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Biometric conversion factors as a unifying platform for comparative assessment of invasive freshwater bivalves

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Abstract

1. Invasive bivalves continue to spread and negatively impact freshwater ecosystems worldwide.

As different metrics for body size and biomass are frequently used within the literature to standardise bivalve related ecological impacts (e.g. respiration and filtration rates), the lack of broadly applicable conversion equations currently hinders reliable comparison across bivalve populations. To facilitate improved comparative assessment amongst studies originating from disparate geographic locations, we report body size and biomass conversion equations for six invasive freshwater bivalves (or species complex members) worldwide: *Corbicula fluminea*, *C. largillierti*, *Dreissena bugensis*, *D. polymorpha*, *Limnoperna fortunei* and *Sinanodonta woodiana*, and tested the reliability (i.e. precision and accuracy) of these equations.

2. Body size (length, width, height) and biomass metrics of living-weight (LW), wet-weight (WW), dry-weight (DW), dry shell-weight (SW), shell free dry-weight (SFDW) and ash-free dry-weight (AFDW) were collected from a total of 44 bivalve populations located in Asia, the Americas and Europe. Relationships between body size and individual biomass metrics, as well as proportional weight-to-weight conversion factors, were determined.

3. For most species, although inherent variation existed between sampled populations, body size directional measurements were found to be good predictors of all biomass metrics (e.g. length to LW, WW, SW or DW: $R^2 = 0.82\text{--}0.96$), with moderate to high accuracy for mean absolute error (MAE): $\pm 9.14\text{--}24.19\%$. Similarly, narrow 95%–confidence limits and low MAE were observed for most proportional biomass relationships, indicating high reliability for the calculated conversion factors (e.g. LW to AFDW; CI range: 0.7–2.0, MAE: $\pm 0.7\text{--}2.0\%$).

4. *Synthesis and applications.* Our derived biomass prediction equations can be used to rapidly estimate the biologically active biomass of the assessed species, based on simpler biomass or body size measurements for a wide range of situations globally. This allows for the calculation of approximate average indicators that, when combined with density data, can be used to estimate biomass per geographic unit-area and contribute to quantification of population-level effects. These general equations will support meta-analyses, and allow for comparative assessment of historic and contemporary data. Overall, these equations will enable conservation managers to better understand and predict ecological impacts of these bivalves.

Keywords:

Allometric relationships, biomass and body size measurements, *Corbicula*, *Dreissena*, freshwater invasive bivalves, *Limnoperna*, *Sinanodonta*, weight conversion equations.

Accepted Article

1. Introduction

Organism biomass is considered an essential ecological variable, and is a key attribute of eco-physiological interactions, and community and food-web regulation (Gruner et al., 2018). Although the estimation, quantification, and cataloguing of organism biomass are common scientific practices, accurate biomass determination can be a laborious and time-consuming process that requires laboratory resources (Ricciardi & Bourget, 1998). For instance, ash free dry-weight (AFDW) is considered a highly accurate method for obtaining standardised biomass data for biologically active tissues, and is frequently used to assess benthic invertebrate species (Ricciardi & Bourget, 1998; Eklöf et al., 2017). However, estimation of AFDW requires the destruction of specimens through oven drying and incineration at high temperatures, resulting in the loss of potentially scientifically valuable specimens. To avoid specimen destruction and reduce processing costs, many studies tend to report mathematical conversion factors that are derived from population subsamples (e.g. Ricciardi & Bourget, 1998). Once established, conversion equations can be used to facilitate the determination of biomass for large quantities of organisms using simple proxy variables that scale predictably with biomass (Ricciardi & Bourget, 1998; Brey et al., 2010). Further, equations can also be used to estimate biomass categories, such as AFDW, based on directional measurements of specimen body size, i.e. length, width or height. In addition, proportional ratio-based weight-to-weight conversion equations allow for estimation of AFDW from a simple living-weight (LW) or wet-weight (WW), or a more accurate but destructive dry-weight (DW; Eklöf et al., 2017). In theory, despite inherent variation, conversion equations can facilitate multidirectional conversion of biomass parameters along a proportional scale of LW to AFDW. However, weight-to-weight conversion equations do not typically account for intraspecific variation of soft and hard tissue growth, i.e. biologically active versus non-active structures (Eklöf et al., 2017). Accordingly, the proportional AFDW to DW ratio may change with body size and ontogeny, which can impact the reliability of estimate-based biomass conversions (Lease & Wolf, 2010).

Invasive freshwater bivalves often display a high degree of physiological and ecological plasticity (Sousa et al., 2014), show indeterminate growth and high fecundity (Labecka & Czarnoleski, 2019), untypical modes of reproduction (Labecka & Domagala, 2018), and have a remarkable capacity for vector-mediated dispersal (Banha et al., 2016). Accordingly, these invaders can represent a major threat to the function and biodiversity of freshwater ecosystems (Sousa et al., 2014; Douda et al., 2017). Once established, invasive bivalves can dominate

macroinvertebrate communities and physically alter benthic habitats (Sousa et al., 2014). However, the functional importance and impacts of invasive bivalve populations on invaded ecosystems often remain poorly understood, insufficiently quantified and unrecorded (Douda et al., 2017). As dominant filter-feeders, most bivalves' ecological impacts are a result of their filtration or particle clearance rates (Sylvester et al., 2005; Marescaux et al., 2016), whereby suspended nutrients, contaminants and organic matter (phytoplankton, zooplankton, bacteria and fine particles) are removed from the water column, which can result in altered nutrient cycling, and increased rates of bioamplification, biomagnification and biodeposition (Sousa et al., 2014). Equally, the simultaneous production of large quantities of faeces and pseudo-faeces results in the transfer of resources from the water column to the sediment (Sousa et al., 2014; Marescaux et al., 2016).

A considerable amount of data detailing bivalve filtration and clearance rates has been reported within the literature, and these are most frequently standardised as units of measurement in relation to grams of DW or AFDW of the study species (e.g. Kryger & Riisgård, 1988; Sylvester et al., 2005). Further, filtration and clearance rates can also be described by their relationship to the LW, WW and shell free dry-weight (SFDW) of bivalves (e.g. Douda & Cadková, 2018; Joyce et al., 2019). Such data enable improved understanding of the dynamic processes shaping both community structure and biodiversity of invaded ecosystems (Sousa et al., 2014). However, extracting data for comparative purposes can be exceedingly difficult, as knowledge of bivalve weight-to-weight conversion parameters is often limited, ambiguous or incomplete. Indeed, the removal of impediments preventing the integration of information obtained from numerous disparate sources is considered essential for the advancement of conservation biogeography (Richardson & Whittaker, 2010). To date, bivalve body size-to-weight and weight-to-weight relationships have not been documented for several widespread invasive freshwater bivalves, or are not readily accessible through systematic searches of major online databases (e.g. Scopus, Web of Science, Google Scholar). Although a number of studies have documented conversion relationships for body length to biomass, most only consider individual populations of *Corbicula* and *Dreissena* species (e.g. Aldridge & McMahon, 1978; Glyshaw et al., 2015; Balogh et al., 2019); while similar studies on other widespread freshwater invasive bivalves such as *Limnoperna fortunei* and *Sinanodonta woodiana* are rare or altogether non-existent. Moreover, most studies have only tended to derive population-specific equations for the conversion of shell length to a limited number of biomass categories, usually specimen dry-weight

(Aldridge & McMahon, 1978; Mackie, 1991; Dermott et al., 1993), dry shell-weight (Aldridge & McMahon 1978), shell free dry-weight (Aldridge & McMahon, 1978; Mackie, 1991; Balogh et al., 2019), or ash free dry-weight (Bonel & Lorda, 2015; Glyshaw et al., 2015; Balogh et al., 2019). Notwithstanding available equations, there is a considerable need for general conversion equations that systematically describe relationships between the most commonly used size and weight variables, being applicable to a wide range of situations.

Additionally, the use of conversion equations derived from a single population alone may not always be appropriate, given that the growth rates and condition index (i.e. soft to hard tissue ratio) of individuals can vary due to the substantial differences in biotic and abiotic conditions experienced by bivalve populations residing at disparate locations. Furthermore, while there is a lack of robust equations available for the conversion of bivalve body size to biomass, body size measurements are especially beneficial, given the relative ease of data collection (Eklöf et al., 2017). Accordingly, location specific and more general, widely-applicable conversion equations for biomass and directional measurements would be a highly useful tool for researchers. In particular, although body size to biomass equations pertaining to independent populations can be found within the literature for some invasive freshwater bivalves, almost no information is currently available for proportional biomass conversion relationships. Reliable conversion equations could improve the assessment of size-biomass based relationships that underpin various aspects of bivalve research, including metabolic rates (Sprung, 1995), individual growth (Karatayev et al., 2006), productivity of discrete cohorts (Joyce et al., 2019), phosphorus and ammonia uptake and release (Lauritsen & Mozley, 1983) and trace metal bioaccumulation (Tang et al., 2017).

In the present study, we report comprehensive biometric conversion equations for six of the most successful and widely studied invasive bivalves (or species complex members, e.g. *Corbicula* lineages): *Corbicula fluminea* (form A/R; Pigneur et al., 2011), *C. largillierti* (form C/S), *Dreissena bugensis*, *D. polymorpha*, *L. fortunei* and *S. woodiana*. These straightforward estimates detail the relationship between body size and biomass, and the parameters of weight-to-weight biomass conversion across multiple and geographically disparate populations of each species within their invaded ranges. Through the capture of inherent variation amongst these populations, we report both general estimates and population-specific biometric conversion factors, to facilitate the unification of biometric information that can be obtained from disparate sources within the literature. We then test the reliability of these equations (i.e. precision and

accuracy). Further, for each species, we also assess whether the AFDW to DW ratio changes with body size.

2. Methods

2.1. Populations sampled

Commonly used body size and biomass measurements were recorded for populations of *Corbicula fluminea*, *C. largillierti*, *Dreissena bugensis*, *D. polymorpha*, *Limnoperna fortunei* and *Sinanodonta woodiana*, ranging across 14 countries in Asia, the Americas and Europe (Figure 1). For each species, populations from up to nine countries were assessed, with up to four populations being sampled for each country. In essence, these populations were opportunistically selected and represent the bivalve populations to which the consortium of collaborators had access. Populations were sampled as the opportunity arose, mostly between late spring and early autumn and encompassed various reproductive stages. For each sampled population, undamaged living individuals of mixed sizes were collected by hand for examination. Whilst no specific protocol was employed to avoid potential size bias, collectors were asked to select as broadly a representative sample of the available size range as possible. To avoid desiccation, specimens were maintained within source water prior to acquisition of measurements (≤ 48 hrs). In some instances, prior to processing, specimens were frozen for transport and/or storage (-20°C). Freezing of organisms is unlikely to have a significant effect on body size and biomass of bivalves (Ricciardi & Bourget, 1998).

2.2. Size and biomass variables

In the laboratory, three measurements of body size and six measurements of biomass were captured. First, any foreign material found adhering to the external surface of specimens was completely removed. If required, specimens were thawed to room temperature. Body size directional measurements of shell length (L), width (W) and height (H) were recorded for every specimen with the aid of callipers (0.01 mm; Figure S1.1). Following this, any excess water was removed from surfaces by drying the external shell with tissue paper. Further, using a scalpel blade and tweezers, excess water was removed from the mantle cavity by gently forcing bivalves to gape, taking care not to cut the adductor muscle or damage tissues. Using high-resolution scales, living-weight (LW) was obtained for each specimen. Then each specimen was fully opened, which in most cases involved cutting of the adductor muscles. To remove additional fluid

from the mantle and other cavities, each specimen was then placed with the valve gape (flesh) facing downwards onto absorbent tissue, for ~5-10 minutes. A wet-weight (WW) was obtained for each specimen. Following this, the soft tissue was dissected from the shell, then both soft tissue and shell were dried together within an oven (60-72 °C) for ~48 hrs, or until they reached a constant weight. Specimens were cooled to room temperature in a desiccator before final weighing. A combined dry-weight (DW) was recorded, as were weights for the soft tissue and shell separately, i.e. shell free dry-weight (SFDW) and dry shell-weight (SW), respectively. While the vast majority of specimens were dissected purely mechanically, in some instances, soft tissues were first softened by submersing specimens in 7% NaOH and then dissected (Rodríguez & Dezi, 1987). These empty shells were then collected, dried again to constant weight, and weighed to obtain SW. This was done mostly for small specimens of *L. fortunei*, for which total or partial dissolution of tissues facilitated dissection without breaking the specimens' thin valves and prevented unwanted retention of soft tissue. In this case, following the establishment of SW, SFDW was calculated subtracting SW from the total DW (i.e. $SFDW = DW - SW$). To obtain an ash-weight (AW), the soft and hard tissue structures of specimens were incinerated (500–550 °C) together within a muffle furnace for 4–6 hrs. In all cases, the ash free dry-weight (AFDW) was then calculated for the entire specimen (soft tissue and shell) by subtracting the AW from DW, i.e. $AFDW = DW - AW$. When soft tissues were dissolved by NaOH, the AFDW is not reported. All samples were cooled to room temperature in a desiccator before final weighing. When weight values were too low to obtain a record or produced an inconsistent result (e.g. $SW \geq \text{total DW}$), the specimen was removed from its corresponding database.

2.3. Relationships between body size and individual biomass

Body size to biomass relationships were examined for each of the six bivalves using non-linear regressions in the form of the power law equation (e.g. Eklöf et al., 2017):

$$\text{Biomass} = \alpha \times \text{size}^\beta$$

where biomass is a measurement of the individual mass category (i.e. LW; WW; DW; SW; SFDW; or AFDW, in g) and size is a directional measurement of body size (L; W; or H, in mm), while α defines a normalization constant, and β is designated as the scaling constant (i.e. the allometric coefficient). As biomass typically scales upwards with body size, non-linear regressions

with heteroscedastic variance were modelled as power functions in relation to mean α and β values, as initial data exploration indicated a superior fit relative to linear and logarithmic exponentiated equations (*sensu* Packard, 2014). However, for the above models, we also report the simpler and more intuitive Pearson's coefficient of determination (R^2) for the linear log–log relationship between body size and biomass as a measure of conversion precision. Mean absolute error (MAE; i.e. the mean difference between actual and predicted values) was additionally calculated for each species to inform upon accuracy of the derived power law equations.

2.4. Proportional weight-to-weight conversion factors

Ratios between six biomass variables (all those measured except AW, which was only used to calculate AFDW) were calculated for each individual specimen. Proportional conversion factors between the biomass variables were then calculated for each population by computing mean and median values for these ratios. Standard deviation, standard error (SE) and 95% confidence interval (CI) values were also calculated for each conversion factor and population as an assessment of data variability, thus informing on the precision of conversion estimates. Using population mean values, an overall grand mean, associated median, SE and 95% CI values were obtained for each species. Further, absolute error calculations were then used to assess the accuracy of the estimated conversion factors in relation to each individual specimen (i.e. the difference between the expected grand mean conversion value and the actual specimen values). An overall MAE was calculated for each species to assess accuracy of conversion factors. Here, we consider a conversion factor to be reliable (precise and accurate) when both a narrow CI ($\leq \pm 10\%$) and low MAE ($\leq \pm 10\%$) are shown.

2.5. Relationship between body size and AFDW/DW ratios

To examine the potential influence of bivalve size on the proportion of body flesh, relationships between body size (L, W, H) and the ratio AFDW/DW were also calculated for all six bivalve species. For each individual species, the relationship between body size and the proportional AFDW to DW ratio was assessed *via* linear regression for all populations, both individually (i.e. population-specific) and combined (i.e. species-wide).

2.6. Data analysis

For each species, the individual variables for body size, biomass measurements and proportional biomass conversion estimates were analysed among all sampled populations using Kruskal–Wallis tests, for a conservative test of possible differences among populations. All data analyses were performed using the base 'stats' package in R v3.4.4 (R Core Development Team, 2018), while non-linear models were created using the 'gnls' function from the 'nlme' package.

3. Results

3.1. Populations sampled

We obtained samples from 44 populations belonging to the six invasive bivalve species studied, from latitudes ranging between 54.61° N and 34.85° S, and longitudes between 112.53° E and 105.63° W (Figure 1; see Table S1.1 in Appendix S1 in Supporting Information). Between 15 and 132 individuals were obtained from each population, accounting for a total of 3731 individuals for all species and populations (Table S1.1). These 44 populations consisted of ten *C. fluminea* ($n = 865$ individuals), two *C. largillierti* ($n = 189$), five *D. bugensis* ($n = 475$), 14 *D. polymorpha* ($n = 1292$), six *L. fortunei* ($n = 619$) and seven *S. woodiana* ($n = 291$).

3.2. Size and biomass variables

We obtained average L for each population, as well as average W and H values with the exception of one population for each of *D. bugensis*, *D. polymorpha* and *L. fortunei* (Table S1.1). Average L, W and H across populations are presented in parentheses, while population-specific means are summarised in Table S1.1: *C. fluminea* (21.9, 14.6, 20.3 mm), *C. largillierti* (16.7, 9.4, 14.6 mm), *D. bugensis* (21.3, 10.8, 12.0 mm), *D. polymorpha* (17.6, 9.4, 8.9 mm), *L. fortunei* (14.8, 6.0, 7.0 mm), and *S. woodiana* (107.0, 41.6, 69.8 mm). Similarly, we obtained data for the six biomass variables for all populations inspected. However, in some instances, only partial information was available for species populations. This was the case for *C. fluminea* (three populations out of 10 studied), *D. bugensis* (one of five), *D. polymorpha* (two of 14), *L. fortunei* (four of six), and *S. woodiana* (one of seven). In such instances, one or more variables were unavailable for the entire population. While the number of populations used to calculate weight-to-weight conversion factors are shown (Tables S1.2–S1.5), we did not attempt to summarize raw biomass information, as raw data for all variables are provided (see Data Accessibility Statement). In general, for all species, significant inter-population variability was observed for directional

measurements and biomass categories (i.e. Kruskal–Wallis, $P < 0.001$; see Table S1.6–S1.8), indicating substantial differences between sampled populations.

3.3. Relationships between body size and individual biomass

Body size to biomass conversion equations and associated model parameters for the examined invasive bivalves are provided in Tables S1.9–S1.11. The best-fit relationships between body size and biomass are shown in Figures S1.2–S1.4. Body size measurements, especially length, were found to be good predictors of all biomass variables in relation to both precision and accuracy (Tables S1.9–S1.12). Although model fits for the prediction of SFDW and AFDW from body size measurements were occasionally poor (all species: $R^2 = 0.63–0.89$), prediction parameters for LW, WW, SW and DW had good predictive power ($R^2 = 0.82–0.96$), indicating high model precision in all cases, excepting for *C. largillierti* ($R^2 = 0.66–0.95$). Low SE was also evidenced for all models (Tables S1.9–S1.11). Similarly, whilst calculated MAE tended to be high for SFDW and AFDW conversion equations (all species: length-based models; $\pm 12.94–59.28\%$), MAE values were generally low to moderate for LW, WW, SW and DW (per length; $\pm 9.14–24.19\%$), indicating relatively high model accuracy for most cases, excepting for *C. largillierti* ($\pm 16.99–31.50\%$; Table S1.12). In some instances, width and/or height-based equations were found to have marginally greater model accuracy than those based on bivalve length (e.g. LW, WW, SW and DW models for *D. polymorpha*; Table S1.12). In all cases, greater MAE values were associated with models showing a larger spread of data around the predicted equations (i.e. the best-fitting relationship; Figures S1.2–S1.4), with larger sized individuals tending to drive the disparity between predicted values and actual biomass measurements. Calculated scaling constants (β) were generally above 2, ranging 1.7–3.8 across all species. Ordinate at origin were very near zero in all cases.

3.4. Proportional weight-to-weight conversion factors

Proportional weight-to-weight conversion factors obtained for all weight measurements and species examined are presented in Tables S1.2–S1.5. Population-specific weight-to-weight conversion factors are provided within Appendix S2. In general, significant inter-population variability was observed for all species in relation to the proportionality of biomass categories (i.e. Kruskal–Wallis, $P < 0.001$; Tables S1.6–S1.8). Low SE, narrow CI and low MAE values were observed for most proportional biomass relationships, indicating both precision and accuracy for

the calculated conversion factors (Figure 2). Nevertheless, large SE, wide CI and large MAE values were produced in some instances, especially for *C. largillierti*. Notably, other than for *L. fortunei*, LW values could be used to reliably predict AFDW (95% CI range: 0.7–2.0, MAE: 0.7–2.0; Table S1.2). Further, the biomass conversion relationship for AFDW (entire specimen) as a proportion of SFDW produced inflated mean values and exceptionally wide CI and large MAE for all species. In contrast, the inverse relationship of SFDW/AFDW is less variable in all cases, although not necessarily reliable (Table S1.5).

3.5. Relationship between body size and AFDW/DW ratios

The overall relationships between body size (length, width or height) and calculated AFDW/DW ratios are given in Appendix S1, Table S1.13. In general, AFDW/DW ratios tended to linearly decrease in relation to larger bivalve body sizes, excepting for positive relationships shown by *C. fluminea* and *L. fortunei* (Figure S1.5; Table S1.13). All species linear relationships were significant ($P < 0.001$), other than for height of *C. largillierti* ($P = 0.058$; Table S1.13). However, inter-population differences in relation to slope direction were observed for all species, excepting *D. bugensis* (see Appendix S3). Similarly, the significance of the relationship between body size and AFDW/DW ratios varied amongst populations (Appendix S3). Overall, R^2 values were exceptionally low (0.02–0.18; Table S1.13). Regardless of direction, calculated linear slopes (m) for species were relatively minor. Calculated slopes show changes to the proportional measurement for AFDW/DW to body size, ranging from 0.07–1.33% (Table S1.13). Similarly, for all species, per-population slope values generally remained quite small for length, width and height ($< 1.8\%$). However, *D. polymorpha* specimens obtained from Lake Maggiore, Italy, showed a higher rate of change ranging from 2.1–4.5% (Appendix S3).

4. Discussion

4.1. Relationships between body size and individual biomass

Body size directional measurements were found to be good predictors of all biomass categories for all species, with body length being especially reliable. In general, derived models show high precision and moderate to high accuracy. However, slightly poorer model fits for SFDW and AFDW suggests the presence of some measurement variability due to laboratory operator and device error when processing these often quite small weights (Eklöf et al., 2017). Although the estimated scaling (β) constants tended to be reasonably similar, the apparent

differences of these calculated coefficients emphasise the need to have species-specific equations rather than reliance on the grouping of species within higher taxonomic classifications for the assessment of body size to biomass relationships (e.g. Ricciardi & Bourget, 1998). In addition, a positive allometric relationship (i.e. $\beta > 1$) between biomass and body size was detected for all species, which indicates that bivalves will get heavier relatively more quickly than their rate of body size increase. Therefore, we argue that the power law equations generated from this study can be used to decipher the biomass categories of the assessed species, but cannot be reliably substituted for related species, or disparate lineages within a species complex. Comparisons with previous studies also highlight differences between populations of the same species, despite the good overall fit of weight-length relationships. For example, previous studies on *C. fluminea* in Lake Arlington (USA) and Río de la Plata (Argentina) arrived at average estimates of the scaling constant between SFDW-L and DW-L of 2.65–3.14 and 3.08, respectively (see Appendix S4). However, our estimations of the same parameters only fall within the lower portion of the ranges, i.e. $2.92 \pm 6.34 \times 10^{-2}$ and $2.70 \pm 2.58 \times 10^{-2}$ ($\beta \pm \text{SE}$). Compared to these two previous studies, our estimates capture the variability of >800 *C. fluminea* specimens from nine populations worldwide. Therefore, we contend that our estimates will constitute better approximations for *C. fluminea* across most scenarios. Similarly, in the case of *D. polymorpha*, our average estimations of β ($\pm \text{SE}$) for WW-L and DW-L relationships ($3.03 \pm 2.40 \times 10^{-2}$ and $3.05 \pm 2.25 \times 10^{-2}$, respectively) fall above the values reported in previous studies for two closely residing populations (2.66 and 2.61–2.98, respectively) (Appendix S4). According to our results, these seem to represent lower-bound situations, while our estimations likely constitute a better representation of the average global picture for *D. polymorpha*.

In contrast, our estimation of the SFDW-L relationship for *D. bugensis* based on five populations from Europe and North America (estimated scaling constant: $\beta = 2.66 \pm 5.26 \times 10^{-2}$) falls within the range measured by previous studies in The Netherlands and Hungary (1.90–3.02: Appendix S4). Similarly, our estimation of the SFDW-L relationship for *D. polymorpha* ($\beta = 2.57 \pm 5.17 \times 10^{-2}$) occupies an intermediate position in the range reported by previous studies on three European ($\beta = 1.78$ – 2.64 : Kryger & Riisgård, 1988; Balogh et al., 2019) and two North American populations of the *D. polymorpha* ($\beta = 2.20$ – 3.0 : Mackie, 1991; Dermott et al., 1993). Our estimate included eight populations from mainland Europe (Belgium, Germany, Italy, Poland and Spain), two non-continental European populations (Great Britain and Ireland), and four populations from distant locations across Canada and the USA. Accordingly, for both *D. bugensis*

and *D. polymorpha*, the relatively close geographic match between source populations likely promotes consistency between the present and previous estimations of their SFDW-L relationships. Further, biometric conversion equations available for *D. polymorpha* have encompassed a wide range of geographic situations, which likely increased the level of agreement amongst past studies and the present results. In the case of *L. fortunei* and *S. woodiana*, previous information is quite rare or nonexistent (but see Bonel et al., 2013; Bonel & Lorda, 2015), and thus the present data provide the only estimations currently available.

The observed inter-population variability can be driven by numerous abiotic and biotic factors (Oliveira et al., 2015), and significant differences between bivalve size-biomass relationships across different sites have previously been reported (e.g. Nalepa et al., 1993; Balogh et al., 2019). In particular, bivalve size-biomass relationships can be altered, even amongst spatially close populations, by a variety of site-specific factors such as water depth, bivalve density, food availability (Nalepa et al., 1993; Glyshaw et al., 2015), pollution (Dumont et al., 1975), genetic differences (Paolucci et al., 2014) and optimal resource allocation for fecundity (Heino & Kaitala, 1996). Time variation, both inter- (Balogh et al., 2019) and intra-annual (Nalepa et al., 1993), can also significantly affect biomass due to abiotic and complex biotic effects. The condition index and reproductive state of organisms (i.e. ovigerous or viviparous versus recently spawned) can also greatly affect weight-size relationships (Aldridge & McMahon, 1978; Nalepa et al., 1993). As such, we argue that the inherent variation surrounding gravid status of these freshwater bivalves is captured to a reasonable extent, which is adequate for general purpose conversion factors. Finally, multiple experimental operators performing data collection likely also increased the variance among estimates of conversion factors and equations.

4.2. Proportional weight-to-weight conversion

Proportional weight-to-weight conversion factors obtained in the present study exhibited a significant inter-population variability, indicating that conversion values obtained for one specific population cannot be liberally used for another population. Additionally, although the AFDW/WW relationship tended to be more precise and accurate than AFDW/DW, as conversion equations were based on proportional change, the biologically relevant margin of error may be greater. Specifically, for example, as biomass of WW was greater than DW, a 1% margin of error for WW could reflect a greater biomass change than 1.5% of DW. While the practical use of conversion estimates with large variance has limitations due to decreased reliability, the results

derived for these species highlight the importance of population variability, and the need to obtain approximate estimates that capture this inherent variability by avoiding underrepresentation of population driven variability through the sampling of multiple disparate populations. Further, excessively large mean conversion, CI and MAE values for the weight-to-weight relationship between AFDW/SFDW for all species, clearly show these variables cannot be used interchangeably. This is likely due to the organic portion of the bivalve shell (i.e. periostracum and hinge ligament), being included in AFDW but removed for SFDW calculations.

4.3. Relationship between body size and AFDW/DW ratios

In general, there was a negative influence of body size on the AFDW/DW ratio, so that with increased body size, the proportional mass of biologically active tissues generally decreased in relation to non-active tissues (Appendix S3). This could mean that larger, generally older, individuals develop thicker shells over time, resulting in a higher shell to tissue mass ratio (Eklöf et al., 2017). Contrastingly, positive slopes indicate a greater investment in soft tissue production, which may include respawning or gravid states. Similarly, abiotic factors such as the availability of calcium or the acidity of water may limit the development of hard tissue structures (Ferreira-Rodríguez et al., 2017). Nevertheless, despite both positive and negative trends existing amongst populations, calculated linear slopes were observed to be small with low R^2 values.

4.4. Study implications and caveats

The biometric conversion equations derived by the present study provide a unifying platform for rapid estimation of biologically active biomass from simpler biomass or body size measurements for six invasive bivalves. In essence, for the first time, researchers will be able to directly compare both inter- and intra-specific studies, from spatially and temporally disparate bivalve populations, where study results have been standardised to discrete weight categories for which no universally applicable conversion equations have previously existed. Nevertheless, although uncertainty is accounted for in relation to precision and accuracy, these general equations need to be taken as approximate average indicators, especially in the context of body size to biomass relationships.

For each of the six assessed bivalves, inherent variation exists amongst bivalve populations concerning proportion of investment made in generating soft or hard tissue structures, which warns us about the risks of indiscriminately extrapolating relationships between populations.

Given that specimens were obtained from populations situated across a large geographical gradient, these discrepancies illustrate that our general estimations will often be preferable to the selection of a body size conversion equation that is based on a single population, which would likely be unacceptably inaccurate, particularly if the equation is sourced from a geographically disparate location. Nevertheless, where possible, we recommend researchers continue to calculate body size to biomass relationships as unique to their study population, with the general equations depicted by the present study being a useful tool when a primary equation cannot be produced.

Our conversion equations will have a large number of applied and theoretical uses (which will ultimately also inform management decisions) including assessments of impact and ecosystem function for meta-analysis purposes. In addition, mass mortality events have been repeatedly described for many invasive freshwater bivalves, including *C. fluminea* (e.g. Bódis et al., 2014; McDowell et al., 2017), *D. polymorpha* (e.g. Churchill et al., 2017) and *S. woodiana* (Bódis et al., 2014). Yet the impact of these events on ecosystem function remains difficult to quantify, especially as soft tissue structures will be rapidly consumed or decompose (McDowell & Sousa, 2019). However, conversion equations can be used to reliably calculate total biomass, which would allow for estimations of nutrients released during mortality events when combined with bivalve stoichiometric data. Other uses include the determination of the impact of these invasive bivalves on the diets of predators, as our equations can be used to predict biomass from partially digested bivalve prey or empty shells extracted from predators. Further, these general equations can be used as a platform to assess historic data, thus allowing comparison with contemporary data. For example, records of bivalve body size data could be used to extrapolate biomass, while older studies using biomass categories of WW could be converted to DW to facilitate comparative assessment, giving greater insight into estimates of physiological rates, secondary production, ecosystem function, services and impacts for these invasive species (that are commonly standardised by different body size and biomass units). Further, these data establish a basis for further in-depth assessment of seasonal and regional differences in bivalve biometric parameters, which in turn could provide for greater insight into fundamental aspects of invasive bivalves ecological roles, and whether or not these roles differ across regions and seasons. To achieve this, repeated sampling of bivalve populations over seasonal temporal scales, as well as data concerning regional biotic and abiotic conditions, rather than simple geopolitical borders, would be required.

From a management perspective, while the prevention of further invader spread is generally accepted as the most optimal and efficient management approach (e.g. Coughlan et al., 2020), an improved understanding of population level effects would allow for more informed decisions concerning the allocation of resources for invader control (Dick et al., 2017). The derived equations can be rapidly employed by managers and policy makers to aid determination of bivalve driven effects and associated ecological risk, as well as the subsequent impact of any management interventions as part of cost-benefit assessments. As an example, basic laboratory experiments can be used to determine bivalve clearance and nutrient cycling rates from a small number of specimens in relation to their biologically active biomass, combined with density data, our equations will then allow bivalve driven effects to be scaled to the level of infestation observed at an invaded site. Such knowledge will aid decision makers in prioritising the allocation of resources across multiple invaded sites. Furthermore, the determination of biologically active biomass within invaded sites (as explained above for fortuitous mass mortalities) can also be used to predict nutrient release by purposefully killed bivalves, which can underpin a more strategic approach to control whereby only a portion of bivalves are actively killed at any one time to mitigate excessive nutrient release. As such, our derived biometric conversion factors can provide a unifying platform for these comparative assessments, as well as management strategies.

4.5. Conclusions

Overall, body size directional measurements are good predictors of bivalve biomass, which has previously been recorded in the literature on a per population basis. Further, proportional weight-to-weight conversion equations can be used with reasonable reliability to estimate biomass of the examined species based on a single known weight. Importantly, our equations capture inter-population variability upon a global scale. However, our results also suggest that general relationships, while in most cases being more appropriate than those arbitrarily or opportunistically picked from the literature, need to be taken as approximate average indicators from which many situations will deviate. Future work should consider the development of more specific models, which could account for, *inter alia*, seasonal weight changes, reproductive stages, and different habitat conditions. Nevertheless, using standard body size measurements, our derived equations can facilitate rapid estimation of biologically active biomass for these examined invasive bivalves. When combined with density data, these equations can be used to estimate biomass per unit area and improve understanding of associated population-level impacts. We

believe these equations will permit comparisons among a large number of studies (e.g. metabolic, reproductive, growth, ecotoxicological studies, meta-analyses, and historical assessments), which will enhance understanding of bivalve-driven ecological processes within invaded ecosystems. Future studies could attempt a systematic analysis of regional and seasonal patterns and consider conversion equations for shell-free AFDW, which has been used within the literature but omitted here.

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6. Authors' contributions

N.E.C. conceived and designed the study; all authors contributed to data collection; N.E.C., E.M.C., R.N.C. and P.W.S.J. performed data analysis; all authors contributed to the interpretation

of results, which was led by N.E.C. and F.S.; and all authors contributed to the writing and editing of the manuscript, which was led by N.E.C. with support from F.S.

7. Data Availability Statement

Data available from the Dryad Digital Repository:

[<https://doi.org/10.5061/dryad.tdz08kq0c>] <https://doi.org/10.5061/dryad.tdz08kq0c> (Coughlan et al., 2021).

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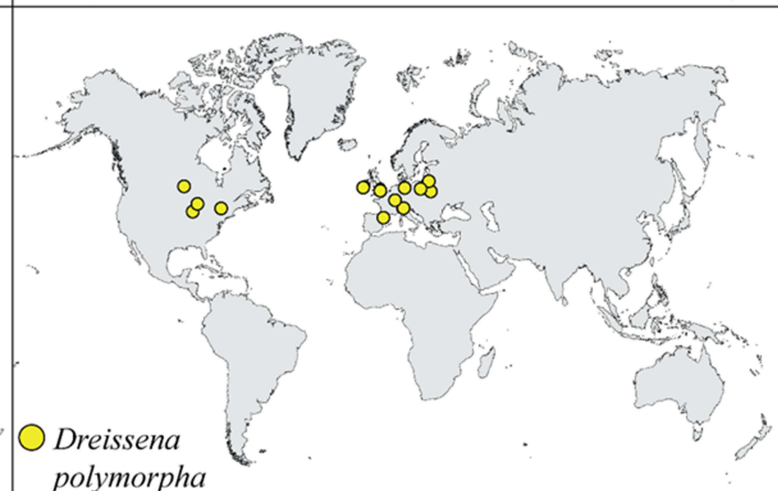
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Figure Legends

Figure 1: Sample site locations for populations of six invasive bivalve species. See Appendix S1 in Supporting Information for more specific site locations (Table S1.1).

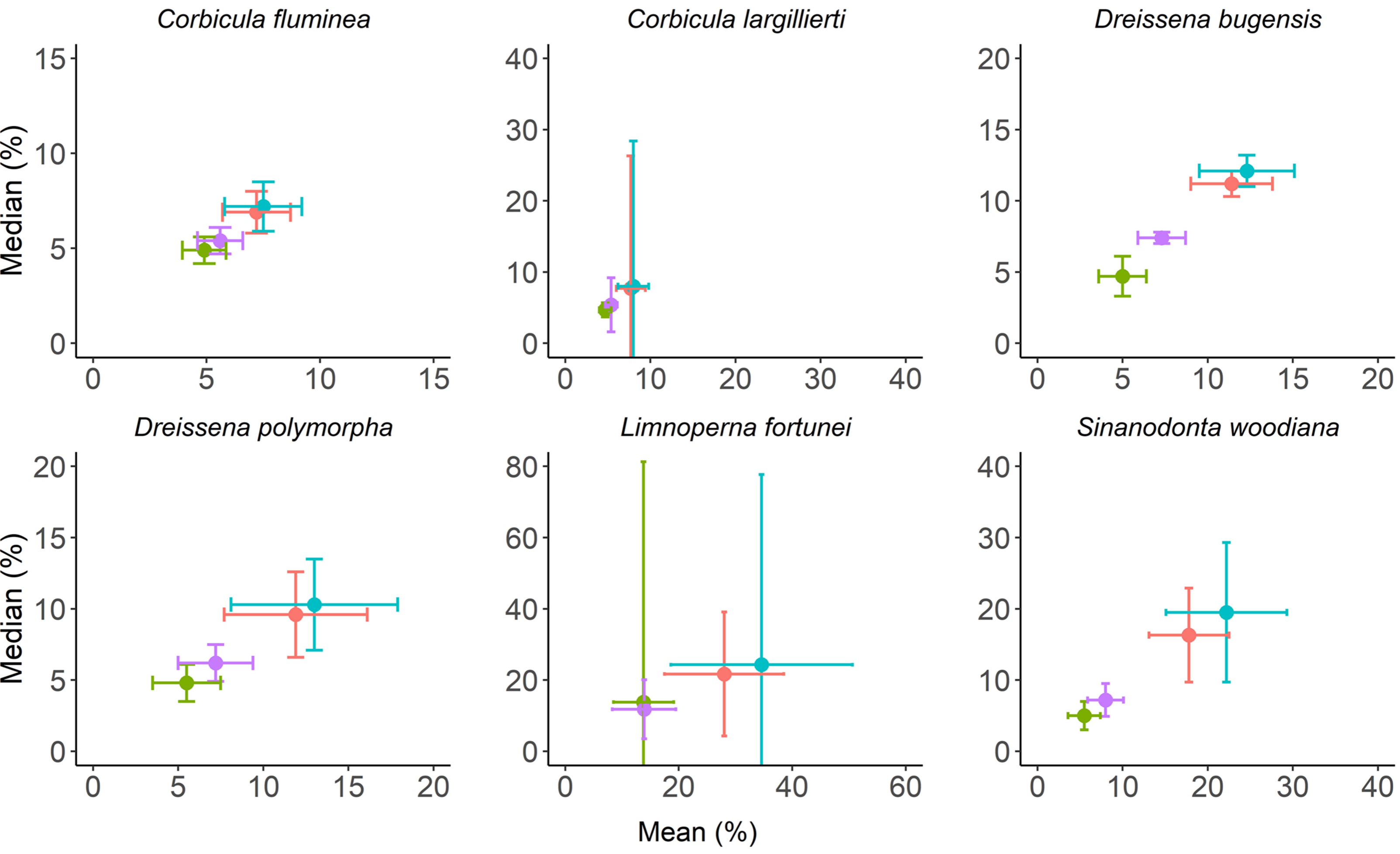
Figure 2: Graphical summarisation of variability in precision and accuracy for selected proportional weight-to-weight conversion factors. All conversion factors obtained are presented in Appendix S1 in Supporting Information (Tables S1.2–S1.5). Note differences in scale for the sake of data visualisation among the inserted panels.



Biomass conversion:



Median biomass conversion (%) ± 95%CI
Precision indicator



Mean biomass conversion (%) ± mean absolute error

Accuracy indicator