

# Geographic intraspecific variation in buoyancy within Antarctic notothenioid fishes

THOMAS J. NEAR<sup>1</sup>, CHRISTOPHER D. JONES<sup>2</sup> and JOSEPH T. EASTMAN<sup>3\*</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology and Peabody Museum of Natural History, Yale University, New Haven, CT 06520-8105, USA

<sup>2</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA

<sup>3</sup>Department of Biomedical Sciences, Ohio University, Athens, OH 45701-2979, USA

\*corresponding author: eastman@ohiou.edu

**Abstract:** We investigated intraspecific geographic variation in buoyancy by obtaining percentage buoyancy (%B) measurements for the Antarctic notothenioid species *Pleuragramma antarcticum*, *Trematomus hansonii*, *T. bernacchii* and *Gymnodraco acuticeps* from both McMurdo Sound in East Antarctica and the South Shetland Islands in West Antarctica. Mean percentage buoyancies in these species ranged from 0.22–0.52% in the neutrally buoyant *P. antarcticum* to 3.34–3.67% in the benthic *T. bernacchii*. Dispersion (1 standard deviation) of percentage buoyancy (%B) values around the mean was  $\pm 0.2$ – $0.5$  %B units for the entire sample. Although intraspecific differences in mean percentage buoyancy were statistically significant ( $P < 0.05$ ) in *P. antarcticum* and *T. hansonii*, we consider these differences as normal variation without substantive biological significance. The dispersion in buoyancy measurements during adult life reflects the density of the fish and this may be influenced, in both the short- and long-term, by gut contents, nutritional condition, and reproductive state. Mitigation of the effects of these variables is not biologically realistic because they constitute normal aspects of the daily and yearly life cycles. The results of our measurements of buoyancy are consistent with what is known about the ecology of these four species and this is considered in the discussion.

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**Key words:** *Gymnodraco*, ontogenetic variation, *Pleuragramma*, *Trematomus*

## Introduction

Differential use of benthic and water column habitats is a major axis of diversification in the adaptive radiation of notothenioid fishes (Eastman & DeVries 1982, Eastman 1993, Eastman & McCune 2000), and the divergent buoyancies of various species reflect occupation of these habitats (Eastman 1993, Eastman & Sidell 2002). Since all notothenioids lack a swim bladder, buoyancy modification is accomplished through reduction of skeletal ossification and/or deposition of lipids as a source of static lift. Measurements of buoyancy are expressed as percentage (or relative) buoyancy (%B), calculated as weight in water/weight in air  $\times 100$ . The range of interspecific variation in this measurement among notothenioids encompasses neutrally buoyant species with no weight in water (%B  $\approx 0$ ) as well as heavy benthic species (%B  $\approx 6.0$ ) (Eastman 1993). Most notothenioids, however, are intermediate between these two extremes (Eastman & DeVries 1982, Eastman & Sidell 2002) and the ancestral benthic habitat is retained by most species (Eastman 1993).

It has been assumed that measurements of buoyancy exhibit sufficiently small levels of intraspecific variation to reliably characterize the ecology of various notothenioid species or species groups. However, there has been no

examination of the magnitude of geographic intraspecific variation in buoyancy in any species. There is a noteworthy example of ontogenetic variation in buoyancy involving the large Antarctic toothfish *Dissostichus mawsoni*. Juveniles of this species (standard length (SL) = 189 mm) are heavy (%B = 5.3), subadults (SL = 200–500 mm) are intermediate (%B = 3–4%) and adults (SL > 800 mm) are neutrally buoyant (Near *et al.* 2003). Such a dramatic change in percentage buoyancy is probably atypical in notothenioids. Nothing is known about the buoyancies of larvae or newly settled juveniles in any notothenioid species. Buoyancy measurements to date have been made on species from single localities - either McMurdo Sound (Eastman & DeVries 1981, 1982) or the South Shetland Islands (Eastman & Sidell 2002). Since the majority of notothenioids have a circum-Antarctic distribution (Gon & Heemstra 1990), there are communities across many shelf areas of the Southern Ocean that share some of the same species. Thus these repeated communities around Antarctica offer the opportunity to examine geographic intraspecific variation in buoyancy in order to better understand this key aspect of notothenioid biology that, with respect to ecology, is the hallmark of the notothenioid radiation.

**Table I.** Summary of data and comparison of measurements of buoyancy for total sample by geographic region. SL = range of standard length measurements in mm (and mean, \* if significant), N = number of specimens, %B = mean percentage buoyancy, SD = standard deviation, SEM = standard error of the mean. Results of *t*-tests for each species are at bottom of table. Significant *P*-value (<0.05) is indicated with an asterisk.

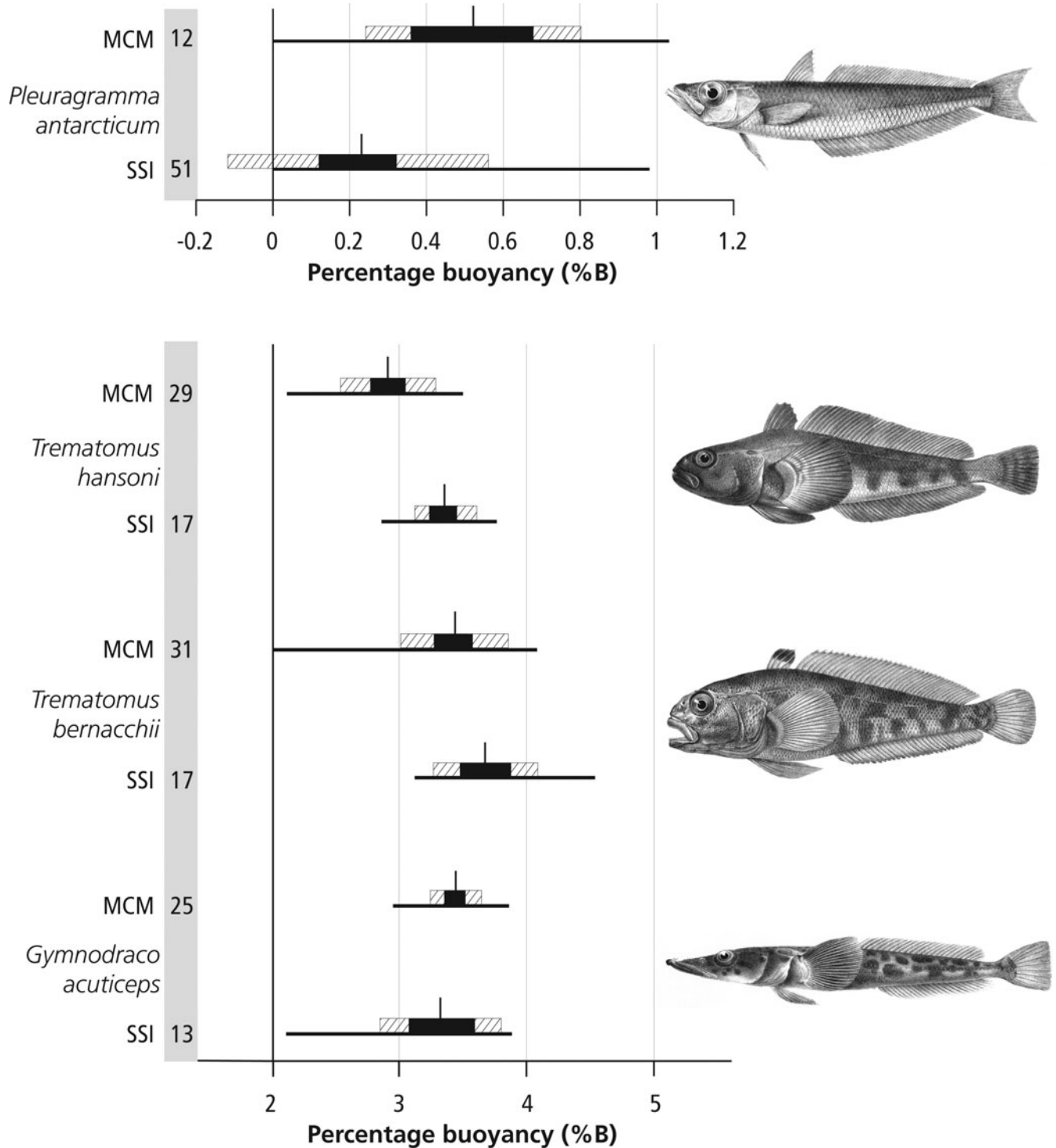
	<i>Pleuragramma antarcticum</i>	<i>Trematomus hansonii</i>	<i>Trematomus bernacchii</i>	<i>Gymnodraco acuticeps</i>
McMurdo Sound				
SL (mean)	82–167 (138)	107–255 (186)	90–221 (151)	204–280 (228)
N	12	29	31	25
%B	0.52	2.91	3.43	3.41
SD	0.277	0.383	0.414	0.204
SEM	0.080	0.071	0.074	0.041
South Shetland Islands				
SL (mean)	107–212 (150)	155–366 (233*)	202–298 (242*)	168–314 (245)
N	51	17	17	13
%B	0.22	3.35	3.67	3.32
SD	0.344	0.237	0.415	0.468
SEM	0.048	0.057	0.101	0.130
<i>t</i> -value	2.824	-4.863	-1.855	0.715
df	61	44	46	14
<i>P</i> -value	0.004*	0.00002*	0.087	0.422

In this paper we present results from a comparison of buoyancy measurements among populations of four notothenioid species sampled at McMurdo Sound in East Antarctica and the South Shetland Islands in West Antarctica. We made these comparisons: 1) to determine if there is geographic intraspecific variation in buoyancy, and 2) to consider whether any documented variation is of substantive significance in the ecology of these species, particularly habitat use.

### Materials and methods

Specimens were collected in the southern Scotia Arc in March 2001 and 2003 and in February–March 2006. These collections were made in conjunction with demersal fish trawl surveys of the South Shetland Islands aboard the RV *Yuzhmorgeologiya*, expeditions conducted by the United States Antarctic Marine Living Resources Program. Specifics regarding fishing gear, primarily a commercial size bottom trawl, and sampling design have been previously reported (Kock & Jones 2002, Near *et al.* 2003, Flores *et al.* 2004). The data for the McMurdo Sound sample was the basis for other publications highlighting these populations (Eastman & DeVries 1981, 1982, Eastman 1993) with the exception that sample sizes were increased for the present study by including some previously excluded gravid specimens of *Trematomus bernacchii* and *T. hansonii*. There were no gravid specimens among our samples from the South Shetland Islands. Eastman & DeVries (1982) provide sampling locations and methods used for specimen collection at McMurdo Sound. These included baited bottom traps, fishing with a hook and line and, in the case of the neutrally buoyant *Pleuragramma antarcticum*, removal of specimens from the stomachs of *Dissostichus mawsoni* Norman, 1937 captured on a set line at 300–500 m.

We targeted four species from major notothenioid clades for comparison, the bathydraconid *Gymnodraco acuticeps* Boulenger, 1902 and the nototheniids *Pleuragramma antarcticum* Boulenger, 1902, *Trematomus bernacchii* Boulenger, 1902 and *Trematomus hansonii* Boulenger, 1902. We made buoyancy and standard length (SL) measurements on freshly captured specimens using previously described methods (Eastman & DeVries 1982, Eastman & Sidell 2002, Near *et al.* 2003). Briefly, this involves weighing heavily anaesthetized fish in air and then in seawater at ambient temperature. To weigh fish in water, we attached a light rod to the balance pan with adhesive clips and tied a line with a barbless hook to the other end of the rod. This apparatus projected off the side of the balance and over an insulated water container. We obtained weight in water by hooking the fish through the lower jaw, lowering it into the container, removing air from oral and branchial cavities and taking the weight when the balance display stabilized. The sample (Table I) consists of 98 specimens from the South Shetland Islands (water temperature = 0–2°C) and 97 specimens from McMurdo Sound (water temperature = -1.9°C). The differences in water temperature are of no consequence because changes in the density of seawater between 0°C and 5°C are < 0.1%. Some notothenioids, including *P. antarcticum*, use neutral lipids as a source of static lift; changes in ambient pressure with depth have relatively little effect on these substances (Bone & Moore 2008, p. 103). Furthermore, errors in buoyancy measurements attributable to changes in salinity, temperature and pressure are small, totalling only about + 0.15% of the weight of fish in air (Corner *et al.* 1969), and usually disregarded (Denton & Marshall 1958). Weights for McMurdo specimens were made in an onshore laboratory with an electronic balance whereas those for South Shetland specimens were taken aboard ship with a mechanical balance. These differences in methodology reflect the reality of Antarctic field research in that buoyancy



**Fig. 1.** Dice-Leraas diagram (modification of Hubbs & Hubbs 1953) showing comparison of measurements of buoyancy for samples of four species from McMurdo Sound (MCM) and the South Shetlands Islands (SSI). Shaded column following locality provides sample size. Heavy horizontal line is the range, short vertical line is the mean, rectangle shows 1 SD on each side of the mean with black portion indicating  $\pm 2$  SEM. For sample sizes  $> 30$ , 2 SEM approximates the 95% confidence limits for the mean (Sokal & Rohlf 1981, p. 152). Therefore when black rectangles overlap, interspecific differences among measurements of buoyancy are not significant. Fish drawings from Boulenger (1902).

measurements now need to be made aboard ship because most species found in the proximity of near shore research stations have been studied.

Prior to statistical analysis we transformed the buoyancy data to natural logarithms (ln) to correct for inequality of variances. Because many of the buoyancy values for *Pleuragramma antarcticum* were 0, we added 0.5 to all values and transformed them to square roots (Sokal & Rohlf 1981, p. 423). Buoyancy values in Table I are untransformed with the 0.5 factor removed, but reported levels of significance are for ln- or square root-transformed data. We performed *F*-tests to ensure that variances between samples were equal and then utilized descriptive statistics and two-sample *t*-tests to summarize and compare measurements of size (standard length) and buoyancy between the McMurdo and South Shetland populations. For each species we tested the null hypotheses that there is no difference in the mean SL and mean percentage buoyancy between McMurdo and South Shetland populations. To determine whether or not there were ontogenetic changes in buoyancy, we used a general linear model to conduct an analysis of covariance for the relationship between mean buoyancy and standard length (the covariate).

## Results

Table 1 provides mean values and descriptive statistics for buoyancy measurements from 195 specimens arranged by species and geographic region. The Dice-Leraas diagram in Fig. 1 shows the distribution of buoyancy measurements and facilitates comparison of the paired samples. Samples showed some departures from normality, common in analyses of morphological data (Simpson *et al.* 1960), with left skewing in *T. bernacchii* from McMurdo and *G. acuticeps* from the South Shetland Islands, and right skewing in *P. antarcticum* from the South Shetlands. When rounded to one decimal place, dispersion (1 standard deviation) of percentage buoyancy values around the mean was  $\pm 0.2$ – $0.5$  %B units for the entire sample. In comparisons of means, two-sample *t*-tests indicated that the mean percentage buoyancy was significantly different between samples of *Pleuragramma antarcticum* and *T. hansonii* from the two localities (Table I). Whether this significance is biologically meaningful is considered below in the discussion.

The South Shetlands samples had larger mean standard lengths and larger size ranges of specimens for all four species (Table I), but two-sample *t*-tests indicated that only the samples of *Trematomus bernacchii* and *T. hansonii* were significantly larger than the McMurdo samples. Bivariate plots of percentage buoyancy against standard length for each of the eight samples (not shown) indicate slight to moderate ontogenetic increases in buoyancy (lower %B) in all species except *G. acuticeps* where buoyancy decreases (higher %B) with standard length. Since we sought to

**Table II.** Analysis of covariance for the relationship between percentage buoyancy and standard length for total sample of each species examined. Significant *P*-values ( $<0.05$ ) indicated with an asterisk.

Species	$r^2$	df	Y-intercept	Slope	<i>P</i> -value
<i>Pleuragramma antarcticum</i>	0.182	61	0.664	-0.003	0.0005*
<i>Trematomus hansonii</i>	0.007	44	2.944	0.001	0.572
<i>Trematomus bernacchii</i>	0.066	46	3.805	-0.002	0.078
<i>Gymnodraco acuticeps</i>	0.210	36	2.216	0.005	0.004*

determine whether these ontogenetic changes were significant, we pooled the data for the two localities for each species and used this in an analysis of covariance with standard length as the covariate. Although the size range of specimens for this analysis was somewhat restricted, the relationship of percentage buoyancy to standard length was significant for *P. antarcticum* and *G. acuticeps* (Table II). Similar to the pattern observed in all other notothenioids studied to date (Eastman & Sidell 2002, Near *et al.* 2003), buoyancy increased with standard length in *P. antarcticum*, but decreased with standard length in *G. acuticeps* (Table II, negative and positive values for slopes, respectively).

## Discussion

### Overview of intraspecific variation in buoyancy

In our intraspecific comparisons of buoyancy measurements from geographically separated samples of four notothenioid species, mean buoyancies were statistically significant in *P. antarcticum* and *T. hansonii*, although we consider these differences as normal biological variation without substantive significance. Buoyancy measurements of  $\pm 1$  standard deviation around the mean encompass the majority ( $\approx 68\%$ , Sokal & Rohlf 1981, p. 102) of the sample. Including data from this and previously published papers, the standard deviations for percentage buoyancy measurements from 23 adequate ( $N \geq 7$ ) samples are  $\pm 0.2$ – $0.6$  %B units, with a modal value of  $\pm 0.4$  %B units. It should not be surprising that there is dispersion in these measurements during adult life because the percentage buoyancy reflects the density of the fish and this may be influenced, in both the short- and long-term, by gut contents, nutritional condition, and reproductive state. Mitigation of the effects of these variables is not biologically realistic because they constitute normal aspects of the daily and yearly life cycles. Furthermore, the influence of these variables may actually be less than expected - reproductive status in particular has been shown to be of little consequence. Sexual dimorphism in percentage buoyancy has been shown to be unusual in notothenioids (Eastman & Sidell 2002). Furthermore, removal of the gonads did not affect percentage buoyancy in the oyster toadfish *Opsanus tau* (Fine *et al.* 1995) and in

zebrafish, *Danio rerio*, gravid and nongravid fish had the same mean densities (Robertson *et al.* 2008). As Fine *et al.* (1995) note, in a negatively buoyant benthic fish spending most of its time on the substrate, as is the case in three of our four species, there is minimal selective advantage for precise control of buoyancy.

Ontogenetic change in percentage buoyancy (a lower %B with growth as measured by weight or length) is another factor contributing to intraspecific variation in this measurement. A size effect on percentage buoyancy in notothenioids is generally detectable if buoyancies are obtained from a sufficiently large size range of the specimens. For example, the effect of weight on buoyancy has been documented in large samples of some nototheniids and channichthyids. In four species with percentage buoyancies of 3–5% and spanning a 3–5-fold range of body weights, there is about a 1% decrease in percentage buoyancy with increasing weight (Eastman & Sidell 2002). The most striking example of an ontogenetic decrease among notothenioids is seen in the large neutrally buoyant nototheniid *Dissostichus mawsoni* where percentage buoyancy falls from 4% in 25 cm SL juveniles to 0% in  $\geq 81$  cm SL adults (Near *et al.* 2003).

The decline in percentage buoyancy with size is probably attributable to the nature of fish growth. Changes in weight are relatively greater than changes in length given the approximately cubic ( $W = aL^3$ ) relationship between length and weight (Busacker *et al.* 1990). Moreover, increasing weight represents growth of relatively low-density muscle and viscera with its contained lipid whereas increase in length represents growth of high-density skeletal tissues (Donaldson *et al.* 1979). Furthermore, the skeleton in teleosts, unlike that in terrestrial vertebrates, comprises a constant (rather than increasing) proportion of the body weight regardless of the size of the individual (Reynolds & Karlotski 1977).

The unexpected finding of an ontogenetic increase in percentage buoyancy in *Gymnodraco acuticeps* may reflect the fact that this species has a notably different shape, with relatively more bone and less soft tissue, than the typical nototheniid (Fig. 1). The head is long and wide and the trunk is narrow with a relatively small amount of muscle. However, the size range of specimens in our sample is only 2-fold and our result should be regarded as provisional.

#### Buoyancy and ecology - *Pleuragramma antarcticum*

The neutrally buoyant *Pleuragramma antarcticum* is the most specialized of the notothenioids for pelagic life as its entire life cycle, including egg and larval stages (Vacchi *et al.* 2004), is confined to the water column or platelet ice. While usually considered neutrally buoyant, its measured percentage buoyancy is 0–1% with means of 0.2–0.5%. There are disadvantages of having no weight in water including the tendency to rise in the water column and

instability or maneuverability problems when motionless, drifting in currents or coasting. Thus fish living in the water column, including *Pleuragramma*, are frequently negatively buoyant (Davenport 1999), with percentage buoyancies somewhat  $>0\%$ .

Our South Shetlands sample of *Pleuragramma* was significantly more buoyant (lower %B) than the McMurdo sample, reflecting the fact that 32 of 51 specimens from this sample had a %B of 0. Although these specimens were not significantly larger than the McMurdo specimens (Table I), they were captured in the summer (versus early spring for McMurdo) and this is probably associated with better condition and a higher lipid content. Although this difference in buoyancy is statistically significant, as noted previously, we regard these small differences in buoyancy as normal variation associated with the life cycle and therefore of little biological consequence.

*Pleuragramma antarcticum* is one of the most lipid-rich notothenioids (Friedrich & Hagen 1994, Hagen *et al.* 2000) and has become a textbook example of the utilization of triacylglycerols as a source of static lift for buoyancy (Bone & Moore 2008, pp. 105–106). The lipid is stored in large sacs and these sequestered lipids are hypothesized to be unavailable for metabolism (DeVries & Eastman 1978, Eastman & DeVries 1989), although *Pleuragramma* also has other lipid stored in typical adipose tissue that may be metabolically labile. There has been no experimental study of energetic use of lipid from either tissue. It has been observed, however, that juvenile *Pleuragramma* (SL = 29–115 mm) exhibit a pronounced ontogenetic lipid accumulation during the winter and maintain a stable amount of lipid according to size, suggesting that they were able to maintain condition by feeding rather than utilizing stored lipids (Hubold & Hagen 1997). Lipid content is also proportionally higher in adult versus juvenile specimens (Friedrich & Hagen 1994), indicating that an ontogenetic change in lipid content could reflect an unobserved change in buoyancy with age in this species. Unfortunately measurements of buoyancy were not performed on these specimens. As mentioned above, this probably accounts for some of the differences between our samples of this species.

#### Buoyancy and ecology - *Trematomus hansonii* and *T. bernacchii*

Both *T. hansonii* and *bernacchii* are benthic species, and at McMurdo Sound both exhibit similar depth preferences (Eastman & DeVries 1982). At 2.9–3.7%, mean percentage buoyancies of our four samples span a wider range (especially at the low end) than might be expected in benthic species. However, as Webb (1990) notes, higher tissue densities (leading to a greater percentage buoyancy) are not always desirable because aspects of a species behavior or life cycle may involve periods of time in the

water column. This is especially true in the case of *T. hansonii*. At both McMurdo Sound and the South Shetland Islands *T. hansonii* is more buoyant than *T. bernacchii*, and the magnitude of the difference between these species is nearly identical in both of the sampled areas (Table I; Fig. 1). There is ample evidence that the greater buoyancy in *T. hansonii* reflects behavioural and ecological differences involving water column activities. For example, when compared to *T. bernacchii*, *T. hansonii* shows more spontaneous swimming activity when kept in captivity (Eastman 1993) and takes more prey from the water column (Montgomery *et al.* 1993, Foster & Montgomery 1993). In the Ross Sea *Trematomus bernacchii* is a generalized benthic feeder on infaunal and epifaunal polychaetes, amphipods and molluscs (Vacchi *et al.* 1994, La Mesa *et al.* 2004) whereas in this same locality *T. hansonii* is planktivorous on small copepods (Foster & Montgomery 1993) or piscivorous on juvenile fish and eggs (La Mesa *et al.* 1997), and can be considered very plastic in its overall feeding behaviour (Pakhomov 1998a).

Unlike *Pleuragramma*, *T. hansonii* and *T. bernacchii* are not lipid-rich. Although *T. bernacchii* has 5–11% lipid (as %dry weight) in its skeleton, there is no significant contribution of lipid to buoyancy (i.e. the skeleton plus lipid is not positively buoyant) in either of these species sampled near Mawson Station in East Antarctica (Phleger *et al.* 1999).

#### Buoyancy and ecology - *Gymnodraco acuticeps*

*Gymnodraco acuticeps* leads a primarily benthic existence, including guarding of its eggs on the bottom (Evans *et al.* 2005). Since bathydraconids have a reduced ascending process on the premaxilla, jaw protrusion is limited (Iwami 1985, Balushkin & Voskoboinikova 1995) and they are less reliant on benthic food sources than are most of the phylogenetically basal notothenioid clades. The pointed jaws and large fang-like teeth of *G. acuticeps* are more suited to impaling swimming prey than for rooting on the bottom. Furthermore, its relatively low percentage buoyancy (3.3–3.4%), falls within the 3.1–3.7% range of channichthyids (Eastman & Sidell 2002), and reflects a preference for feeding in the water column. In McMurdo Sound *G. acuticeps* feeds primarily on water column fishes including *Pleuragramma antarcticum* and *Pagothenia borchgrevinkii* (Eastman 1985). In the Indian Ocean sector of the Southern Ocean, *G. acuticeps* consumes mostly mesopelagic myctophids (Pakhomov 1998b) and at the South Shetland Islands it eats primarily nototheniid fish (Takahashi & Iwami 1997).

During one of our cruises (Eastman & Lannoo 2003) we obtained video (viewable at <http://www.oucom.ohiou.edu/dbms-eastman/bathydraconid.htm>) showing a bathydraconid, probably *Bathydraco macrolepis*, holding position a few

metres off the bottom at a depth of 1200 m. It is headed into the current, with the trunk horizontal to the substrate and only the pectoral fins moving. If such hovering behaviour proves to be a common foraging strategy in some bathydraconids, it would explain lower than expected percentage buoyancy measurements.

In summary, we have detected statistically significant intraspecific differences in buoyancy for two of four notothenioid species sampled from two widely separated near-shore regions of Antarctica. However, these intraspecific differences are sufficiently small, a few tenths of a percent, such that they are of no biological significance as far as the ecology of these species is concerned. The water column of the Southern Ocean is a vast space that is seasonally productive but underutilized by fishes, and the evolutionary diversification in buoyancy within several notothenioid clades has produced species able to permanently or temporarily utilize these water column resources.

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