 1.8-fold difference in average relative intestine lengths which are most frequently 50–70% of body length and never exceed body length (Ojeda 1986; Eastman and DeVries 1997; Moreira 2015). Interpretation of the high RILs obtained for the primarily carnivorous *P. charcoti* and *C. aceratus* (no algae consumption) is uncertain. Given the reduction in pyloric caeca in these two phyletically derived species, RIL may compensate for the loss of mucosal surface area in the caeca and be unrelated to diet.

Specialization in the alimentary canal

Examples of specialization in the alimentary canal among non-notothenioids include the stomach functioning as a gizzard and utilizing the consumed detritus for mechanical breakdown of food as in mugilids (mullets), and the loss of the stomach in cyprinids (minnows) and catostomids (suckers). Intestinal length in herbivorous fishes is usually at least threefold greater than body length (Bone and Moore 2008). Greater intestinal length allows for the longer processing time needed for plant material in herbivores but it also compensates for the inorganic component of ingested detritus in detritivores. The North American cyprinid (minnow) *Campostoma anomalum* is an example of specialization associated with ingesting a load of detritus along with its diet of algae, especially diatoms. Like all minnows, it lacks oral teeth and a stomach, but the lower jaw has a

prominent cartilaginous ridge suitable for scraping. The intestine, nearly eightfold greater than the body length, is accommodated in the body cavity by being wound around the swim bladder (Jenkins and Burkhead 1993). In coral reef fishes, convergent patterns of dietary-related morphological variation were evident across three families—Labridae, Chaetodontidae and Pomacentridae—with corallivores possessing long and narrow intestines, carnivores relatively short and wide intestines and herbivores relatively long and wide intestines (Elliott and Bellwood 2003). In a marine perciform more suitable for comparing with notothenioids, the marblefish, *Aplodactylus punctatus* (Aplodactylidae) from ≈33°S on coast of Chile, provides a perspective on the degree of alimentary canal specialization for herbivory. The diet of *A. punctatus* consists of about 98% macroalgae, primarily the brown kelp *Lessonia trabeculata* (Benavides et al. 1994). Depending on body size, the mean alimentary canal is 2.3–4.8-fold total length or 195–565% of total length. In an ontogenetic series of this species ranging in length from 22–42 cm TL, the exponent of the allometric equation is 2.01 (Benavides et al. 1994), nearly twice that of *N. coriiceps* in our present study. Through experimentation, they concluded that the advantage of a longer intestine was that the transit time was increased by 2.6-fold and the digestibility of algae increased from 38 to 80%.

Detritivory

There are probably factors other than herbivory that influence the length of the intestine. For example during benthic browsing, detritus may be ingested necessitating a longer intestine, with *G. gibberifrons* as the example among notothenioids. Among the nine species we studied, and notothenioids in general, *G. gibberifrons* is the quintessential benthic browser as evidenced by its depressed body shape with a flattened ventral surface, subterminal mouth, dorsally located eyes, mottled pigmentation pattern and habitation of mud substrates where it feeds on infauna (Targett 1981; Daniels and Lipps 1982). Although there has been no ecomorphological study of its feeding mode, it has been characterized as a "slurp-feeder" (compiled in Barrera-Oro 2002, p. 297/Table III). Therefore, it is not surprising that its intestinal contents include mud and small rock fragments that were inadvertently swallowed as it grubbed through sediment (Targett 1981; Daniels 1982; Casaux et al. 1990). Our data and that of Ojeda (1986) identify *G. gibberifrons* as having the greatest relative intestine length of any notothenioid examined to date at 87.8% and 90.9% of SL, respectively. In this case, the relatively long intestine is not attributable to herbivory (only 5% of algae in W%), but instead is probably compensation for the decrease in mucosal surface area caused by the large inorganic component of the swallowed

detritus. The mud and rocks mix with and dilute the organic component necessitating a longer intestine for increased processing and absorption time for the organic component.

Herbivory

In fishes, there is no known microbial gut flora that is responsible for producing cellulase for algal digestion. However, if gastric pH is low, acid hydrolysis can rupture plant cell walls and release cytoplasmic contents for digestion and absorption (Wilson and Castro 2011). The absence of gastrointestinal specialization in many bony fish species has long been recognized: "the ecological situation of fish may often favour a generalized rather than a highly specialized digestive system" (Barrington 1957), with digestive system in this context meaning alimentary canal. Targett and Radtke (1984) analysed the gastric and intestinal pH in *N. coriiceps* and concluded that gastric pH is sufficient to lyse algal cell walls and that some components of macroalgae cells can be assimilated by the fish. Reported levels of algae assimilation by fish range between 20% (Montgomery and Gerking 1980) and 90% (Horn 1989). Fish that have a longer intestinal length have a higher capacity to digest algae (Ojeda 1986; Eastman and DeVries 1997).

Final remarks

Our present study on some aspects of the trophic ecology of the Antarctic notothenioids provides evidence of the opportunistic feeding behaviour and dietary plasticity, exemplified by the omnivory in species such as *N. coriiceps* and *N. rossii*. This reflects what is available to them at a particular time in their ontogeny and in a particular location (Potter Cove) at a certain time of the year (summer). Without a specialized diet, there will probably be little specialized morphology evident in the alimentary canal. For example, there will be no obvious morphology associated with intermittent herbivory on kelp, and attempts to correlate diet with stomach length, intestine length, number of pyloric caeca will be inconclusive. In addition to the macroalgae consumption reported here for *N. coriiceps*, trap fishing at a depth of 36 m in the kelp beds around Bouvetøya, caught large (50–60 cm TL) *N. coriiceps* with stomachs packed with red and green algae (Eastman, personal observation, 2004 ICE-FISH Cruise, NBP 04-04). Dietary plasticity may be the norm in species living in an environment where competition from non-notothenioids is reduced and food is not limiting. In *N. coriiceps* and *N. rossii*, the alimentary canal can process food on a scale ranging from carnivory to omnivory including intermittent herbivory, although perhaps less efficiently than if the alimentary canal was more specialized.

Nevertheless, all food provides some nutrition and while algae may be a low quality in terms of energetic and nitrogen content, if it is consumed and processed, there is probably some assimilation and some energy is obtained.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

References

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141–159. https://doi.org/10.3354/meps294141

Atkinson A, Siegel V, Pakhomov E, Rothery P, Loeb V, Ross RM, Quetin LB, Schmidt K, Fretwell P, Murphy EJ, Tarling GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic krill. Mar Ecol Prog Series 362:1–23. https://doi.org/10.3354/meps07498

Bakke AM, Glover C, Krogdahl A (2011) Feeding, digestion and absorption of nutrients. In: Grosell M, Farrell AP, Brauner CJ (eds) Fish physiology, vol 30. Academic Press, London, pp 57–110

Barrera-Oro E (2002) The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. Antarct Sci 14:293–309

Barrera-Oro ER, Casaux RJ (1990) Feeding selectivity in *Notothenia neglecta*, Nybelin, from Potter Cove, South Shetland Islands, Antarctica. Antarct Sci 2:207–213

Barrera-Oro ER, Piacentino GLM (2007) Feeding habits of juvenile *Trematomus newnesi* (Pisces, Nototheniidae) at Potter Cove, South Shetland Islands, Antarctica. Polar Biol 30(6):789–796

Barrera-Oro ER, Winter D (2008) Age composition and feeding ecology of early juvenile *Notothenia rossii* (Pisces, Nototheniidae) at Potter Cove, South Shetland Islands, Antarctica. Antarct Sci 20:339–341

Barrera-Oro E, Moreira E, Seefeldt M, Valli Francione M, Quartino ML (2019) The importance of macroalgae and associated amphipods in the selective benthic feeding of sister rockcod species *Notothenia rossii* and *N. coriiceps* (Nototheniidae) in West Antarctica. Polar Biol 42:317–334

Barrington EJW (1957) The alimentary canal and digestion. In: Brown ME (ed) The physiology of fishes, vol 1. Academic Press, New York, pp 109–161

Benavides AG, Cancino JM, Ojeda FP (1994) Ontogenetic changes in gut dimensions and macroalgal digestibility in the marine herbivorous fish, *Aplodactylus punctatus*. Funct Ecol 8:46–51

Bone Q, Moore RH (2008) Biology of fishes, 3rd edn. Taylor & Francis, New York

Casaux R (1998) The contrasting diet of *Harpagifer antarcticus* (Notothenioidei, Harpagiferidae) at two localities of the South Shetland Islands, Antarctica. Polar Biol 19(4):283–285

Casaux R, Barrera-Oro E (2013) Dietary overlap in inshore notothenioid fish from the Danco Coast, western Antarctic Peninsula. Polar Res 32(21319):1–8. https://doi.org/10.3402/polar.v32i0.21319

Casaux RJ, Mazzotta AS, Barrera-Oro ER (1990) Seasonal aspects of the biology and diet of nearshore notothenioid fish at Potter Cove, South Shetland Islands, Antarctica. Polar Biol 11:63–72

Casaux R, Barrera-Oro E, Baroni A, Ramón A (2003) Ecology of inshore notothenioid fish from the Danco Coast, Antarctic Peninsula. Polar Biol 26:157–165

Clements KD, Raubenheimer D (2006) Feeding and nutrition. In: Evans DH, Clairborne JB (eds) The physiology of fishes, 3rd edn. CTC Press, Boca Raton, pp 47–82

Clements KD, Raubenheimer D, Choat JH (2009) Nutritional ecology of marine herbivorous fishes: ten years on. Funct Ecol 23:79–92. https://doi.org/10.1111/j.1365-2435.2008.01524.x

Daniels RA (1982) Feeding ecology of some fishes of the Antarctic Peninsula. Fish Bull US 80:575–588

Daniels RA, Lipps JH (1982) Distribution and ecology of fishes of the Antarctic Peninsula. J Biogeogr 9:1–19

Eastman JT (2005) The nature of the diversity of Antarctic fishes. Polar Biol 28:93–107

Eastman JT, DeVries AL (1997) Morphology of the digestive system of Antarctic nototheniid fishes. Polar Biol 17:1–13

Eastman JT, Barrera-Oro E, Moreira E (2011) Adaptive radiation at a low taxonomic level: divergence in buoyancy of the ecologically similar Antarctic fish *Notothenia coriiceps* and *N. rossii*. Mar Ecol Prog Ser 438:195–206

Elliott JP, Bellwood DR (2003) Alimentary tract morphology and diet in three coral reef fish families. J Fish Biol 63:1598–1609. https://doi.org/10.1046/j.1095-8649.2003.00272.x

Foster BA, Montgomery JC (1993) Planktivory in benthic nototheniid fish in McMurdo Sound, Antarctica. Environ Biol Fish 36:313–318

Gon O, Heemstra PC (eds) (1990) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahams Town

Gröhsler T (1994) Feeding habits as indicators of ecological niches: investigations of Antarctic fish conducted near Elephant Island in late autumn/winter 1986. Arch Fish Mar Res 42:17–34

Harmelin-Vivien ML (2002) Energetics and fish diversity on coral reefs. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp 265–274

Horn MH (1989) Biology of marine herbivorous fishes. Oceanogr Mar Biol 27:167–272

Hossain A, Dutta HM (1988) Embryology of intestinal caeca in the bluegill (*Lepomis macrochirus*). Can J Zool 66:998–1003

Iken K, Barrera-Oro ER, Quartino ML, Casaux RJ, Brey T (1997) Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. Antarct Sci 9:386–391

Jenkins RE, Burkhead NM (1993) Freshwater fishes of Virginia. American Fisheries Society, Bethesda

Juares MA (2013) Biología reproductiva y ecología trófica de dos especies simpátricas del género Pygoscelis en las Islas Shetland del Sur, Antártida. Tesis Doctoral. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina. https://hdl.handle.net/10915/27166

Kiest KA (1993) A relationship of diet to prey abundance and the foraging behavior of *Trematomus bernacchii*. Polar Biol 13:291–296

Kock KH (2005) Antarctic icefishes (Channichthyidae): a unique family of fishes. A review. Part I Polar Biol 28:862–895

Kock KH, Kellermann A (1991) Reproduction in Antarctic notothenioid fish. Antarct Sci 3:125–150

Kock KH (1992) Antarctic fish and fisheries. Cambridge University Press, Cambridge

Kock KH, Barrera-Oro E, Belchier M, Collins MA, Duhamel G, Hanchet S, Pshenichnov L (2012) The role of fish as predators of krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. CCAMLR Sci 19:115–169

Korovina VM (1986) Anatomical-histological perculiarities of the intestine of *Patagonotothen ramsayi* (Nototheniidae). J Ichthyol 26:48–54

Korovina VM, Prirodina VP (1986) Anatomical-histological features of the intestine of the sculpin spinecheek, *Cottoperca gobio*, (Bovichthyidae, Notothenioidei). J Ichthyol 26:130–136

Korovina VM, Neyelov AV, Bondarenko EP (1986) Structure of intestine of *Chaenocephalus aceratus* (Lönnberg) (Channichthyidae, Notothenioidei). USSR Acad Sci Proc Zool Inst Leningrad 162:110–114 **[In Russian]**

Korovina VM, Neyelov AV, Bondarenko YP (1991a) The anatomy and histology of the intestine of the Patagonian toothfish (*Dissostichus eleginoides* Smitt). J Ichthyol 31:34–40

Korovina VM, Neyelov AV, Bondarenko YP (1991b) Intestinal anatomy and histology of the marbled notothenia, *Notothenia rossii marmorata*. J Ichthyol 31:79–90

Korovina VM, Voronina EP, Neelov AV (2004) Comparative characteristics of the alimentary tract of toothfishes of the genus *Dissostichus* (Nototheniidae). J Ichthyol 44:239–244

Marina TI, Salinas V, Cordone G, Campana G, Moreira E, Deregibus D, Torre L, Sahade R, Tatian M, Barrera-Oro E, De Troch M, Doyle S, Quartino ML, Saravia L, Momo FR (2018) The food web of Potter Cove (Antarctica): complexity, structure and function. Estuar Coast Shelf Sci. https://doi.org/10.1016/j.ecss.2017.10.015

McKenna JE (1991) Trophic relationships within the Antarctic demersal fish community of South Georgia Island. Fish Bull US 89:643–654

Montgomery WL, Gerking SD (1980) Marine macroalgae as food for fishes: an evaluation of potential food quality. Environ Biol Fish 5:143–153

Moreira E (2015) Ictiofauna Antártica: Ecología de estadíos juveniles de especies del Suborden Notothenioidei de Caleta Potter, Isla 25 de Mayo. Tesis doctoral. FCNyM, Universidad Nacional de la Plata. https://sedici.unlp.edu.ar/handle/10915/50216

Moreira E, Juáres M, Barrera-Oro E (2014) Dietary overlap among early juvenile stages in an Antarctic notothenioid fish assemblage at Potter Cove, South Shetland Islands. Polar Biol 37:1507–1515. https://doi.org/10.1007/s00300-014-1545-3

Moreno CA (1980) Observation on food and reproduction in *Trematomus bernacchii* (Pisces: Nototheniidae) from the Palmer Archipelago, Antarctica. Copeia 1:171–173

Near TJ, MacGuigan DJ, Parker E, Struthers CD, Jones CD, Dornburg A (2018) Phylogenetic analysis of Antarctic notothenioids illuminates the utility of RADseq for resolving Cenozoic adaptive radiations. Mol Phylogen Evol 129:268–279. https://doi.org/10.1016/j.ympev.2018.09.001

Nybelin O (1947) Antarctic fishes. Sci Results Nor Antarct Exped 1927–1928(26):1–76

Ojeda FP (1986) Morphological characterization of the alimentary tract of Antarctic fishes and its relation to feeding habits. Polar Biol 5:125–128

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Siegel V, Watkins JL (2016) Distribution, biomass and demography of Antarctic Krill Euphausia superba. Biology and ecology of Antarctic Krill. Springer, Berlin

Sokal R, Rohlf F (1981) Biometry, 2nd edn. W.H. Freeman, San Francisco, CA

Targett TE (1981) Trophic ecology and structure of coastal Antarctic fish communities. Mar Ecol Prog Ser 4:243–263

Targett TE, Radtke RL (1984) Growth and feeding ecology studies on coastal Antarctic fishes. Antarct J US 19:147–149

Voronina EP (1999) Some specific features of the structure of the digestive tract of *Gvozdarus svetovidovi* (Pleuragramminae, Nototheniidae). J Ichthyol 39:127–129

Voronina EP, Balushkin AV (1998) Morphological features of the digestive tract in four genera of notothenioid fishes (Nototheniidae). J Ichthyol 38:781–788

Voronina EP, Neelov AV (2001) Structural traits of alimentary tract of fishes of the family Channichthyidae (Notothenioidei). J Ichthyol 41:778–788

Wilson JM, Castro LFC (2011) Morphological diversity of the gastrointestinal tract in fishes. In: Grosell M, Farrell AP, Brauner CJ (eds) Fish physiology, vol 30. Academic Press, London, pp 1–55

Zamzow JP, Aumack CF, Amsler CD, McClintock JB, Amsler MO, Baker BJ (2011) Gut contents and stable isotope analyses of the Antarctic fish, *Notothenia coriiceps* (Richardson), from two macroalgal communities. Antarct Sci 23:107–116. https://doi.org/10.1017/s095410201000091x