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1	Size matters: relationships between body size, dry weight and ash-free dry							
2	weight of common coastal, aquatic invertebrates in the Baltic Sea							
3 4	Short title: Body size affects weight estimations							
5								
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26 ABSTRACT (410 words)

27 **Background**. Organism biomass is one of the most important variables in ecological studies, 28 making estimations of organism weight one of the most common laboratory tasks. Biomass of 29 small macroinvertebrates is usually estimated as dry (DW) or ash-free dry weight (AFDW); a 30 laborious and time consuming process, that often can be speeded up using easily measured and 31 reliable proxy variables like wet/fresh weight and/or body size. Another common way of 32 estimating AFDW - which is the most accurate but also time-consuming estimate of 33 biologically active tissue weight - is the use of AFDW/DW ratios or conversion factors. So far, 34 however, these ratios typically ignore the possibility that the relative weight of biologically 35 active vs. non-active support tissue (e.g. protective exoskeleton or shell) - and therefore, also 36 the AFDW/DW ratio - may change with body size, as previously shown for taxa like spiders, 37 vertebrates and trees.

Methods. We collected samples of aquatic, epibenthic macroinvertebrates (>1 mm) in 32 shallow bays along a 360 km stretch of the Swedish coast along the Baltic Sea; one of the largest brackish water bodies on Earth. We then estimated statistical relationships between the body size (length or height in mm), dry weight and ash-free dry weight for 14 of the most common taxa; five gastropods, three bivalves, three crustaceans and three insect larvae. Finally, we statistically estimated the potential influence of body size on the AFDW/DW ratio per taxon.

45 Results. For most of the taxa, non-linear regression models describing the power relationship 46 between body size and i) DW and ii) AFDW fit the data well (as indicated by low SE and high 47 R²). Moreover, for more than half of the taxa studied (including the vast majority of the shelled 48 molluscs), body size had a negative influence on organism AFDW/DW ratios.

49 **Discussion**. The good fit of the modelled power relationships suggest that the constants 50 reported here can be used to more quickly estimate organism dry- and ash-free dry weight

51	based on body size, thereby freeing up considerable work resources. However, the considerable
52	differences in constants between taxa emphasize the need for taxon-specific relationships, and
53	the potential dangers associated with either ignoring body size or substituting relationships
54	between taxa. The negative influence of body size on AFDW/DW ratio found in a majority of
55	the molluscs could be caused by increasingly thicker shells with organism age, and/or
56	spawning-induced loss of biologically active tissue in adults. Consequently, future studies
57	utilizing AFDW/DW (and presumably also AFDW/wet weight) ratios should carefully assess
58	the potential influence of body size to ensure more reliable estimates of organism biomass.
59	
60	Keywords: allometry; biometry; estuary; epifauna; infauna; isometric scaling; length:weight
61	relationship; submerged aquatic vegetation; seagrass.

- 62
- 63

64 INTRODUCTION

Organism biomass is inarguably one of the more important variables in ecology, playing a central role in studies ranging from ecophysiology and population dynamics, to community interactions, food web regulation and whole-ecosystem metabolism. As a consequence, to accurately estimate organism biomass constitutes one of the most common and important tasks in ecological studies (Rosillo Callé, 2008).

70 Small invertebrates retained on 0.5-1 mm sieves (hereafter 'macrofauna') make up a 71 major part of animal density, diversity and biomass in many ecosystems; e.g. insects and 72 arachnids in terrestrial ecosystems; epibenthic, aquatic crustaceans, echinoderms and molluscs 73 in stands of aquatic vegetation; and infaunal (sediment-dwelling) worms, crustaceans and 74 molluses in marine sediments. Macrofauna biomass is typically reported as dry- or ash-free dry 75 weight per unit area (e.g. g per m^2), which requires observers to repeatedly identify, sort, dry 76 and weigh individual or pooled organisms; a time-consuming, expensive and tedious process. 77 Many studies have shown that more easily measured proxy variables scale predictably with dry 78 weight and therefore can be used to speed up biomass estimations; e.g. wet (fresh) weight 79 (Brey, Rumohr & Ankar, 1988; Ricciardi & Bourget, 1998) and body size, based on either 80 exact length measurement (Smock, 1980; Frithsen, Rudnick, & Doering, 1986; Sabo, Bastow, 81 & Power, 2002) or retention on sieves of certain mesh sizes (Widbom 1984; Edgar 1990; 82 Casagranda & Boudouresque, 2002). While wet weight can be a very good proxy, we argue 83 that body size (e.g. length) holds several advantages. First, ecological theory supported by empirical data suggest biomass scales predictably with length in the form of power relations 84 85 (Smock, 1980; Sabo, Bastow, & Power, 2002). Second, while freezing/thawing and fixation in 86 conservation liquids (e.g. EtOH or formalin) can affect both organism wet weight (Howmiller 87 1972; Mason, Lewis, & Weber, 1983; Leuven, Brock, & van Druten, 1985) and length 88 (Hjörleifsson & Klein-MacPhee, 1992; Kapiris, Miliou, & Moraitou-Apostolopoulou, 1997),

wet weight is also very sensitive to blotting, centrifugation (to remove excess water), and
exposure to air and light before and during weighing (Howmiller 1972, Mason, Lewis, &
Weber, 1983; Leuven, Brock, & van Druten, 1985). Third, body size (e.g. length or height)
estimations can more easily be automated, using e.g. image analysis software (Paavo et al.,
2008, Mallard, Bourlot, & Tully, 2013), to rapidly process multiple individuals at a time.

94 Ash-free dry weight (AFDW) is typically regarded as the most accurate predictor of 95 macrofauna biomass, as it only includes biologically active tissue. Since AFDW estimations 96 require the incineration of dried samples in a furnace at high temperature, adding considerable 97 time and costs to analyses, many studies have reported how AFDW scales with estimations of 98 wet- and dry weight, usually in the form of simple 'conversion factors' (e.g. AFDW/DW, in 99 %) (Rumohr, Brey, & Ankar, 1987; Ricciardi & Bourget, 1998). However, these ratios 100 typically ignore the possibility that the relative weight of biologically active vs. non-active 101 support tissue (e.g. protective exoskeleton or shell) - and therefore the AFDW/DW ratio - may 102 change with macrofauna body size, as previously shown for disparate taxa like spiders 103 (Andersen, 1979), vertebrates (Miller & Birchard, 2005) and trees (Niklas, 1995). This issue is 104 important not only for obtaining accurate biomass conversions and estimations, but also for 105 understanding how organismal investment in one type of structure may limit or constrain 106 investment in other structures across ontogenetic development stages (Lease & Wolf, 2010).

Here we estimate and report relationships between body size, dry-weight and ash-free dry weight for 14 of the most common aquatic, epibenthic invertebrate taxa found in shallow, vegetated habitats of the central Baltic Sea; one of the largest brackish water bodies on Earth. For each taxon we also assess whether the ash-free dry-weight/dry weight ratio changes with body size. Our aim is to provide simple yet reliable size-based relationships that can be used to rapidly estimate organism biomass.

113

114 METHODS

115 Study area

The Baltic Sea is a 415 000 km² large marginal sea situated in northern Europe (53-66° N; 10-116 117 30° E). A main feature is the presence of strong horizontal and vertical gradients in salinity, 118 temperature and oxygen, that also undergo considerable temporal (e.g. seasonal) fluctuations 119 (Voipio 1981). The Baltic Sea is evolutionary very young (ca 6000 years), and the shallow 120 coastal areas have since the last glaciation been colonized by a mixture of marine, freshwater 121 and brackish organisms, including crustaceans, gastropods, bivalves, polychaetes, hirudineans, 122 nemerteans and insect larvae (Hansen, Wikström, & Kautsky, 2008). As many marine and 123 freshwater organisms in the Baltic Sea live near their physiological tolerance limits, they grow 124 slower and smaller than in their original environment; e.g. the blue mussel Mytilus edulis 125 (Tedengren & Kautsky, 1986). As a consequence, their size ranges - but potentially also 126 size:weight relationships and AFDW/DW ratios - could differ from those reported for 127 conspecifics in marine or freshwater areas (Rumohr, Brey, & Ankar, 1987).

128

129 Field sampling

130 During summer (May-Aug) we collected aquatic invertebrate macrofauna (>1mm) in 32 131 shallow bays situated along a 360 km stretch of the central, Swedish Baltic Sea coastline (Fig. 132 1). The salinity in the area is generally low (ca. 5-7 psu) but fluctuates strongly with freshwater 133 runoff and upwelling events. In each bay, a snorkeler sampled submerged aquatic vegetation 134 and epibenthic macrofauna in 3-8 randomly selected stations (>30 m apart), by gently placing 135 a 20×20 cm frame (with a 1mm-mesh bag attached) on the sea bed, and collecting all organisms 136 (primarily vegetation and associated invertebrates) found above or on top of the sediment 137 surface. The bag content was immediately transferred to a plastic bag, which was kept cold on 138 ice until frozen (-20° C), in most cases within 1-3 hours.

139

140 Length estimations

141 Following thawing in room temperature, we identified intact invertebrate organisms to the 142 highest taxonomic resolution feasible using standard literature. For the 14 most common taxa 143 we then selected and measured the body size of 12-459 individuals per taxa (3220 individuals 144 in total), chosen to capture the full range of body sizes found across the 32 bays. The taxa 145 included five gastropods (Theodoxus fluviatilis, Hydrobia spp., Radix balthica, Potamopyrgus 146 antipodarum, Bithynia tentaculata), three bivalves (Mytilus edulis, Limecola (Macoma) 147 balthica and Cardidae spp. [numerically dominated by Parvicardium hauniense], three 148 crustaceans (Amphibalanus improvisus, Idotea spp., Gammarus spp.) and three insects (larval 149 stages of Chironomidae spp., Agraylea spp. and Limnephilidae spp.) (see also Table 1). Body 150 size (to the nearest 1 mm) was measured (based on standard procedures) as; i) gastropod height 151 along the central shell axis, ii) bivalve length from anterior to posterior side, iii) total length of 152 Gammarus and Idotea spp. from tip of rostrum to last urosome, iv) body width for 153 Amphibalanus improvisus, and v) total length of insect larvae from end of head to last segment. 154 A higher size accuracy is definitely possible (e.g. to 0.1 or 0.01 mm using calipers or stereo 155 lenses), but as most studies utilizing this type of data (including ours) will depend on 1000s of 156 length measurements, the accuracy chosen was a realistic trade-off between time and precision. 157

158 Estimations of dry- and ash-free dry-weight

Following size estimations, the measured individuals were transferred to pre-dried and weighed (nearest 0.0001 g) porcelain crucibles. For most size classes (except for very large and rare individuals), multiple individuals were typically pooled into the same crucible. This step underestimates actual biomass variability between individuals, but was necessary as the low individual weights (particularly AFDW) were near or below the reliable detection limit of

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164 the scale. We included multiple estimations of the same sizes, so that the number of weight 165 estimations (N) ranged from 10 to 42 per taxa. Samples were then dried at 60 °C for >48h (until 166 constant weight), and cooled to room temperature in a desiccator before weighing. To estimate 167 ash-free dry weight, the crucibles were then transferred to a muffle furnace, incinerated (550 °C for 3 hours), cooled and weighed again. Ash-free dry weight was calculated as dry weight 168 169 minus ash weight. 170 171 **Statistical analyses** 172 We estimated taxon-specific body size:biomass relationship using non-linear regression in 173 the form of the power equation: $biomass = \alpha \times size^{\beta}$ 174 175 where *biomass* is the individual weight (mg DW or AFDW), *size* is the body size (length/height, in mm), α is a normalization constant, and β is the scaling constant. Individual 176 177 biomass typically scales with size in a power relationship, and initial data exploration showed that power equations provided a superior fit compared to linear, log or exponential 178 relationships. As regression coefficients (R^2) are an inadequate measure of fit for non-linear 179 180 regression models (Spiess & Neumeyer, 2010), we report SE for α and β . However, for the sake of simplicity we also estimated the linear log-log relationship between body size and 181 biomass, and report the R^2 for those models (see e.g. Lease & Wolf, 2010). 182 183 For each taxon we also calculated the mean $(\pm 1 \text{ SE})$ AFDW/DW ratio (in %); a 184 commonly used conversion factor in macroinvertebrate studies (see e.g. Ricciardi & Bourget, 185 1998). We then used linear regression to test whether body size (in mm) affected the

186 AFDW/DW ratio. Prior to analyses we checked assumptions of normality (by plotting

187 predicted vs. observed quantiles) and homoscedasticity (by plotting predicted vs. observed

residuals). All analyses were conducted in R v. 3.2.3 (R Core Team, 2016).

189

190 **RESULTS**

191 Relationships between body size and individual biomass

192 The relationships between body size (mm), individual dry weight (mg DW) and ash-free dry 193 weight (mg AFDW) for all 14 taxa are displayed in Figure 2a-h, and the parameters (and their 194 fit) are presented in Table 1. For most of the taxa, body size was a very good predictor of individual DW, as demonstrated by low SE and R² near 1. The model fits were slightly poorer 195 for the three insect taxa ($R^2 = 0.60-0.82$) and the gastropod *Bithynia tentaculata* ($R^2 = 0.85$) 196 197 than for the other ten taxa. For a majority (12 out of 14) of the taxa, the scaling constants (β) were well above 2 (2.110-3.590). The exceptions were the small gastropod Potamopyrgus 198 antipodarum and chironomid larvae, that had constants closer to 1 ($\beta = 1.368$ and 1.383, 199 200 respectively).

Body size was also a very good predictor of AFDW, even though model fits (based on SE and R²) were slightly poorer than for DW (Table 1). Just as for DW relationships, the model fits (based on SE and R²) were best for gastropods, molluscs and crustaceans. The scaling constants (β) were for most taxa quite similar to those reported for the DW relationships, with the exception of a higher constant for *P. antipodarum* (β = 2.447) and a lower constant for *Bithynia tentaculata* (β = 1.360).

207

208 Influence of organism body size on AFDW/DW ratios

The AFDW/DW ratios (mean %±SE) per taxa are also presented in Table 1. As expected, there were consistent differences between the four major taxonomic groups studied, with low AFDW content in bivalves and gastropods (12-27%), who's calcium carbonate shell makes up the major part of whole-body biomass, to higher AFDW content in chitin-shelled crustaceans (ca 60%), and the highest content in insect larvae (86-92%).

214 Results of simple linear regression showed that for more than half (8 out of 14) of the 215 taxa surveyed, body size clearly affected the AFDW/DW ratio (Table 1, Fig. 2i-l). For four out 216 of five gastropods, two out of three bivalves, as well as the sessile, calcite-shelled crustacean 217 Amphibalanus improvisus, the AFDW/DW ratio decreased linearly with body size. For the 218 small gastropod Potamopyrgus antipodarum body size instead had a positive influence on 219 AFDW/DW. However, the P. antipodarum size range was very narrow (2-4mm) and the 220 intercept was not different from 0 (Table 1), suggesting a relatively poor model. Moreover, 221 there was no size effect found in the blue mussel *Mytilus edulis* (Table 1). Finally, in contrast 222 to the size effects found for most of the hard-shelled molluscs, there was no influence of body 223 size on AFDW/DW in any of the chitin-shelled crustaceans or insect larvae (Table 1, Fig 2i-l).

224

225 **DISCUSSION**

226 Estimating organism biomass is one of the most common, important but also resource-227 consuming tasks in ecological work, particularly when it comes to small-bodied, highly 228 abundant and diverse macroscopic invertebrates. Many previous studies have successfully 229 shown that more easily measured variables like invertebrate wet (fresh) weight (e.g. Ricciardi 230 & Bourget, 1998) or body size (e.g. Smock, 1980) can be used as proxies to reliably predict 231 both the dry- and ash-free dry weight, thereby simplifying and speeding up biomass 232 estimations. Here, we first complement this literature by reporting how individual biomass 233 scales with body size for 14 of the most common epibenthic invertebrate taxa found in shallow 234 coastal areas of the Baltic Sea. Moreover, we demonstrate that for a majority of the studied 235 molluses, the ratio between organism dry- and ash-free dry weight – an often-used conversion 236 factor (Rumohr, Brey, & Ankar, 1987; Ricciardi & Bourget, 1998) - decreases predictably with 237 body size. Thus, our results can be used to quickly estimate the biologically active biomass of

individual organisms based on their size, and when combined with density data, accuratelyestimate biomass per unit area.

240

241 Body size as a proxy for dry- and ash-free dry weight

242 For a majority of the studied taxa, body size was a good predictor of both dry weight and ash-243 free dry weight. The model fits were slightly poorer for ash-free dry weight (AFDW); most 244 likely a consequence of the fact that even though multiple individuals of the same size were 245 pooled, the low individual AFDW of many organisms (in the vicinity of 1 mg) challenged the 246 accuracy of the scale. Comparisons between the 14 taxa studied (Table 1) show that particularly 247 within the gastropods and crustaceans, the scaling (β) constants differ quite substantially 248 between taxa (see the different slopes in Fig. 2 and β coefficients in Table 1). These differences 249 emphasize the need for taxon-specific relationships to accurately predict biomass, and the 250 potential dangers in either ignoring body size or substituting relationships between taxa. 251 Consequently, our power equations (Table 1) can be used in a simple yet reliable way to 252 estimate organism dry- or ash-free dry weight based on standard body size measurements. Size-253 based biomass estimations are likely to speed up laboratory work considerably; for example, 254 Casagranda and Boudouresque (2002) showed that sieve-based size estimations speeded up 255 estimations of body biomass of the gastropod Hydrobia ventricosa by 20-30 times. 256 Consequently, our size-based estimations of invertebrate biomass are likely to free up 257 considerable work resources (time, man-power, money) that can be used to e.g. collect and 258 process more samples.

259

260 The influence of body size on AFDW/DW ratios

For most of the taxa with a calcium-carbonate (molluscs) or calcite shell (the barnacle *Amphibalanus improvisus*), we found a significant negative influence of body size on the

263 AFDW/DW ratio; a commonly reported and often-used conversion factor in invertebrate 264 studies (Rumohr, Brey, & Ankar, 1987; Ricciardi & Bourget, 1998). In other words, the 265 proportional weight of biologically active vs. non-active tissue (shell, hard mouth parts, etc.) 266 decreased with body size. There are at least two possible and complementary explanations for 267 this relationship. First, while mollusc shell length increase per unit of time typically decreases 268 with age, new shell layers are consistently added on a yearly basis (Negus, 1966). This results 269 in increasingly thicker, and therefore disproportionally heavier, shells with mussel length, and 270 a higher shell:tissue weight ratio. Second, our sampling was conducted during summer; a 271 season when a majority of adult molluscs (here represented by the larger individuals per taxa) 272 most likely had spawned and temporarily lost a considerable proportion of their biologically 273 active tissue (Kautsky, 1982). The slopes of the significant regressions (Table 1, median = -274 1.26) suggest that failing to incorporate the potential influence of body size can strongly reduce 275 the accuracy of AFDW estimations based on dry weight (and presumably also wet weight) -276 particularly if there is considerable variability in body size in the samples. The somewhat 277 surprising lack of size influence in the common blue mussel Mytilus edulis was not investigated 278 in detail, but could be caused by i) the lack of small shell-crushing mussel predators in the area 279 (e.g. crabs), who otherwise are known to trigger thicker mussel shells (Freeman, 2007), and/or 280 ii) the relatively low salinity, which results in that the small, osmotically stressed *M. edulis* 281 invests considerably more energy into osmosis and soft tissue production, than in thicker shells 282 (Kautsky, Johannesson, & Tedengren, 1990).

In contrast to the results for molluscs, there was no size effect on AFDW/DW ratios for the chitin-shelled insects and crustaceans. These results fit well with those reported in previous studies, for example of terrestrial insects, for which exoskeletal chitin scales isometrically (1:1) with body size (Lease & Wolf, 2010). In summary, our results suggest that body size can play an important but hitherto underestimated role when estimating organism AFDW based on dry

- 288 (and possibly, wet) weight, particularly for shelled molluscs.
- 289

290 Conclusions

291 Using samples of epibenthic macroinvertebrates collected in 32 shallow bays along a 360 km 292 stretch of the Swedish Baltic Sea coastline, we show that for 14 of the most common 293 macrofauna taxa, organism body size scales predictably with individual dry weight and ash-294 free dry weight in the form of power relations. The good model fits suggest the taxon-specific 295 equations reported here can be used to predict individual biomass based on organism size, 296 thereby speeding up estimations of macrofauna biomass. Moreover, for the vast majority of the 297 molluses studied, we find a negative relationship between body size and AFDW/DW ratio; a 298 commonly used conversion factor in macrofauna studies. Consequently, future studies utilizing 299 AFDW/DW ratios should carefully assess the potential influence of body size to ensure reliable 300 biomass estimations.

301

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308

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Table 1. Results of regression analyses estimating i) the non-linear power relationship between body size and dry weight (DW) and ii) ash-free dry weight (AFDW), iii) the mean \pm 1SE AFDW/DW ratio (in %), and iv) the linear relationship between body size and AFDW/DW ratio (in %). α and β : normalization and scaling constant for power equations, respectively. ns: p>0.05, *: p<0.05, *: p<0.01, ***: p<0.001. Values in bold mark those significant (at α = 0.05). Note: R² were derived from linear log-log models.

			Bod	ody size vs. DW		Body size vs. AFDW			AFDW/DW	Body size vs. AFDW/DW		
Taxon	Class	Ν	æ±se	β ±SE	R ²	α±SE	β ±se	R ²	Mean %±1SE	Intercept±SE	slope±SE	R ²
Bithynia tentaculata L.	Gastropoda	25	$0.598{\pm}0.484^{ns}$	2.117±0.351***	0.847	0.479±0.511 ^{ns}	1.36±0.472**	0.668	19.133±2.207	33.162±3.878***	-1.91±0.452*	0.424
Hydrobia spp.	Gastropoda	24	0.239±0.041***	2.134±0.095***	0.952	0.079±0.029*	1.441±0.22***	0.758	13.737±1.155	19.791±2.855***	-0.633±0.715*	0.155
Potamopyrgus antipodarum Gray	Gastropoda	17	0.479±0.511 ^{ns}	1.360± (0.472**	0.919	0.021±0.012 ^{ns}	2.447±0.395***	0.898	16.051±1.399	6.063±4.616 ^{ns}	2.653±1.180*	0.202
Radix balthica L.	Gastropoda	20	0.137±0.035**	2.355±0.115***	0.956	0.046±0.018*	2.119±0.177***	0.906	27.087±2.233	35.338±3.558***	-1.794±0.650*	0.258
Theodoxus fluviatilis L.	Gastropoda	29	0.221±0.065**	2.683±0.148***	0.9492	0.015±0.006*	2.915±0.194***	0.912	13.044±1.083	18.52±2.396***	-0.242±0.494*	0.159
Cardidae spp.	Bivalvia	33	0.134±0.094 ^{ns}	2.848±0.347***	0.924	0.014±0.013 ^{ns}	2.806±0.486***	0.879	12.358±0.852	18.075±1.468***	-0.429±0.325*	0.364
Limecola balthica L.	Bivalvia	18	0.069±0.024*	2.820±0.134***	0.991	0.001±0.002 ^{ns}	3.479±0.673***	0.92	12.717±1.934	21.429±2.98***	-0.264±0.372*	0.383
Mytilus edulis L.	Bivalvia	24	0.030±0.015*	2.933±0.153***	0.991	0.006±0.003*	2.844±0.147***	0.978	14.189±0.504	13.162±1.044***	0.078±0.069 ^{ns}	0.011
Amphibalanus improvisus Darwin	Crustacea	13	0.314±0.205 ^{ns}	2.515±0.289***	0.976	0.036±0.022 ^{ns}	2.289±0.276***	0.961	8.939±0.550	11.044±1.064***	-0.397±0.179*	0.246
Gammarus spp.	Crustacea	37	0.047±0.032 ^{ns}	2.111±0.265***	0.926	0.033±0.028 ^{ns}	2.05±0.32***	0.863	58.966±1.519	63.062±2.616***	-0.389±0.307 ^{ns}	0.017
Idothea spp.	Crustacea	42	0.001±0.001 ns	3.592±0.200***	0.949	0.001±0.001 ^{ns}	3.850±0.249***	0.919	61.505±1.659	66.183±3.457***	-0.550±0.358 ns	0.032
Agraylea spp. (larvae)	Insecta	13	0.001±0.002 ^{ns}	3.410±0.721**	0.820	0.001±0.002 ^{ns}	3.432±0.769***	0.833	85.967±3.769	88.893±7.725***	0.570±1.277 ^{ns}	-0.097
Chironomidae spp. (larvae)	Insecta	38	0.014±0.016 ^{ns}	1.383±0.290***	0.600	0.008±0.006 ^{ns}	1.544±0.321***	0.533	79.307±2.643	78.633±6.947***	0.070±0.688 ^{ns}	-0.027
Limnephilidae spp. (larvae)	Insecta	10	0.001±0.001 ^{ns}	3.176±0.649***	0.746	0.001±0.001 ^{ns}	3.207±0.611***	0.789	91.851±2.137	86.64±3.558***	0.382±0.185 ^{ns}	0.290



Fig. 1. Maps of Sweden (small image) and the sampling area, marking the position of the 32 bays with black circles.

Fig. 2. Best-fitting relationships between body size (length or height, see methods) and a-d) dry weight (mg. DW), e-h) ash-free dry weight (mg. AFDW) and i-l) AFDW/DW ratio (% AFDW), for 14 taxa - five gastropods, three bivalves, three crustaceans and three insect larvae - sampled in coastal areas of the central Baltic Sea. For model parameters and estimates of fit, see Table 1.

