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Measurements of buoyancy for some Antarctic notothenioid fishes from the South Shetland Islands

Accepted: 2 May 2002 / Published online: 12 June 2002
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Abstract Buoyancy was measured for 258 specimens representing 13 species of adult and sub-adult nototheniids, bathydraconids, and channichthyids from the South Shetland Islands. Measurements were expressed as percentage buoyancy ($%B = W_{\text{water}}/W_{\text{air}} \times 10^2$). There were no neutrally buoyant species and mean values for $%B$ were 3.07–6.11%, with channichthyids at the low end and benthic nototheniids and bathydraconids at the high end. All species showed an ontogenetic decrease in $%B$ with increasing body weight. With the exception of *Champscephalus gunnari*, there was no sexual dimorphism in $%B$ within this sample. With some exceptions, values for $%B$ were consistent with life-history information. Sub-adult *Dissostichus mawsoni* were not neutrally buoyant, as are large adults. *Notothenia rossii* had a significantly lower $%B$ than closely related *N. coriiceps*. Benthic *Gobionotothen gibberifrons* had a lower $%B$ than semipelagic *Lepidonotothen larseni*. Although they exhibit some diversification in life history, the four channichthyids in the sample were similar in $%B$. Neutral buoyancy is rare in notothenioids and may be confined to a single nototheniid clade.

Introduction

Fish of the perciform suborder Notothenioidei dominate diversity, abundance and biomass in the subzero waters

of the Antarctic continental shelf. Here the 96 Antarctic species show an adaptive radiation (Eastman 1993, 2000; Clarke and Johnston 1996) and possibly form a species flock (Eastman and Clarke 1998; Eastman and McCune 2000). It has long been recognized that notothenioids, for example certain species of the family Channichthyidae, reside temporarily or seasonally in the water column and prey on krill (Regan 1913; Nybelin 1947; Olsen 1955; Kock 1985). Although notothenioids lack a swim bladder, this phyletic constraint was overcome by a suite of density-lowering modifications (Eastman and DeVries 1982), and subsequent diversification was keyed to the utilization of unfilled niches in the water column, especially pelagic or partially pelagic zooplanktivory and piscivory. With little competition from the sparse non-notothenioid fauna, notothenioids filled these niches, as well as remaining the dominant benthic group. While the acquisition of antifreeze glycopeptides was the key physiological innovation enabling notothenioids to inhabit ice-laden water (DeVries 1988; Cheng 1998), the ecological hallmark of the radiation was the evolutionary alteration of buoyancy and the morphological diversification associated with filling most available niches on the Antarctic shelf.

In the large and diverse family Nototheniidae, about one-half of the 33 Antarctic species temporarily or permanently inhabit the water column, rather than the ancestral benthic habitat (Eastman 1993). The family exhibits a variety of life-history or ecomorphological types, ranging from benthic species with percentage buoyancies of 2.9–4.4%, to cryopelagic, semipelagic and epibenthic (benthopelagic) species with reduced weight (2.3–2.8%), to a few pelagic species with near neutral (0–0.6%) buoyancy (Eastman and DeVries 1982). Ekau's (1991) morphometric analysis ranked many of these species on a benthic-pelagic scale and validated the ecomorphological designations for these nototheniids. Additional work indicated that pelagicism, the evolutionary tailoring of morphology for life in the water column, arose independently in different nototheniid clades (Klingenberg and Ekau 1996). However, a more

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recent cladogram (Balushkin 2000) unites the neutrally buoyant species in a single clade. The mechanism of density reduction involves lipid deposition and reduction of skeletal ossification (DeVries and Eastman 1978; Eastman and DeVries 1981), with heterochrony, specifically paedomorphy, likely important in the latter process (Voskoboinikova 1994, 2001; Voskoboinikova et al. 1994). Finally, the notothenioid diversification is noteworthy among fish radiations because, in addition to phyletic diversity, it also exhibits considerable morphological and ecological diversity (Brooks and McLennan 1991; Mayden 1992).

To date, only 14 notothenioid species have been measured for buoyancy, and 10 of these are nototheniids (DeVries and Eastman 1978; Eastman and DeVries 1981, 1982; Eastman 1993, 1999). In this study, we sought to enlarge the taxonomic base of buoyancy measurements, by including additional species such as icefishes of the family Channichthyidae. In this paper, we present measurements of buoyancy for 258 specimens, representing 13 species of nototheniids, bathydraconids and channichthyids, and examine the influence of body weight and sex on buoyancy.

Materials and methods

Collection and maintenance of specimens

We collected specimens during cruise 01–05 of the ARSV *Laurence M. Gould* (11 June to 16 July 2001) in the vicinity of the U.S. Palmer Station on Anvers Island in the South Shetland Islands. Our primary fishing site was in Dallmann Bay, Brabant Island (64°09–11'S, 62°44–46'W) at depths of 100–200 m. We used a 5.5-m otter trawl towed at a speed of 2.5–3 knots, with a bottom time of 20 min. We also deployed semi-conical commercial traps (pots) measuring 80 cm high and 200 cm in diameter, and consisting of a steel frame covered with mesh. A funnel entrance was located on the side. Traps were baited with pieces of fish, buoyed (including a flashing light and radar reflector) and left in place on the bottom for 12–36 h. They collected primarily *Notothenia coriiceps* and *N. rossii*. Water temperature at the fishing sites was –0.8 to –1.1°C.

In order to ensure a supply of specimens in good condition, we conducted four fishing trips from Palmer Station to Dallmann Bay during the period 15 June to 4 July. After capture, we maintained fish in circulating seawater tanks aboard ship for 1–3 days. They were subsequently transferred to circulating seawater tanks in the aquarium facility at Palmer Station. We held them for another 1–3 days before making measurements of buoyancy. During this period, water temperature in the aquarium facility was +0.5 to –0.1°C. We also made note of swimming activity while specimens were in captivity.

Nomenclature and measurements

Scientific nomenclature for notothenioids follows Gon and Heemstra (1990), with the emendation of Schneppenheim et al. (1994) concerning *Lepidonotothen*. For each specimen, we obtained total length (L_t), standard length (L_s), weight in air (W_{air}) and weight in seawater (W_{water}). We used a Mettler Toledo top-loading electronic balance (model PG2002-S) with a capacity of 2,100 g and accuracy of ± 0.01 g. To assess buoyancy, we weighed heavily anesthetized (200 mg l⁻¹ of ethyl 3-aminobenzoate methanesulfonate salt, MS-222) specimens in aquarium seawater at ambient

temperature. To weigh fish in water, we attached a 3.5-mm-diameter, 405-mm-long aluminum rod to the balance pan with adhesive cable clips. We tied a length of thread and a barbless hook to the end of the rod. This apparatus weighed 11 g and was tested for accuracy in transmitting load to the balance by suspending weights from the hook. The apparatus extended off the side of the balance and projected over a 50-cm-tall, 38-l insulated water container that held the fish. We obtained W_{water} by attaching the hook to the lower jaw, lowering the fish into the container, ensuring that the oral and opercular cavities were free of air bubbles, and taking the reading when the fish was motionless and the balance display had stabilized.

As in previous (Eastman and DeVries 1982) and comparable work (Fine et al. 1995), we expressed our measurements as percent (or relative) buoyancy (%B) – i.e., the percentage of the weight in air supported when in the water:

$$\% B = W_{WATER}/W_{AIR} \times 10^2$$

We also calculated a Fulton-type condition factor (Anderson and Gutreuter 1983) as an index of weight per unit length and as a proxy for body shape:

$$I_K = (W/L_T^3) \times 10^5$$

where W = body weight in grams and L_t = total length in millimeters. Larger values for I_K indicate greater weight per unit length associated with a thicker body. As another indicator of body shape and weight as a function of length, we used these same variables to compute a length-weight relationship for each species:

$$W = aL_T^b$$

We obtained the values for the power function by least-squares regressions of ln-transformed data. Values for $b > 3$ indicate positive allometry, and higher values also suggest a more rotund body shape – greater weight per unit length.

Stomach contents and reproductive state

While stomach contents could affect density and therefore buoyancy, it was not possible to evaluate the contents in our specimens. However, all fish were weighed at approximately the same time interval after collection, allowing for evacuation of gut contents and for minimization of the variation in fullness. We sexed specimens by opening the body cavity and examining the gonads, under magnification if necessary. We assessed gonadal maturity based on a five-point scale specific for notothenioids (Everson 1977, 1994; Kock and Kellermann 1991) as follows: 1, immature; 2, adolescent; 3, mature/developing; 4, mature/ripe (male) or gravid (female); 5, mature/spent. Our sample contained one specimen of *N. coriiceps* in stage 4, four *Gobionotothen gibberifrons* in stages 3–4, and three *Lepidonotothen larseni* in stages 3–4 (Table 1). We therefore concluded that this small number of ripe or gravid specimens had not biased our measurements of buoyancy.

Statistical analysis

We used the software program SYSTAT (5.2.1) to analyze data. Prior to analysis, we visually examined the data with bivariate scatter plots. For statistical analysis, we transformed data to natural logarithms (ln), and thus reported levels of significance are for ln-transformed data. Logarithms have the advantage of linearizing the data and correcting for heteroscedasticity. We utilized descriptive statistics and independent t -tests to summarize and compare morphological data between the sexes. Measurements were not independent since we took four measurements or weights and derived one ratio for each fish. We therefore used the Bonferroni adjustment to ensure that we accepted a conservative P -level as significant. This P -level was $0.05/5 = 0.01$. We used least-squares regressions to investigate the relationship between W_{water} and W_{air} and between %B and W_{air} . We employed one-way

Table 1. Size and life-history information for sample of 13 notothenioid species. Order of species as in Fig. 1 from light to heavy based on percentage buoyancy

Species	No.	Mean L_t , mm (range)	Mean W_t , g (range)	% of max. reported L_t	Mature at L_t , mm	Developmental stage	Gonadal maturity stage	Sex ratio (F/M) ^b
<i>Champscephalus gunnari</i>	26	396 (305–490)	406 (153–790)	46–74	350	Adult	1 to 3	11/15 = 0.73
<i>Chionodraco rastrospinosus</i>	32	374 (361–456)	402 (208–591)	61–84	330–370	Adult	1 to 2	9/23 = 0.39*
<i>Notothenia rossii</i>	12	394 (361–455)	757 (573–1224)	39–49	380–400	Adult	1 to 3	4/8 = 0.50
<i>Chaenodraco wilsoni</i>	7	268 (250–285)	124 (87–160)	58–66	230	Adult	2	4/3 = 1.33
<i>Chaenocephalus aceratus</i>	13	395 (351–434)	379 (219–538)	60–74	460–570	Adult	1 to 2	0/13 = 0.00*
<i>Dissostichus mawsoni</i>	5	325 (290–398)	296 (181–596)	14–20	1000	Sub-adult	–	–
<i>Trematomus eulepidotus</i>	3	250 (242–259)	185 (163–226)	71–76	–	Adult	2 to 3	2/1 = 2.00
<i>Notothenia coriiceps</i>	8	283 (252–348)	391 (230–693)	41–56	340–350	Sub-adult and adult	2 to 4	3/5 = 0.60
<i>Gobionotothen gibberifrons</i>	74	269 (216–392)	195 (87–655)	39–71	360	Sub-adult and adult	1 to 3–4	36/38 = 0.95
<i>Lepidonotothen squamifrons</i>	2	182 (181–182)	51 (50–52)	36	340–360	Sub-adult	1	2/0
<i>Lepidonotothen larseni</i>	56	170 (140–203)	45 (22–76)	58–85	110–120	Adult	1 to 3–4	33/23 = 1.44
<i>Parachaenichthys charcoti</i>	7	191 (163–258)	31 (19–73)	35–56	–	Sub-adult and adult	1 to 2	4/3 = 1.33
<i>Lepidonotothen nudifrons</i>	13	143 (118–183)	32 (15–69)	62–96	90–95	Adult	1 to 3	7/6 = 1.17

^aGon and Heemstra (1990)

^bAsterisk denotes χ^2 -test indicating sex ratio significantly different from unity at level of at least $P < 0.02$

ANOVAs (F -tests) and t -tests to evaluate levels of significance for exponents. To evaluate the influence of sex on W_{water} and $\%B$, for each species we tested the homogeneity of slopes between males and females for the dependent variables (W_{water} , $\%B$) using single-factor ANCOVAs with W_{air} as the covariate. In all cases, the null hypothesis was that there was no difference.

Results

Data for our sample of eight nototheniids, four channichthyids, and one bathydraconid are summarized in Table 1. All specimens were adults or sub-adults and most were between 40 and 75% of maximum reported total length (L_t). The mean $\%B$ for the 13 species in our sample ranges from 3.07% to 6.11% (Fig. 1, Table 2), with intraspecific variation of 1–2% for most species. Figure 1 indicates that in the 4 species with sample sizes of at least 26, measurements of buoyancy approach statistical adequacy in terms of the ratio of dispersion (standard deviation) to reliability (standard error of the mean) (Hubbs and Hubbs 1953). For samples of this size, twice the SEM approximates the 95% CI (confidence interval) for the mean. Therefore, when black rectangles overlap (Fig. 1), differences among measure-

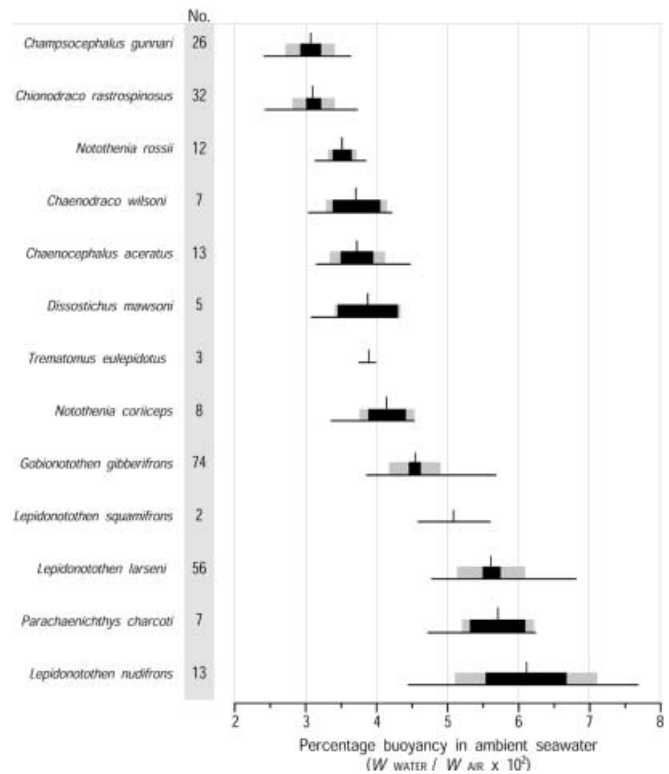


Fig. 1. Comparison of measurements of buoyancy among 13 species of notothenioids in a Dice-Leraas diagram (modification of Hubbs and Hubbs 1953). Heavy horizontal line is the range; short vertical line is the mean; rectangle shows 1 SD on each side of the mean with black portion indicating ± 2 SEM. For sample sizes approaching 30, 2 SEM approximates the 95% CI for the mean. Therefore when black rectangles overlap, interspecific differences among measurements of buoyancy are not significant

Table 2. Percentage buoyancy (%B), condition factor (I_k) and length-weight relationship for sample of 13 notothenioid species. Order of species as in Fig. 1 from light to heavy based on %B

Species	No.	Mean %B (SD) ^a	Mean I_k (SD) ^b	Length-weight relationship ^c			
				Coefficient (a)	Exponent (b)	r^2	P
<i>Champscephalus gunnari</i>	26	3.07 (0.34)	0.62 (0.05)	2.46×10^{-7}	3.54	0.99	< 0.0001
<i>Chionodraco rastrispinosus</i>	32	3.12 (0.29)	0.76 (0.07)	3.30×10^{-6}	3.14	0.87	< 0.0001
<i>Notothenia rossii</i>	12	3.52 (0.20)	1.22 (0.06)	8.57×10^{-7}	3.44	0.98	< 0.0001
<i>Chaenodraco wilsoni</i>	7	3.72 (0.42)	0.63 (0.05)	1.43×10^{-8}	4.09	0.96	0.0003
<i>Chaenocephalus aceratus</i>	13	3.73 (0.38)	0.61 (0.13)	2.50×10^{-6}	3.14	0.63	0.0133
<i>Dissostichus mawsoni</i>	5	3.88 (0.46)	0.80 (0.09)	1.17×10^{-7}	3.73	0.98	0.0028
<i>Trematomus eulepidotus</i>	3	3.89 (-)	1.17 (-)				
<i>Notothenia coriiceps</i>	8	4.15 (0.38)	1.63 (0.18)	7.91×10^{-7}	3.54	0.95	0.0003
<i>Gobionotothen gibberifrons</i>	74	4.54 (0.36)	0.91 (0.08)	1.11×10^{-6}	3.38	0.98	< 0.0001
<i>Lepidonotothen squamifrons</i>	2	5.09 (-)	0.85 (-)				
<i>Lepidonotothen larseni</i>	56	5.62 (0.47)	0.89 (0.09)	2.22×10^{-7}	3.72	0.94	< 0.0001
<i>Parachaenichthys charcoti</i>	7	5.71 (0.50)	0.41 (0.02)	3.02×10^{-6}	3.06	0.99	< 0.0001
<i>Lepidonotothen nudifrons</i>	13	6.11 (0.99)	1.01 (0.09)	1.08×10^{-6}	3.45	0.99	< 0.0001

^a% buoyancy = $W_{\text{water}}/W_{\text{air}} \times 10^2$

^b $I_k = (W/L_t^3) \times 10^5$ where W = body weight (g) and L_t = total length (mm)

^c $W = aL_t^b$ where W = body weight (g) and L_t = total length (mm)

ments of buoyancy are not significant. In Fig. 1, the means for %B for most species cluster into three groups. For example, *Champscephalus gunnari* and *Chionodraco rastrispinosus* are relatively light species and %B does not differ significantly between them. However, these two species are significantly lighter than an intermediate group of seven species, *N. rossii* to *G. gibberifrons* in Fig. 1, many of which do not differ among themselves. A heavier group consisting of *L. larseni*, *Parachaenichthys charcoti* and *L. nudifrons* also does not differ among themselves but they are significantly heavier than the intermediate group.

Bivariate plots (not shown) and least-squares regressions of W_{water} against W_{air} indicate that this relationship is linear and negatively allometric. For the 11 species with sample sizes = 5, slopes are 0.60–0.95 and values for r^2 are 0.83–0.99. The 95% CI for the slope includes 1.00 only in *Chionodraco rastrispinosus*, *Chaenocephalus aceratus*, *N. rossii*, and *N. coriiceps*. Hence, as W_{air} increases with fish growth, W_{water} increases at less than unity and therefore the %B ratio decreases with ontogeny such that heavier specimens have a lower %B. Bivariate plots of %B against W_{air} indicate that this trend is evident for all species (not shown) represented by five or more specimens. Plots illustrating this trend are shown (Fig. 2) for the 4 species with large sample sizes and considerable ranges in body weight (7.5-fold for *G. gibberifrons*, 5.2-fold for *Champscephalus gunnari*, 3.4-fold for *L. larseni*, and 2.8-fold for *Chionodraco rastrispinosus*).

All species in our sample were sexed except *Dissostichus mawsoni*. We analyzed L_t , L_s , W_{air} , W_{water} , and

%B with respect to sex for the nine species with sample sizes = 7, excluding the all-male sample of *Chaenocephalus aceratus*. With the exception of one species, independent t -tests showed no significant differences between the sexes in L_t , L_s , W_{air} , W_{water} , and %B. Although females of *L. larseni* were significantly longer ($t = 3.514$; $P = 0.001$) and heavier in air ($t = 3.929$; $P = 0.0003$) and in water ($t = 4.386$; $P = 0.0001$), there was no difference in %B ($t = 1.718$; $P = 0.62$). Since t -tests indicated that the P -levels for W_{water} and %B approached significance in *Champscephalus gunnari* and *Chionodraco rastrispinosus*, we used single-factor ANCOVAs for additional exploration of sexual differences in all species. We tested the hypothesis of homogeneity of slopes for males and females with either W_{water} or %B as the dependent variable and W_{air} as the covariate. The assumption of non-significant differences in the slopes was satisfied for all species with the exception of *Champscephalus gunnari* and *Chionodraco rastrispinosus*, where the slopes were different between males and females. *Champscephalus gunnari* females had significantly higher values for W_{water} ($F_{1,23} = 7.01$; $P = 0.014$) and for %B ($F_{1,23} = 7.11$; $P = 0.014$) than males. However, *Chionodraco rastrispinosus* females had significantly lower values for W_{water} ($F_{1,29} = 4.34$; $P = 0.046$) and for %B ($F_{1,29} = 4.36$; $P = 0.046$) than males. Thus, with the exception of these two instances, sex did not affect %B in the species in our sample. We should note, however, that since the sex ratio of the sample of *Chionodraco rastrispinosus* was significantly different than unity (Table 1), the difference in %B was probably an artifact.

Discussion

The 14 notothenioids measured in previous studies (Eastman 1993, 1999) had %*B* in the range of 0–5.9%. Our 13 species from the South Shetland Islands ranged from 3.1 to 6.1%, with the majority falling between 3.0 and 4.5%. No species were close to neutral buoyancy although *Champocephalus gunnari*, the oft-cited example of a water-column channichthyid, was the lightest species in the sample.

Intraspecific values for %*B* exhibit variability or scatter that is typical for these measurements, and show a decrease with increasing body weight (Fig. 2). Fish exhibit indeterminate growth (Weatherley 1972), and since the %*B* ratio is derived from growth parameters, the decline in %*B* may be 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 (Bussacker 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). This is especially true in notothenioids since the diet includes lipid-rich crustaceans and fishes (Clarke 1980; Kattner et al. 1996; Hagen et al. 2000), and because species with significant amounts of lipid also show an ontogenetic increase in lipid content (Friedrich and Hagen 1994).

Are values for measurements of buoyancy consistent with information on life history?

Although values for %*B* are in general agreement with known aspects of the life history for most species, there are a few cases that merit discussion. For example, the small sub-adult *D. mawsoni* in our sample (mean $W_{\text{air}} = 0.30$ kg) were not neutrally buoyant as are large adults ($W_{\text{air}} = 35.25$ kg) from McMurdo Sound that live and feed in the water column (Eastman and DeVries 1981; Eastman 1985). Our sub-adult specimens weighed 118-fold less than the McMurdo specimens and had a %*B* of 3.9%. This species exemplifies the ontogenetic decrease in %*B*, especially marked in this instance because its life cycle involves a progressively more pelagic and oceanic existence with increasing age and size (Yukhov 1982).

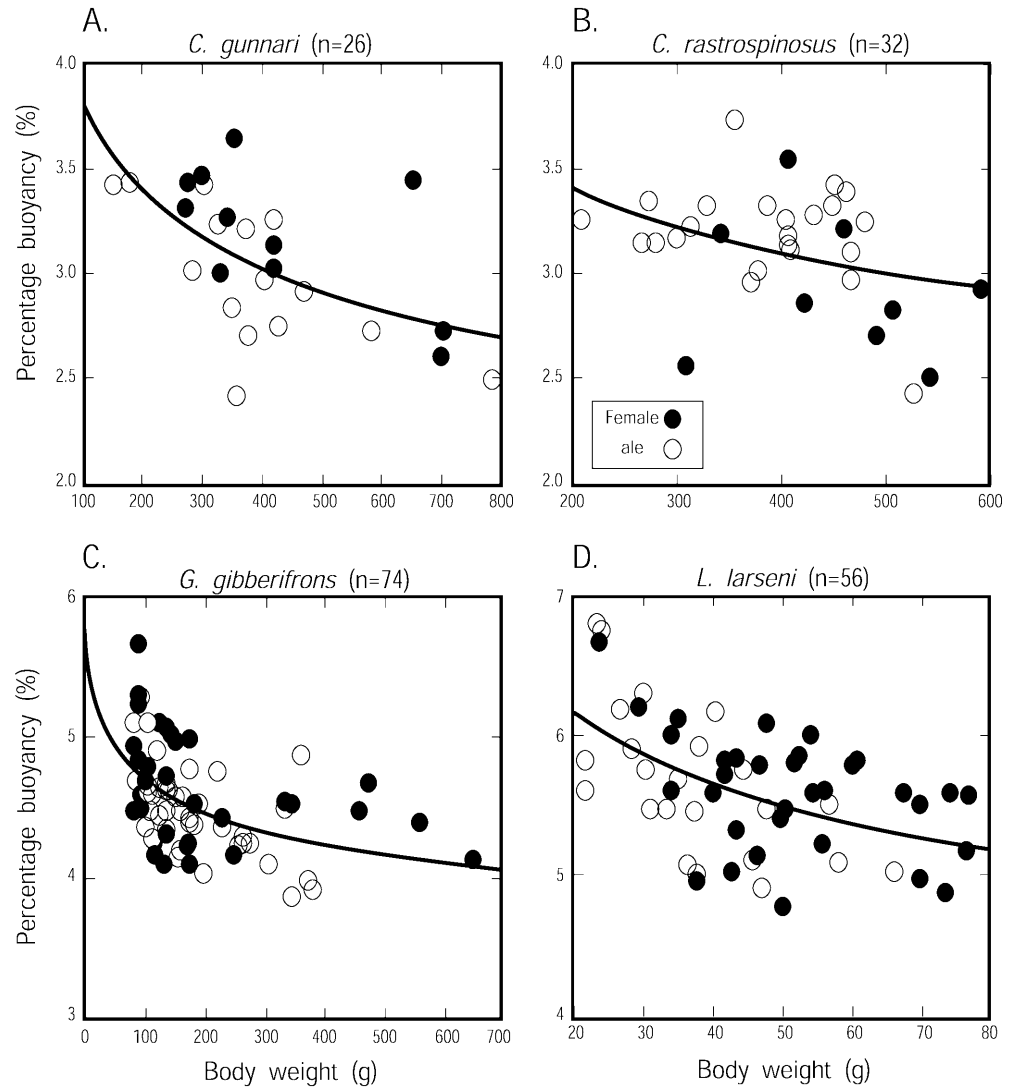
In the sympatric nototheniids, *N. rossii* and *N. coriiceps*, measurements of %*B* are consistent with inferences from body shape and morphology. The two species are closely related, possess similar pelagic fingerling stages but have diverged in adult morphology and life history. *N. rossii* is semipelagic, with a migratory period during its life cycle (DeWitt et al. 1990) and has a significantly lower %*B*. It also feeds heavily on krill (Kock 1985). Compared to the more benthic *N. coriiceps*, *N. rossii* also possesses a more streamlined body and a narrower head,

exhibits less modification of the pelvic fins for substrate contact and shows more spontaneous activity in captivity. The less rotund body of *N. rossii* is also reflected in the lower condition factor and the smaller exponent in the length-weight relationship (Table 2).

For other species, body shape does not accurately predict where the species will fall in the continuum of buoyancy measurements (Fig. 1, Table 2). For example, *L. larseni* possesses a compressed fusiform body with large dorsolaterally directed eyes and a terminal mouth, and thus has the appearance of a pelagic or semipelagic species. Dietary studies indicate that *L. larseni* feeds primarily on krill and other water-column organisms (Permitin 1970; Permitin and Tarverdiyeva 1972; Takahashi and Iwami 1997), although other research indicates that *L. larseni* also feeds on benthos (Shust and Pinskaya 1978; Daniels 1982; Gröhsler 1994). Given its appearance, *L. larseni* would be expected to have a relatively low %*B*. *G. gibberifrons* exemplifies a benthic nototheniid: the ventral aspect of the body is flattened; the mouth protrudes anteroventrally and the fleshy lips appear specialized for benthic browsing. Surprisingly, however, *G. gibberifrons* has a significantly lower %*B* than *L. larseni*. The condition factors for the two species are nearly identical but the exponent for the length-weight relationship is smaller in *G. gibberifrons*, although this is not necessarily associated with a lower %*B* in all species (Table 2). While *G. gibberifrons* feeds on infauna (DeWitt et al. 1990), it also feeds on active organisms like krill when available (Kock 1985; DeWitt et al. 1990; Takahashi and Iwami 1997). Another implication of lower than expected %*B* is that *G. gibberifrons* may be in the water column moving above the substrate when browsing on infauna. In spite of their seemingly specialized external morphology, both species are probably sufficiently opportunistic that they are capable of feeding in the water or on the substrate. It should also be noted that krill are sometimes found close to the bottom (Gutt and Siegel 1994) and are an important component of the diet of notothenioids living on or near the bottom (Pakhomov 1997).

Our sample of channichthyids included species spanning the relatively restricted range of morphological and ecological diversity in this family. Although we observed no differences in the amount of spontaneous swimming while our specimens were in captivity, *Champocephalus gunnari* and *Chaenodraco wilsoni* are usually considered more pelagic than *Chionodraco rastrospinosus* and *Chaenocephalus aceratus* (Iwami and Kock 1990). The four species were remarkably similar in %*B*, clustering in the range 3.1–3.7% (Fig. 1, Table 1). *Champocephalus gunnari* feeds on krill in the water column (Olsen 1955; Kock 1985; Kock et al. 1994; Kock and Everson 1997) and undergoes diurnal vertical migrations (Kock and Everson 1997; Trunov et al. 2000). The streamlined body and vertical banding on the trunk also suggest a life history oriented to the water column, and *Champocephalus gunnari* did have the lowest %*B* in our sample. Although *Chaenocephalus aceratus* is one of

Fig. 2. Bivariate scatter plots of percentage buoyancy versus body weight for females (●) and males (○) of *Champscephalus gunnari* (A), *Chionodraco rastrispinosus* (B), *Gobionotothen gibberifrons* (C), and *Lepidonotothen larseni* (D). Some values are hidden in C. Because the body weight (W_{air}) variable contributes to an exponential function in the length-weight relationship characterizing fish growth, the power-smoothing option in SYSTAT was chosen to display the line showing the decrease in %B with increasing W_{air}



the more benthic channichthyids (Iwami and Kock 1990), its %B is only about 0.6% greater than *Champscephalus gunnari*. We suspect that these small differences are not biologically meaningful and that %B may not reflect the combined pelagic-benthic life styles of many species. There are no obligatory benthivores among channichthyids (Voronina and Neelov 2001). There is also remarkable similarity in morphology, ecology, and behavior (Iwami 1994), with most species showing active vertical migration to feed on pelagic prey (Iwami and Kock 1990), especially fish and krill (Pakhomov 1997). Furthermore, heterochrony, and especially paedomorphy, have been important in the evolution of notothenioids in general (Balushkin 1984) and channichthyids in particular (Iwami 1994). Among notothenioids, delayed ossification of bones is most pronounced among channichthyids (Voskoboinikova 1997), and is “a mechanism of paedomorphic evolution” (Voskoboinikova 1994). Skeletal underdevelopment with the persistence of cartilage allows development of secondary pelagism (Voskoboinikova 2001) such as that

seen in channichthyids. Because channichthyids have extensive cartilage in the skeleton as adults (Iwami 1985), interspecific differences in density and therefore buoyancy would tend to be minimized.

The little-studied channichthyid, *Dacodraco hunteri*, is an exception to the foregoing discussion. It is the only other channichthyid whose buoyancy has been measured and, at 1.3% (Eastman 1999), it is significantly lower than other channichthyids. This small, streamlined species exhibits extensive skeletal reduction, including a partially persistent notochord. *Dacodraco* feed on pelagic *Pleuragramma*, and their life history may be keyed to a more permanent life in the water column than is the case with other channichthyids.

Concluding remarks: neutral buoyancy is uncommon in notothenioids

Our buoyancy data for an additional 13 species, including channichthyids, provide a wider perspective on

the frequency and distribution of neutral buoyancy among notothenioids. While an evolutionary novelty in this benthic suborder, neutrally buoyant species are widely distributed and ecologically important. For example, *Pleuragramma antarcticum* is the most abundant pelagic fish in high-Antarctic shelf waters (Hubold 1984). There are 122 species of notothenioids, including 96 Antarctic species, but only 5 have been proven or hypothesized to be neutrally buoyant. Weights at or close to neutral buoyancy have been validated only for *Pleuragramma antarcticum* (DeVries and Eastman 1978) and *Dissostichus mawsoni* (Eastman and DeVries 1981). On the basis of morphology, *Aethotaxis mitopteryx* (Eastman and DeVries 1982; Kunzmann and Zimmermann 1992), *Dissostichus eleginoides* (Oyarzún et al. 1988), and *Gvozdarus svetovidovi* (Eastman 1993) have been hypothesized as being possibly neutrally buoyant. Neutrally buoyant notothenioids have substantial amounts of somatic lipid, usually in subcutaneous and muscular locations (Eastman 1993). Whole-body analyses indicate that most of the lipid is stored in the carcass of gutted fish and that *Aethotaxis* has an extremely high lipid content – 61.4% of dry weight, the highest of any notothenioid reported to date (Friedrich and Hagen 1994; Hagen et al. 2000). The lipid content of *Pleuragramma* is also high at 37.7% of dry weight (Hagen et al. 2000). These analyses also indicate that these species exhibit a pronounced ontogenetic lipid accumulation with increasing size (Friedrich and Hagen 1994).

Neutrally buoyant species also have poorly ossified skeletons, frequently with extensive areas of cartilage. Neutral buoyancy may only be possible when skeletal paedomorphy, especially reduction in mass and density through persistent larval features, which is common in a number of notothenioid species, is coupled with substantial somatic lipid deposition, which is not common. In a recent phylogenetic analysis of a morphological data set for notothenioids, *Dissostichus*, *Pleuragramma*, *Aethotaxis*, and *Gvozdarus* are united in the notothenioid subfamily Pleuragramminae (Balushkin 2000). Thus, as far as our current knowledge extends, neutral buoyancy in notothenioids is confined to this single clade.

Acknowledgements We thank the captain, crew, and personnel of Raytheon Polar Services aboard the ARSV *Laurence M. Gould* for their assistance during the cruise. We are also indebted to the personnel at the U.S. Palmer Station for additional help. We are grateful to Danette Pratt for producing Figs. 1 and 2 and to three referees for their constructive comments. This work was supported by National Science Foundation grant OPP 99-09055 (B.D.S.), National Science Foundation grant OPP 94-16870 (J.T.E.), and Ohio University Presidential Research Scholar Award (J.T.E.).

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