

# Biology and phenotypic plasticity of the Antarctic nototheniid fish *Trematomus newnesi* in McMurdo Sound

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**Abstract:** *Trematomus newnesi* inhabited inshore (<20 m) subzero waters in McMurdo Sound where it fed in the water column on *Euphausia crystallorophias* and fishes. This sample included the largest reported specimens of this species. The length–weight relationship was  $\text{Weight} = 3.17 \times 10^{-6} (\text{Standard Length})^{3.34}$ ,  $n = 67$ ,  $r^2 = 0.95$ . The population was phenotypically plastic, with two distinct morphs easily separated by visual inspection – the typical morph and a large mouth/broad headed morph comprising 28% of the sample. The large mouth morph had a wider and blunter head, longer upper jaw, wider gape, more heavily ossified jaws and darker colouration. To document this morphology, four views of the head are illustrated. Inference from morphology and measurements suggested that the large mouth morph was more benthic than the typical semipelagic morph. Museum specimens from Cape Adare confirmed the presence of the large mouth morph 700 km north of McMurdo Sound. This is the first clear example of phenotypic plasticity in any species of marine fish and its discovery extends the bounds of the nototheniid adaptive radiation to the population level. This finding suggests ecological and evolutionary parallels between the inshore waters of the high Antarctic shelf and the low diversity ichthyofaunas of Arctic, boreal and some temperate lakes. Although there is no data on genetic diversification, an alternate interpretation of the phenotypic plasticity is that the large mouth morph is a cryptic or sibling species.

Received 4 July 1996, accepted 31 October 1996

**Key words:** Antarctic, diet, large mouth morph, McMurdo Sound, Nototheniidae, phenotypic plasticity

## Introduction

The common nototheniid fish *Trematomus newnesi* Boulenger has a circumantarctic distribution in cold, shallow shelf waters of the continent and adjacent islands (DeWitt *et al.* 1990). Initially recognized as semipelagic by Richardson (1975), *T. newnesi* exhibits considerable trophic plasticity, feeding in the water column and occasionally on the substrate. As the first described species in the genus, it stands as the type for *Trematomus* (Boulenger 1902). Recent research indicates, however, that *T. newnesi* differs from the other predominantly benthic and epibenthic species of *Trematomus* in features of the skeleton and cephalic lateral line, and that there are grounds for considering generic isolation (Balushkin 1984, 1992). Other work has revealed differences in the blood vascular system. For example, *T. newnesi* is the only species of *Trematomus* without an ocular rete mirabile (Eastman 1988). Furthermore, *T. newnesi* has three haemoglobin components, including two major components one of which (Hb C) is present in only trace amounts in other notothenioids (D'Avino *et al.* 1994). This haemoglobin multiplicity exceeds that of all other trematomids and is consistent with an active semipelagic life. Given this intrageneric heterogeneity, it is not surprising that morphological (Klingenberg & Ekau 1996) and molecular (Ritchie *et al.* 1996) data sets provide different phylogenetic hypotheses concerning the position of *T. newnesi* relative to the main

trematomid radiation. Our data on phenotypic plasticity reveal another unusual aspect of its biology.

Some populations of *T. newnesi* from West Antarctica are reasonably well characterized with respect to food habits and growth (Richardson 1975, Targett 1981, Daniels 1982, Radtke *et al.* 1989). A recent study of the diet of *T. newnesi* at Terra Nova Bay provides the first insight into the biology of this species at high latitude in East Antarctica (Vacchi & La Mesa 1995). Although known from ice covered McMurdo Sound since early in the century (Regan 1913), *T. newnesi* has been infrequently collected from ice holes with traps and jigs. For example, a sample of 200 specimens of the 11 most common notothenioid species included only one specimen of *T. newnesi* (Eastman & DeVries 1982). However, recent ice fishing in inshore water (<20 m) has produced a sufficiently large sample of *T. newnesi* to allow us to investigate its biology in McMurdo Sound near the southern limit of its distribution.

Although conforming to the taxonomic and meristic description of *T. newnesi*, about 28% of the specimens in our sample were separable by eye as a distinct morphological form. Phenotypic plasticity, sometimes involving the appearance of pelagic and benthic morphs, has recently been recognized in many species of temperate and boreal lacustrine fish (Meyer 1987, Ehlinger & Wilson 1988, Wainwright *et al.* 1991, Robinson *et al.* 1993, Skúlason & Smith 1995).

These studies indicate that environmental factors such as diet, feeding mode and competition may determine phenotypic expression. This paper documents the first report of discrete phenotypic plasticity in any marine fish, and our discovery highlights another aspect of fish diversity in high Antarctic shelf waters by extending the bounds of the nototheniid adaptive radiation (Eastman 1993, Clarke & Johnston 1996, Klingenberg & Ekau 1996) to the population level.

### Materials and methods

Five samples of *Trematomus newnesi* were collected over a period of four years (Table I) at two different localities near the US McMurdo Station (77°51'S, 166°40'E) in the southwestern Ross Sea. One site was near the southern end of Hut Point Peninsula, the other was 22 km north at Inaccessible Island. Water temperature was -1.9°C at both localities. At both sites we fished through holes drilled in the sea ice and located 10–100 m from shore using hooks baited with green plastic worms. The bottom at the capture sites was rocky and water depth was 16–18 m. Fish were taken in the lower one-half of the water column, usually within a few meters of the bottom but occasionally within 5 m of the surface. Although anchor ice was common in the vicinity of the holes, the bottom immediately beneath each hole was ice-free.

The fish were fixed in 10% formalin for 3–5 days immediately after capture. The only exception was the sample from October 1995 which was held in an aquarium for 1–3 days before fixation. After washing out the formalin, they were stored in 70% ethanol for periods of 4–6 weeks prior to weighing (nearest 0.01 g) and measuring total (TL) and standard (SL) lengths (nearest 1 mm). All weights and measurements of fish, organs and stomach contents came from these ethanol-stored specimens. Counts of meristic and trophic characters and morphometric measurements following procedures outlined by Hubbs & Lagler (1964). We counted vertebrae on left lateral radiographs produced using a Hewlett-Packard Faxitron soft X-ray machine with a dual cabinet. Following the alizarin red S procedure of Taylor (1967), three specimens of the typical morph and two specimens of the large morph were cleared and stained.

Morphometric measurements were straight line distances taken to the nearest 0.1 mm with a needle point dial calipers: head length, head depth, body depth, body width (equivalent to head width in this species), upper jaw length, gape width, snout length, orbit length, interorbital width, pectoral fin length, pelvic fin length and caudal peduncle depth. Some measurements were used in proportions derived by dividing raw measurements by standard length, head length or body width and expressed as percentages. We used proportional measurements shown to have ecomorphological predictive value in fishes in general (Gatz 1979) and in nototheniids in particular (Ekau 1988, 1991, Klingenberg & Ekau 1996).

The individual prey items contained in the stomach were identified, counted and dried at 60°C. As recommended in the BIOMASS Handbook No. 13 (Anonymous 1983), dietary items are given by frequency of occurrence, number and dry weight. A dietary coefficient Q (Hureau 1970, p. 142) was calculated from the product of the percentage by weight and the percentage by number for each prey item.

Prior to statistical analysis the data were transformed to natural logarithms (ln) to reduce variance, skewness, kurtosis and the coefficient of variation of meristic counts, measurements and ratios. Levels of significance are reported for ln-transformed data. Raw and ln-transformed data were examined for normality and linearity using probability plots against a normal distribution and bivariate plots. The software programs Microsoft Excel (5.0) and SYSTAT (5.2.1) were used for statistical analyses. From regressing ln-transformed meristic and morphometric characters (the dependent variables) against standard length (the independent variable), the resulting slopes provided estimates of nature of allometry associated with body size. Univariate ANOVAs and independent *t*-tests were used in comparing meristic and morphometric data between the two morphs. An ANCOVA was not conducted on morphometric measurements because the homogeneity of slopes assumption was not satisfied. Measurements were not independent since there were three meristic counts and 14 measurements on each fish. We therefore used the Bonferroni adjustment to ensure that a conservative *P*-level was accepted as significant (Tables II, IV, V).

To test the existence of two morphs, we used as the null

**Table I.** Samples of *Trematomus newnesi* from McMurdo Sound with data for sex, gonadosomatic index (GSI) and incidence of large mouth morph. Samples arranged from early to late in the season.

? = sex not determined in this large mouth specimen (although length-weight data were available for inclusion in Fig. 1).

Date	Locality	<i>n</i>	Sex				Large mouth morph	
			Male	GSI	Female	GSI	Male	Female
27–29 Oct. 1995	Inaccessible Island	26	14	0.07	12	2.41	5	0
26 Nov. 1995	Inaccessible Island	13	10	0.09	3	2.38	4	0
Nov. 1992	Hut Point (intake jetty)	11	3	0.13	8	3.24	3	1
early Dec. 1991	Hut Point (intake jetty)	2			1	3.40	?	
26 Jan.–7 Feb. 1994	Hut Point (intake jetty)	15	5	0.12	10	5.07	4	1
Totals		67	32		34		16	2

**Table II.** Untransformed size and meristic data for *Trematomus newnesi*, with sample separated by morph and sex. Numbers of specimens are 47–48 for typical morph and 16–19 for large mouth morph. *P*-level determined by independent *t*-tests on ln-transformed data. Asterisks denote significance at the Bonferroni-adjusted *P*-level of 0.05/6 = *P*<0.0083.

Character		Total sample	Typical	Morph Large mouth	<i>P</i>	Male	Sex Female	<i>P</i>
Total length (mm)	Mean	184.85	177.42	203.63	0.007*	174.76	194.65	0.013
	SD	35.43	32.31	36.85		37.33	30.96	
	Range	113–280	113–232	141–280				
Std. length (mm)	Mean	155.66	149.48	171.26	0.014	145.72	165.29	0.008*
	SD	32.27	29.82	33.73		32.86	29.00	
	Range	93–239	93–201	116–239				
Weight (g)	Mean	80.67	67.26	114.55	0.006*	72.67	88.43	0.066
	SD	59.39	45.59	76.24		64.43	53.87	
	Range	11.87–258.00	11.87–175.61	27.42–258.00				
Vertebrae	Mean	54.37	54.44	54.21	0.144	54.27	54.47	0.179
	SD	0.60	0.62	0.54		0.52	0.66	
	Range	53–56	53–56	53–55				
Gill rakers	Mean	24.11	24.15	24.00	0.739	23.68	24.50	0.029
	SD	1.51	1.62	1.24		1.35	1.56	
	Range	21–27	21–27	22–26				
Pyloric caeca	Mean	6.54	6.56	6.50	0.848	6.44	6.65	0.275
	SD	0.79	0.85	0.62		0.80	0.77	
	Range	5–9	5–9	6–8				

**Table III.** Stomach contents of 15 *Trematomus newnesi* (captured 26 Jan.–7 Feb 1994) with percentage frequency of occurrence (F), percentage by number (N), percentage by dry weight (W) and the dietary coefficient (Q) for each prey item. One stomach was empty and not included in the analysis.

Prey item	F (%)	N (%)	W (%)	Q
Euphausiids				
<i>Euphausia crystallorophias</i>	50.0	88.1	39.2	3454
Fishes (Total)	78.5	11.9	60.8	724
<i>Trematomus</i> sp.	42.9	8.1	41.6	337
<i>Pleuragramma antarcticum</i>	7.1	1.3	3.9	5
<i>Pagothenia borchgrevinki</i>	7.1	0.4	4.4	2
Unidentifiable fish	21.4	2.1	10.9	23

**Table IV.** ANOVAs comparing differences in measurements between typical and large mouth morphs of *Trematomus newnesi*. Data were ln-transformed; degrees of freedom are 1 and 61–64. Asterisks denote significance at the Bonferroni-adjusted *P*-level of 0.05/14 = *P*<0.0036.

Measurement	<i>F</i> -ratio	<i>P</i>
Body depth	7.08	0.010
Head length	12.15	0.001*
Head depth	11.28	0.001*
Body width	10.02	0.002*
Upper jaw length	27.19	0.000*
Gape width	22.68	0.000*
Snout length	17.21	0.000*
Interorbital width	17.49	0.000*
Orbit length	6.00	0.017
Pectoral fin length	5.95	0.018
Pelvic fin length	17.37	0.000*
Caudal peduncle depth	11.76	0.001*
Intestine length	2.18	0.145
Stomach length	4.10	0.047

**Table V.** Proportional measurements of *Trematomus newnesi*, with sample separated by morph. Ratios are for untransformed data expressed as percentages. Numbers of specimens are 47 for typical morph and 18 for large mouth morph. *P*-level determined by independent *t*-tests on ln-transformed data. Asterisks denote significance at the Bonferroni-adjusted *P*-level of 0.05/12 = *P*<0.0042.

Measurement		Typical	Morph Large mouth	<i>P</i>
Gape width/head length	Mean	38.01	45.91	0.000*
	SD	4.04	5.37	
Upper jaw length/head length	Mean	46.96	53.29	0.000*
	SD	2.98	3.01	
Snout length/head length	Mean	28.62	30.42	0.000*
	SD	1.76	1.61	
Orbit length/SL	Mean	7.28	7.24	0.761
	SD	0.45	0.59	
Interorbital width/body width	Mean	48.44	49.06	0.613
	SD	4.25	4.50	
Body depth/body width	Mean	138.43	130.33	0.001*
	SD	9.77	7.56	
Body depth/SL	Mean	23.50	24.64	0.001*
	SD	1.42	1.02	
Pectoral fin length/SL	Mean	25.58	25.45	0.696
	SD	1.56	1.44	
Pelvic fin length/SL	Mean	18.08	18.55	0.437
	SD	2.03	2.04	
Caudal peduncle depth/SL	Mean	7.66	8.13	0.005
	SD	0.44	0.59	
Intestine length/SL	Mean	58.39	59.74	0.392
	SD	9.38	6.82	
Stomach length/SL	Mean	14.60	14.98	0.437
	SD	1.59	1.71	

hypothesis: size, sex ratio, slopes and intercepts of the length–weight relationship and meristic, morphometric and trophic characters did not differ between morphs. This was a two-sided test. An additional null hypothesis was that morphometric measurements were isometric relative to SL.

## Results

### Length–weight relationship and sex ratio

The sample included the largest reported specimens of *Trematomus newnesi*, with one male measuring 280 mm TL, 239 mm SL and weighing 258 g (Table II). When untransformed data were graphed (Fig. 1), the length–weight relationship conformed to the power function  $Weight = a(SL)^b$ . The intercept and slope resulting from the linear regression of the ln-transformed data were equivalent to the values for the coefficient (a) and the exponent (b) of the power function given in Fig. 1. As weight increased more than the cube of SL, growth showed slight positive allometry. We also computed separate length–weight relationships for the two morphs described in the section below (typical morph:  $Weight = 4.28 \times 10^{-6} (SL)^{3.28}$ ;  $N = 48$ ;  $r^2 = 0.96$ ; large mouth morph:  $Weight = 3.82 \times 10^{-6} (SL)^{3.32}$ ;  $N = 19$ ;  $r^2 = 0.90$ ). *t*-tests comparing slopes and intercepts gave no significant differences in the length–weight relationship between the two morphs (slopes:  $t = 0.220$ ;  $df = 63$ ;  $P > 0.80$ ; intercepts:  $t = 0.124$ ;  $df = 63$ ;  $P > 0.90$ ).

Males had low (0.07–0.13%) gonadosomatic indices (GSI) characteristic of an inactive stage in the gonadal cycle

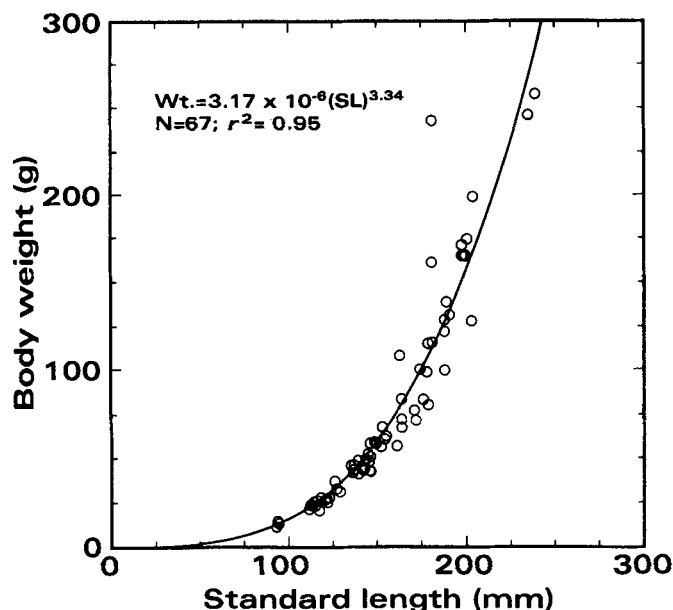


Fig. 1. Length–weight relationship for *Trematomus newnesi* (sexes and morphs combined). Curve drawn by power smoothing option in SYSTAT using untransformed data. Values for power function obtained by linear regression of ln-transformed data.

(Table I). Values for females were 2.38–5.07%, and showed an increasing trend from October through February. These ovaries were therefore in the spent to early developing stages. The sex ratio for the total sample of 32 males/34 females ( $= 0.94$ ) was not significantly different from unity ( $\chi^2 = 0.06$ ,  $df = 1$ ,  $P > 0.5$ ). Females were longer and heavier than males, but values were significant only in the case of standard length (Table II). The sexes did not differ in other meristic and trophic characters (Table II). The ratio of males/females was 16/32 in the typical morph and 16/2 in the large mouth morph, but these departures from unity were probably artifacts of the small size of the samples (Table I).

### Diet

The sample from January–February 1994 was suitable for a complete dietary analysis (Table III). Dietary diversity was low with *Euphausia crystallorophias* dominant by number and fishes (40–48 mm SL) dominant by dry weight. On the basis of a dietary coefficient ( $Q$ )  $> 200$ , *E. crystallorophias* and *Trematomus* were preferential prey items. The diet of the four specimens (the fifth had an empty stomach) of the large mouth morph was skewed toward fishes (present in four of four stomachs) and away from *E. crystallorophias* (present in only one of four).

The diet of 13 specimens taken at Inaccessible Island on 26 November 1995 also consisted of zooplanktonic organisms, but not fish. Contents were not well preserved but prey items were still recognizable at higher taxonomic levels. All stomachs contained calanoid copepods, eight contained pteropod molluscs, three contained hyperiid amphipods and two contained *E. crystallorophias*. There was no difference in the diets of the two morphs.

### Meristics counts and morphometric measurements

Meristic data are summarized in Table II. Values for some meristic and trophic characters were not influenced by body size (standard length = SL). Linear regression analysis indicated that the slopes for number of vertebrae, pyloric ceca and gill rakers were not significantly different from zero ( $P = 0.111$ – $0.480$ ;  $r^2 = 0.01$ – $0.04$ ). On the other hand, the slopes for all morphometric measurements (Table IV) were significantly different from zero ( $P < 0.000$ ), and indicated a strong relationship to SL in all cases ( $r^2 = 0.77$ – $0.96$ ). With respect to SL, slopes suggested strong positive allometry for intestine length (1.46), gape width (1.33) and body width (1.24); moderate positive allometry for stomach length (1.13), body depth (1.10), head depth (1.09); isometry for upper jaw length (1.04), snout length (1.01) and interorbital width (1.01) and negative allometry for head length (0.94), caudal peduncle depth (0.91), pectoral fin length (0.85), orbit length (0.80) and pelvic fin length (0.61).

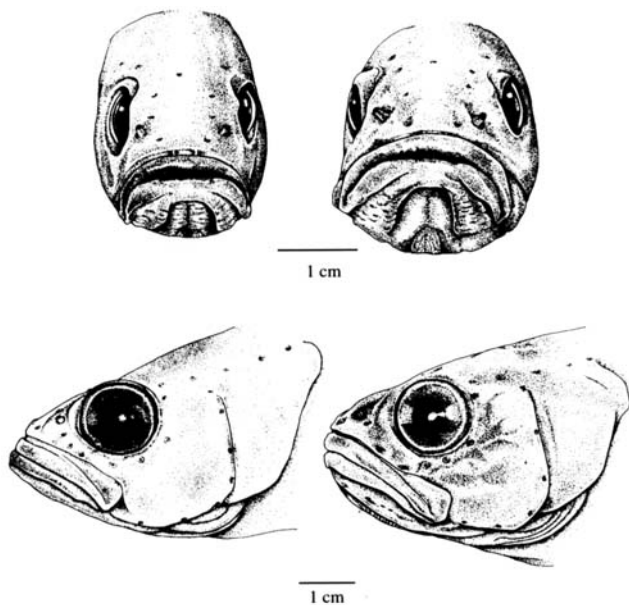


*Two morphs in McMurdo Sound*

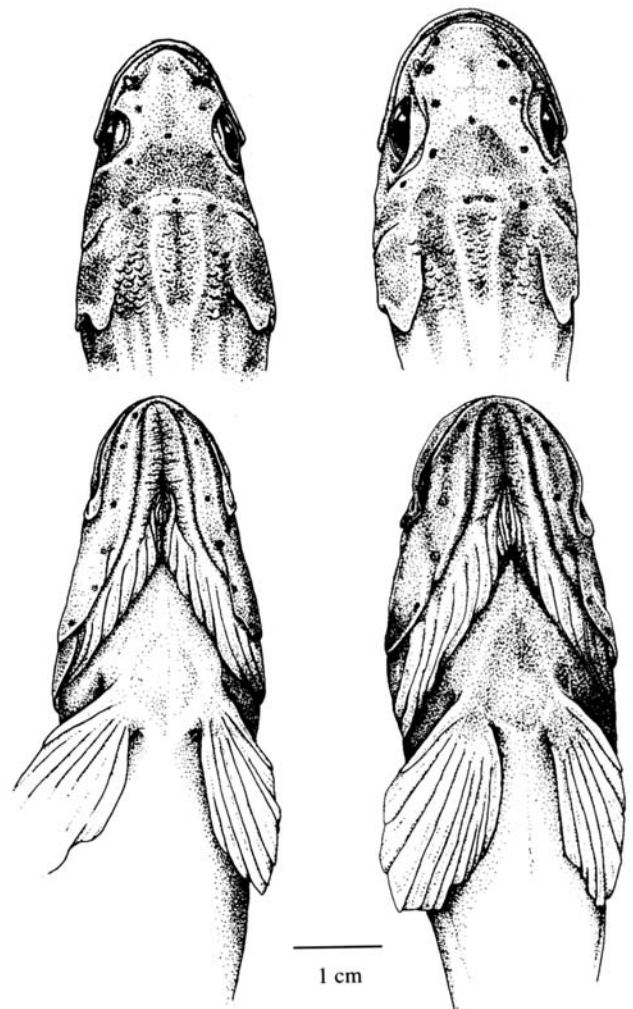
In McMurdo Sound *T. newnesi* was phenotypically plastic (Figs 2 & 3), consisting of the typical morph and a large mouth/broad headed morph in the ratio 48/19. We use the term “typical morph” to indicate that this morph was identical to the illustrated holotype of *T. newnesi* (Boulenger 1902, plate XI), and considered this morph as the form of *T. newnesi* described by Boulenger. The large mouth morph also keyed out as *T. newnesi* (Fischer & Hureau 1985, DeWitt *et al.* 1990), but was easily distinguished from the typical morph in a side-by-side comparison (Figs 2 & 3).

Collected over a period of four years, all of our samples contained representatives of both morphs. The two morphs did not differ in meristic and trophic characters but the sample of large mouth morphs was significantly larger in total length and in weight than the typical morph (Table II). However, the large mouth morphology was not simply a size or age related change as specimens of this morph were distinct and separable by eye over the full size range of the sample (large mouth morphs were 116–239 mm SL;

27–258 g). For example, the specimen in Figs 2, 3 is a small sized example (136 mm SL) of the large mouth morph. All specimens in the samples could be assigned to one of the two morphs by inspection of four profiles (Figs 2 & 3) of head shape and relative width, and by size and position of the mouth. Dorsal and ventral views of head shape were especially important characters in separating the morphs – the head was wide and U-shaped in the large mouth morph and more tapered and V-shaped in the typical morph (Fig. 3). Although intermediate morphs were not apparent, some smaller specimens (<125 mm SL) of the typical morph resembled the large mouth morph in lateral view. They did not, however, possess a U-shaped head or the colouration of the large mouth morph. With a sex ratio of 16 males/2 females (Table I), the



**Fig. 2.** Comparison of anterior (top) and lateral (bottom) head and jaw morphology in similarly-sized morphs of *Trematomus newnesi* from McMurdo Sound. Typical morph on left and large mouth morph on right. Indication of darker pigmentation pattern in large mouth morph also illustrated. The large mouth morph has nine instead of the expected 10 preopercular-mandibular pores, but this is within the normal range of variation for *T. newnesi*. Difference in pupil diameter is artifactual. Typical morph is a female measuring 137 mm SL and weighing 47.5 g. The large mouth morph is a male measuring 136 mm SL and weighing 42.7 g. Specimens were collected from the same ice hole near Inaccessible Island on 27–29 October 1995. x 0.9 (top) and x 0.7 (bottom).



**Fig. 3.** Comparison of dorsal (top) and ventral (bottom) head morphology in similarly-sized morphs of *Trematomus newnesi*. Typical morph on left and large mouth morph on right. Same specimens as in Fig. 2. The large mouth morph has four instead of the expected three supratemporal pores, but this is within the normal range of variation for *T. newnesi*. x 1.0.

sample of the large mouth morphs was significantly different from unity ( $\chi^2$ ,  $c^2 = 10.89$ ,  $df = 1$ ,  $P < 0.001$ ).

The position of the posterior margin of the maxilla relative to the eye was also important in distinguishing the two morphs (Fig. 2). In 94% of specimens of the large mouth morph, the maxilla projected posterior to the middle of the eye (or pupil). More specifically, in 61% of specimens the maxilla projected to the posterior margin of the pupil, and in 33% of specimens it projected past this point into the posterior one-quarter of the eye. In the typical morph, this landmark fell in the middle of the eye (or pupil) in 68% of specimens, at the posterior margin of the pupil in 26% and in the anterior one-third of the eye in 6%. In his original description of *T. newnesi*, Boulenger (1902, p. 177) also noted variability in this character.

Upper and lower jaws were more heavily ossified in the large mouth morph. For example, in a comparison of two individuals of the same length, the dentaries were 31% heavier in the large mouth morph (SL = 164 mm, Wt. = 73.5 g) than in the typical morph (SL = 163 mm, Wt. = 109.4 g). In addition, the gape angle of the closed mouth was at a greater angle from the horizontal (*i.e.*, more vertical) in the large mouth morph than in the typical morph (Fig. 2).

There were also statistically significant morphometric differences between the two morphs. Nine of 14 morphometric measurements were significantly greater in the large mouth morph (Table IV). The large mouth morph had a longer, deeper and wider head, larger gape and upper jaw, longer pelvic fins and a deeper caudal peduncle. These differences were also reflected in relative proportions, with significant differences in jaw and snout length and body depth, and a nearly significant difference in caudal peduncle depth (Table V). Although relative gape width and upper jaw length did not scale isometrically with head length, they were useful measures of trophic morphology and separated the morphs in nearly bimodal fashion (Fig. 4). Some of the scatter in the histogram for gape width was attributable to fixation artifact.

A number of other trophic, sensory and osteological structures were dissected without finding any differences between the two morphs. For example, the pattern of intestinal coiling, the length of the gill rakers and the size and appearance of the teeth in the jaws and in the upper and lower pharyngeal tooth plates were similar. Furthermore, there were no differences in absolute or relative lengths of the stomach or intestine (Tables IV & V). The colour of the parietal peritoneum ranged from black to light gray in both morphs; dark grey was the most common colour. Both morphs also lacked an ocular rete mirabile, possessed a similar degree of dark pigmentation in the meninges around the spinal cord and had identical gross brain morphology. There was no difference in the size of the notochordal foramen (20–25% of centrum diameter in 163–164 mm SL specimens) in the vertebral centrum or in the number and degree of fusion of elements in the caudal skeleton.

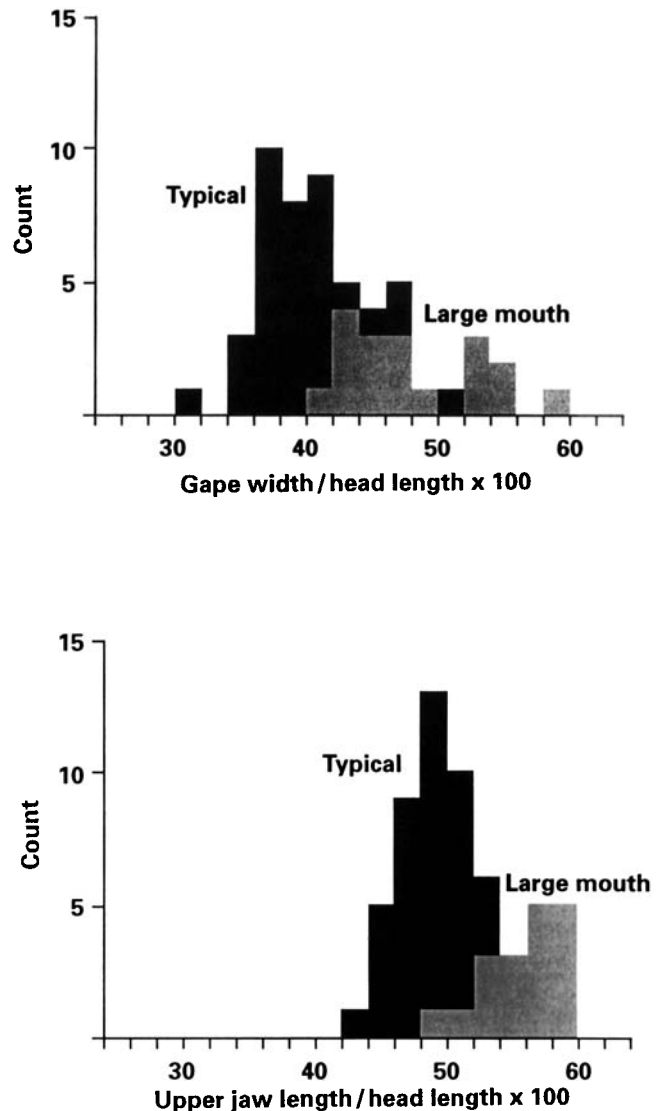


Fig. 4. Histograms showing bimodal distribution of relative measurements for gape width and upper jaw length in the typical (black) and large mouth (grey) morphs. Vertical lines above histograms are means; horizontal lines are 95% confidence intervals.

The pores of the cephalic lateral line system were larger in the large mouth morph (Figs 2 & 3), a consequence of the positive allometry in head width (= body width) and in head depth relative to standard length. The pattern of the cephalic lateral line in the large mouth morph conformed to that described for *T. newnesi* (Jakubowski 1970, Andersen 1984, DeWitt *et al* 1990). The canals were complete without divisions or reductions. In a sample of 16 specimens of the large mouth morph, the supraorbital canal invariably had four pores, the temporal canal had five pores and the coronal commissure had one pore. Some variation was encountered in the other components of the cephalic lateral line, but within the range of variation encompassing *T. newnesi*. The infraorbital canal had seven pores (or eight in 19% of the sample), the preopercular-mandibular canal had 10 pores (or

nine in 31%), and the supratemporal canal had three pores (or four in 25%).

Finally, the background colour of the large mouth morph was darker, with more uniform pigmentation and less mottling than the typical morph (Figs 2 & 3). This was especially marked along the ventral margin of the body – the large mouth morph was more darkly pigmented over the cheeks, opercles, posterior portions of upper and lower jaws, pelvic girdle and fins and near the origin of anal fin.

#### *Morphs of Trematomus newnesi in other Antarctic localities*

To determine whether or not the large mouth morph was found outside McMurdo Sound, all cataloged specimens of *T. newnesi* at the Smithsonian Institution (USNM), Washington, DC were examined. This material consisted of 12 collections totaling 26 specimens, of which two collections contained representatives of the large mouth morph. One of the three specimens in USNM 197680 was a large mouth morph. The specimen was a 165 mm SL female collected in 1956 in Robertson Bay (71°25'S, 177°00'E), Cape Adare. In USNM 50563, one of five specimens was a large mouth morph. This 127 mm SL specimen was collected in 1899 at Duke of York Island (71°38'S, 170°04'E), Cape Adare by members of the Southern Cross Expedition. The viscera were too soft to allow determination of sex.

#### Discussion

The *T. newnesi* from McMurdo Sound includes the largest reported individuals of the species. The coefficient and exponent for the power function of the length–weight relationship are closer to values for similarly sized *T. bernacchii* from Terra Nova Bay (La Mesa *et al.* 1996) than to values for smaller *T. newnesi* captured near the tip of the Antarctic Peninsula (Radtke *et al.* 1989). The exponent (3.9) reported by Radtke *et al.* is unusually large and, if accurate, suggests that in this population weight is increasing at a much greater rate than that required to maintain constant body proportions. This may be a reflection of greater food availability in the vicinity of the Antarctic Peninsula compared with McMurdo Sound.

As is also true for specimens from Terre Adélie (66°40'S, 140°01'E) and the Vestfold Hills region (68°33'S, 78°15'E), *T. newnesi* in McMurdo Sound is most common in water less than 20 m deep (Hureau 1962, Williams 1988). However, at Terra Nova Bay (74°50'S, 164°30'E), about 235 km north of McMurdo, *T. newnesi* schools at depths of 92 m (Vacchi & La Mesa 1995). The diet of the McMurdo population consists of *Euphausia crystallorophias* and fish, but does not include a large component of cannibalism as is true for *T. newnesi* in Terra Nova Bay (Vacchi & La Mesa 1995). Little is known about the biology of *T. newnesi* in the high latitude waters of the Weddell Sea (Kock *et al.* 1984, Ekau 1990).

The data allow rejection of the null hypothesis that *T. newnesi* is morphologically homogeneous and suggest instead that the population in McMurdo Sound includes two distinct morphs. Proportional measurements and colouration, suggest that the large mouth morph leads a more benthic existence than the typical semipelagic morph. With a blunt head and less streamlined more depressed body, the large mouth morph possesses characters typically associated with benthic morphs in other phenotypically plastic fish (Skúlason & Smith 1995, p. 367). In shallow areas free of anchor ice the large mouth morph of *T. newnesi* may live on the bottom as an ambush predator on both benthic and water column organisms. The large mouth and head allow the consumption of larger prey as well as a wider variety of prey. The typical *T. newnesi* morph schools and feeds predominantly in the water column.

Although their morphology implies niche diversification, field observations and information on stomach contents from this small sample do not substantiate differences in habitat or diet between the two morphs. Both morphs we caught at the same localities and times. Without documentation of habitat or dietary differences between the two morphs and without experimental demonstration that large mouth/blunt head morphology is a response to a different diet, we cannot state that these morphs of *T. newnesi* are a documented example of habitat or trophic induced phenotypic plasticity.

The large mouth/blunt head morphology could have a developmental basis since the large mouth morph becomes more distinctive with increasing body size. Study of small specimens will be necessary to determine whether allometric growth is involved in producing the large mouth morph and at what stage of development this morphology becomes evident. Heterochronic processes involving changes in the timing of developmental events are suspected to have played a role in the divergence of some nototheniid species (Balushkin 1984, p. 127–128), sometimes beginning in larval life (Klingenberg & Ekau 1996). However, changes can also begin in the juvenile stage, or even later. In trophically polymorphic pumpkinseed sunfish, the positive allometry in the pharyngeal apparatus is not manifest until 40–80 mm SL (Wainwright *et al.* 1991).

Although the McMurdo sample of the large mouth morph is dominated by males, the inclusion of two females indicates that the differences between the morphs are not attributable to sexual dimorphism. This was further supported by the female specimen of the large mouth morph from Cape Adare (USNM 197680).

It is possible that the large mouth morph is a cryptic or sibling species, a valid species exhibiting only slight morphological divergence from *T. newnesi*. Decoupling of morphological and ecological divergence may lead to the formation of sibling species, now recognized as more common than previously suspected (Knowlton 1993). We prefer a conservative taxonomic approach and are not convinced that there are sufficient grounds for recognition of a new species.



We have therefore interpreted the variation within *T. newnesi* as an example of phenotypic plasticity, which does not imply the existence of underlying genetic variation. Since we lack data on whether the large mouth morph is reproductively isolated and exhibits genetic differentiation, we cannot fully evaluate its potential as a biological species.

Dunbar (1968) suggested that the relatively high incidence of phenotypic plasticity (or morphism) among Arctic and subarctic marine organisms was evidence of continuing development within relatively young high latitude ecosystems. Phenotypic plasticity is now known to be geographically widespread, with many good examples of morphs among various lineages of fishes from temperate and boreal freshwater habitats. Most exhibit phenotypic plasticity in trophic morphology, sometimes without genetic divergence. Differences among the morphs of these freshwater species are of a magnitude similar to that displayed by morphs of *T. newnesi*. Lacustrine species containing trophic morphs include the cichlids *Cichlasoma minckleyi* from Cuatro Ciénegas, Mexico (Sage & Selander 1975, Kornfield *et al.* 1982, Liem & Kaufman 1984) and *Cichlasoma managuense* from Nicaragua (Meyer 1987), the characoid *Saccodon* from Central and South America (Roberts 1974), the goodeid *Ilyodon* from Mexico (Turner & Grosse 1980), the centrarchid *Lepomis gibbosus* from North America (Wainwright *et al.* 1991, Robinson *et al.* 1993) and the Arctic char (*Salvelinus alpinus*) from Lake Thingvallavatn (64°N), Iceland (Jonsson *et al.* 1988, Skúlason *et al.* 1989). Heterochrony has been suggested as the mechanism responsible for the formation of trophic morphs in *S. alpinus* (Balon 1984, Meyer 1987, Skúlason *et al.* 1989).

At first glance lakes appear to share few biological characteristics with the polar marine environment. However, reduced competition associated with a low diversity fish fauna may be a common factor in the origin of morphs in both lacustrine fishes and in *T. newnesi*. For example, the Arctic char, *Salvelinus alpinus*, resembles *T. newnesi* in having a high latitude circumpolar distribution. The population in Lake Hazen (82°N), Ellesmere Island, Northwest Territories is perhaps the most northerly of any freshwater species (Nelson 1994, p. 192). This species has repeatedly diversified into benthic and limnetic morphs in postglacial Arctic and boreal lakes with few fishes (Skúlason & Smith 1995). Trophic and morphological diversification predominate in species-poor fish communities, suggesting that the absence of competition allows niche expansion (Robinson & Wilson 1994, p. 604).

Notothenioids are unusual among marine fishes in their ecological and morphological diversity and in their dominance of shelf and upper slope habitats within their range. The suborder and the family Nototheniidae are adaptive radiations of about 120 and 50 species, respectively (Eastman 1993, Clarke & Johnston 1996, Klingenberg & Ekau 1996). The shelf and upper slope of the Southern Ocean support only 174 species of fishes, and about 55% of these are notothenioids

(Gon & Heemstra 1990, Eastman 1993). In the shallow (20–50 m) waters at the highest latitudes, exemplified by McMurdo Sound (78°S), diversity is further reduced. Here non-notothenioids are absent and notothenioids are few, mostly trematomids (*Trematomus newnesi*, *T. bernacchii*, *T. nicolai*, *T. hansonii* and *T. pennellii*) and the bathydraconid *Gymnodraco acuticeps* (Eastman & DeVries 1982). The phenotypic plasticity in *T. newnesi* is a small scale radiation within the larger diversifications of notothenioids and nototheniids. It implies that, at the highest latitudes, shallow inshore waters are underutilized by trematomids. This is also the first reported example, in any marine fish species, of the recognition of a morph based on gross morphology rather than on meristic counts.

### Acknowledgements

We thank Jocelyn Turnbull and Mike Kuiper for their efforts in fishing. Susan Jewett was most helpful during a visit to the Division of Fishes at the Smithsonian Institution. We are grateful to Danette Pratt for applying her talents to Figs 1–4. We also thank Erik Eastman for assistance in the lab. The manuscript benefited from conversations with Michael J. Lannoo and from the reviews of Ofer Gon and Jean-Claude Hureau. This work was supported by National Science Foundation grants OPP 94-16870 to JTE and OPP 93-17629 to ALD.

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