Improving the estimation of deep-sea megabenthos biomass: dimension to wet weight conversions for abyssal invertebrates

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ABSTRACT: Deep-sea megafaunal biomass has typically been assessed by sampling with benthic sledges and trawls, but non-destructive methods, particularly photography, are becoming increasingly common. Estimation of individual wet weight in seabed photographs has been achieved using equations obtained from measured trawl-caught specimens for a limited number of taxa. However, a lack of appropriate conversion factors has limited estimation across taxa encompassing whole communities. Here we compile relationships between measured body dimensions and preserved wet weights for a comprehensive catalogue of abyssal epibenthic megafauna, using ~47 000 specimens from the Porcupine Abyssal Plain (NE Atlantic) housed in the *Discovery Collections* (National Oceanography Centre, Southampton, UK). The practical application of the method is demonstrated using an extremely large dataset of specimen measurements from seabed photographs taken in the same location. We also collate corresponding field data on fresh wet weight, to estimate the impact of fixation in formalin and preservation in industrial denatured alcohol on the apparent biomass. Taxa with substantial proportions of soft tissues lose 35 to 60% of their wet weight during preservation, while those with greater proportions of hard tissues lose 10 to 20%. Our total estimated fresh wet weight biomass of holothurians and cnidarians in the photographic survey was ~20 times the previous estimates of total invertebrate biomass based on trawl catches. This dramatic uplift in megabenthic biomass has significant implications for studies of standing stocks, community metabolism, and numerical modelling of benthic carbon flows.

KEY WORDS: Biomass · Invertebrate · Preservation · Wet weight · Photograph · Deep sea · Porcupine Abyssal Plain

INTRODUCTION

Deep-sea epibenthic invertebrate megafaunal biomass has typically been assessed by sampling with sledges and trawl nets (Gage & Bett 2005). Our current understanding of the ecology of these assemblages is based on these techniques, including studies of community dynamics over time (Billett et al. 2001) and space (Alt et al. 2013), food web interactions (van Oevelen et al. 2012), the potential links between resource availability and community dynamics (Ruhl et al. 2014), and their contributions to large-scale and global assessments of standing stocks (Rex et al. 2006, Wei et al. 2010). Although trawling and similar approaches are necessary to obtain specimens for taxonomy, histology, and genet-

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ics, such samples have major quantitative uncertainty in terms of the seabed area sampled, and likely do not accurately represent the megabenthic community present (Rice et al. 1979, Bett et al. 2001).

The investigation of deep-sea communities has increasingly favoured non-destructive methods, primarily photography (Jamieson et al. 2013), which can produce quantitative data on the megabenthos (Jones et al. 2009, Smith & Rumohr 2013). Trawling has long been known to provide semi-quantitative sampling of megabenthic biomass, as a result of variable coverage and poor quantification of the seabed area sampled by trawls (Gage & Tyler 1991), lower catching efficiency of trawls, and body-size- and tissue-type-based variation in trawl efficiency (Owen et al. 1967, Rice et al. 1979, Smith & Hamilton 1983, Bett et al. 2001, Durden et al. 2015b). Large photographic surveys of the seabed have revealed substantially higher standing stocks of deep-sea megabenthos than corresponding trawl catch data (Morris et al. 2014, Durden et al. 2015a), thus the use of seabed photography to improve quantification of biomass is logical and of potentially substantial significance to our understanding of deep-sea ecology in general, and carbon budgets in particular. For example, consider the expectation that the distribution of biomass in marine communities may be constant across logarithmic size classes (Sheldon et al. 1972), or increase continuously in logarithmic classes among the benthos (Bett 2013, Kelly-Gerreyn et al. 2014). Consequently, a substantial fraction of standing stock carbon may be represented by the megabenthos that are currently grossly underestimated from trawl catch data.

Some previous photographic studies have estimated megafaunal biomass using abundances estimated from photographs in combination with mean wet weights of trawled specimens, largely in high-level taxonomic groupings for key faunal groups (e.g. Smith & Hamilton 1983, Thresher et al. 2011). Detailed estimation of abyssal invertebrate wet weights from dimensions measured in seabed photographs has been achieved for echinoderms (Ruhl et al. 2014), and for high-level taxonomic groupings at the Mid-Atlantic Ridge (Alt et al. 2013) and the northeast Atlantic (Christiansen & Thiel 1992). Further conversions between body length wet weight from trawl-caught specimens have been published for individual species (e.g. *Enypniastes eximia*; Bailey et al. 1994). However, a lack of appropriate conversion factors for many taxa has limited estimation across complete megafaunal communities.

Here we establish a comprehensive compilation of relationships between measured body dimensions

and preserved wet weights for abyssal epibenthic megafauna from the Porcupine Abyssal Plain (PAP; NE Atlantic). We accessed specimens from the exceptional archive of trawl-caught megabenthos housed in the *Discovery Collections* at the National Oceanography Centre, Southampton, UK. We develop links between those data and an extremely large dataset of specimens measured from seabed photographs taken in the same location, to test the practical application of the method. We collate corresponding field data on fresh wet weight, to estimate the impact of preservation on the apparent biomass of the megabenthos assemblage. Finally, we illustrate the significance of our approach by comparison with previously published estimates of PAP megafaunal biomass.

MATERIALS AND METHODS

Dimension to wet weight conversions from trawled specimens

Conversions were created using ~47 000 specimens collected in the vicinity of the Porcupine Abyssal Plain Sustained Observatory Site (PAP; 48° 50' N, 16° 30' W, 4850 m water depth; Hartman et al. 2012) using a semi-balloon otter trawl (Billett et al. 2001) on a number of research cruises between August 1996 and October 2002: RRS 'Discovery' 222 (Rice 1996), 226 (Rice 1997), 229 (Bett 1998), 231 (Rice 1998), 237 (Sibuet 1999), and 266; and RRS 'Challenger' 135 (Billett 1998) and 142 (Billett 2000). Specimens were fixed in borax-buffered 10% formalin-seawater at sea, and subsequently transferred to 80% industrial denatured alcohol for long-term preservation once ashore (generally within 2 months of sample collection). For the analyses presented here, specimens were reduced to those considered to be complete and intact (e.g. including coelemic fluid in the case of holothurians). Damaged and/or partial specimens were excluded, except in the case of ophiuroids and brisingids, for which no complete, intact specimens were available. Recommendations for the processing of fluid-preserved specimens (Simmons 2014) were generally followed.

Physical dimensions and wet weights were recorded for each specimen. The dimension selected was generally the linear 'length' (Table 1). In asteroids, the radius from the centre of the disk to the end of an outstretched arm was measured. A similar measurement was made for ophiuroids, and the disk diameter was also measured. The column diameter

Table 1. Dimension to preserved wet weight conversions created from specimens collected in trawls of the form: preserved wet weight (g) = A × dimension (mm)^B (see Eq. 1), where A and B are coefficients fitted using linear regression of the logarithm of the formula. Measured dimensions, not including appendages (e.g. tentacles, papillae, antennae, etc.): L = length, D = diameter, R = radius from centre of disk to end of arm

Taxon	Measured dimension (mm)	A (×10^{-4})	B	R^2	n	Dimension range (mm)	Preserved wet weight range (g)
ANNELIDA							
Laetmonice spp.	L	2	2.307	0.756	170	22–91	0.10–9.40
ARTHROPODA							
Cirripedia	Rostral L	0.3	3.440	0.824	26	13–35	0.22–7.57
Pycnogonida	Leg L	0.06	2.843	0.980	6	68–154	8.00–15.00
Munida spp./*Munidopsis* spp.	Body L	6	2.747	0.923	16	6.5–47	0.09–31.20
Isopoda	L	0.4	3.047	0.976	11	18–46	0.22–4.03
CNIDARIA							
Actiniaria	Column D	26	2.360	0.748	683	5–80	0.02–171.7
Iosactis vagabunda (Riemann-Zürneck 1997b)[a]	Column D	788	0.961	0.215	140	5–11	0.23–1.39
Parasicyonis biotrans (Riemann-Zürneck 1991)[a]	Column D	530790	0.235	0.1	18	35–80	92.70–171.70
Daontesia porcupina (Riemann-Zürneck 1997a)[a]	Column D	159	1.696	0.462	62	9–28	0.85–5.56
Actinauge abyssorum (Carlgren 1934)	Column D	9	2.802	0.896	156	7–35	0.11–17.73
Amphianthus bathybium (Hertwig 1882)[a]	Column D	12	2.578	0.890	137	6–26	0.11–5.03
Sicyopus commensalis (Gravier 1918)	Column D	5	2.678	0.909	144	5–23	0.02–2.75
Segonzactis platypus (Riemann-Zürneck 1979)	Column D	11	2.260	0.774	23	9–22	0.16–1.82
Fungiacyathus spp.	D	6	2.357	0.667	10	21–29	0.73–1.87
Umbellula spp.	L	103	1.010	0.725	52	27–1319	0.11–12.91
ECHINODERMATA							
Asteroidea							
Pythonaster atlantidis (Clark 1948)	R	2601	0.917	0.414	10	15–143	16.25–48.58
Styracaster chuni (Ludwig 1907)/*Styracaster horridus* (Sladen 1883)	R	26	2.133	0.929	126	6–60	0.14–18.66
Dytaster grandis grandis (Verrill 1884)	R	11638	0.778	0.413	52	106–180	40.69–74.17
Hyphalaster inermis (Sladen 1883)	R	26	2.172	0.949	191	5–79	
Holothuroidea							
Amperima rosea (Perrier 1886) / *Ellipinion* spp. /*Kolga* spp.	L	6	2.497	0.958	30614	6–69	0.06–20.01
Benthodytes sp. / *Benthodytes sordida* (Théel 1882)	L	3	2.451	0.938	22	38–418	2.10–805.70
Deima validum validum (Théel 1879)	L	27	2.256	0.877	161	20–107	2.30–122.00
Zygothuria candelabra (Hérouard 1923)	L	17	2.241	0.616	53	50–115	6.64–96.00
Oneirophanta mutabilis (Théel 1879)	L	4	2.508	0.933	5659	15–220	0.18–223.00
Paroriza prouhoi (Hérouard 1902)	L	2	2.539	0.922	244	30–325	0.66–619.00
Peniagone spp./*Peniagone diaphana* (Théel 1882)	L	15	1.999	0.835	364	17–115	0.45–25.30
Pseudostichopus aemulatus (Solis-Marin & Billett in Solis-Marin et al. 2004)/*Molpadiodemas villosus* (Théel 1886b)	L	0.5	2.856	0.918	5179	13–248	0.09–804.00
Psychropotes longicauda (Théel 1882)	L	2	2.652	0.942	2339	16–290	0.28–1574.00
Molpadia blakei (Théel 1886a)	L	12	2.349	0.841	72	26–138	2.01–97.53
Ophiuroidea							
	R	21	1.764	0.877	89	5–95	0.02–3.94
	Disk D	5	2.821	0.797	89	4–26	0.02–3.94
ECHIURA	L	281	0.990	0.520	24	17–146	0.20–8.04
MOLLUSCA							
Cephalopoda	Arm L	3	2.438	0.597	6	55–255	3.60–555.00
Gastropoda	L	21	1.940	0.797	15	12–78	0.27–15.26

[a]Dimensions corrected using values in Table 3 prior to conversion

was measured in anemones. The length of the longest leg was measured in pycnogonids. Otherwise, appendages were excluded, particularly those that are flexible or retractable, such as the vellum and papillae in holothurians. Visible surface liquid was removed by blotting using absorbent towel prior to weighing. Wet weights of crustaceans, echinoderms, and molluscs included the shells. In taxa for which dimensions could not be reproducibly measured (Table 2), only wet weights were recorded.

Power relationships were established between the measured dimension and the preserved wet weight of the specimen, with the form:

$$P = A \times L^B \qquad (1)$$

where P is the preserved wet weight (g), L is the measured dimension (mm), and A and B are coefficients fitted using linear regression of the logarithm of the formula above. An R^2 value was computed to evaluate the goodness of fit. Preliminary relationships were presented in Durden et al. (2015a).

Application to seabed photographs

These conversions were applied to individuals identified and measured in 28 200 seabed photographs (representing some 3.6 ha of seabed) from the PAP site obtained with the Autosub6000 autonomous underwater vehicle from RRS 'Discovery' research cruise 377 (Ruhl 2013, Morris et al. 2014). Methods for image processing and annotation are detailed in Morris et al. (2014); in brief, distinctly identifiable megafauna were classified and measured in vertical seabed photographs, following processing of the images to correct for camera orientation. Image pixel dimensions were converted to physical units using the altitude and orientation of the camera (Jones et al. 2009, Morris et al. 2014).

Invertebrates were identified to the lowest practicable taxonomic levels, which was not always to the same detail for specimens in photographs as for those caught in trawls. Matching morphotypes identified in photographs to taxa identified in the trawl catches was not always straightforward. Some morphotypes differ in appearance as a result of trawl capture and subsequent fixation (e.g. retraction of tentacles and contraction of oral disk in anemones, retraction of papillae in holothurians). In cases where specimens from multiple species were grouped, this is indicated in Tables 1 & 2.

Some morphotypes presented difficulties in the selection of a measured dimension that was practical in the photographs, and matched the dimension measured of the preserved specimens. Fig. 1 shows examples of the measured dimensions in images that were also possible in preserved specimens. For certain anemones, a common measured dimension in both the photographs and preserved specimens was not practical, so a further conversion between the dimension measured in preserved specimens (column diameter) and the dimension measured in photographs (oral disk diameter) was applied (Fig. 1).

Table 2. Individual specimen preserved wet weight data for Porcupine Abyssal Plain taxa where reliable dimension measurement was not possible

Taxon	Range (g)	Median (g)	n
TUNICATA			
Culeolus spp.	0.01–2.02	0.34	1599
CNIDARIA			
Zoantharia	0.01–0.43	0.10	538
ECHINODERMATA			
Freyastera spp./*Freyella* spp.	0.07–17.67	0.87	312
Pterasteridae	0.33–8.67	4.5	2
Crinoidea	0.05–1.59	0.7	13
PORIFERA	5.23–11.57	8.0	3

These conversions were established by measuring both dimensions in a subset of images where both dimensions could be observed, and were applied to image measurements prior to wet weight conversion. Power relationships were established between the column diameter and the disk diameter (Table 3), with the form:

$$C = G \times D^H \qquad (2)$$

where C is the column diameter (pixels), D is the oral disk diameter (pixels), and G and H are coefficients fitted using linear regression of the logarithm of the formula above. An R^2 value was computed to evaluate the goodness of fit. The underestimation of the measured dimension is acknowledged in taxa where legs or arms may not be extended fully in photographs (e.g. pycnogonids, brisingids), but measurements of preserved specimens would be of extended appendages.

Preserved to fresh wet weight conversions

Conversions between fresh wet weights, measured at sea, and preserved wet weights following fixation in buffered formalin and preservation in industrial denatured alcohol were established using batch wet weights of trawl-caught specimens, aggregated by taxon, collected from RRS 'Discovery' 237 (Sibuet 1999), RRS 'Discovery' 229 (Bett 1998), and RRS 'Challenger' 142 (Billett 2000). Again, recommendations for the processing of fluid-preserved specimens (Simmons 2014) were generally followed. Note that these batch weights included all specimens (including both damaged and intact specimens) in the determinations of both preserved and fresh weights. Con-
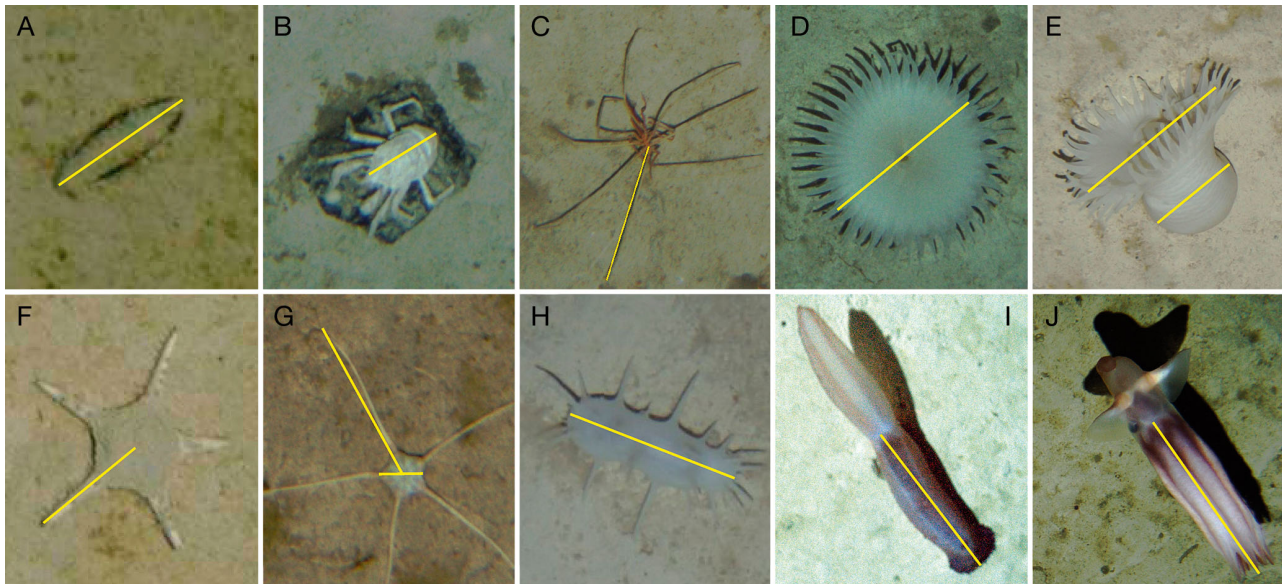
Fig. 1. Example measured dimensions (in yellow) of representative morphotypes: (A) body length of Annelida – *Laetmonice* spp.; (B) length of Arthropoda – *Munidopsis* spp.; (C) leg length of Pycnogonida; (D) oral disk diameter of Cnidaria – *Parasicyonis* sp., see also (E) the disk and column diameters as measured in trawl-caught specimens (see Table 2); (F) radius from body centre to end of arm of Echinodermata, Asteroidea – *Styracaster* spp.; (G) alternate measurements of disk diameter and radius from body centre to end of arm of Echinodermata – Ophiuroidea; (H) body length of Echinodermata, Holothuroidea – *Oneirophanta mutabilis*, also note (I) body length excluding sail of *Psychropotes longicauda*; (J) arm length of Mollusca – Cephalopoda

Table 3. Conversion from photograph-measured dimension (oral disk diameter, D, pixels) to preserved specimen dimension (column diameter, C, pixels). Conversion is in the form: $C = G \times D^H$ (see Eq. 2), where G and H are factors in a relationship determined from n individuals, with goodness of fit, R^2

Morphotype	G	H	R^2	n
Iosactis vagabunda	0.414	1.075	0.81	45
Parasicyonis biotrans	0.015	1.614	0.86	5
Daontesia porcupina	2.527	0.599	0.71	5
Amphianthus bathybium	0.114	1.283	0.83	8

sequently, apparent data outliers (e.g. samples for which fresh wet weights included attached clinker in anemones) were identified, evaluated using Q-Q plots and Cook's distance in R software (R Core Team 2015), and removed. Following this data editing, relationships were established of the form:

$$P = J \times F \qquad (3)$$

where P is the preserved wet weight (g), F is the fresh wet weight (g) and J is a coefficient determined by linear least-squares regression fitted in R (R Core Team 2015) with zero intercept.

Total biomass (g fresh wet weight ha^{-1}) was calculated by converting the measured dimension for each

specimen observed in the seabed photographs to fresh wet weight using the methods detailed above, and summing for each morphotype. For morphotypes for which no specific conversions were available, estimates were based on conversions for the nearest morphological analogue.

RESULTS AND DISCUSSION

Dimension to preserved wet weight conversions for 34 taxa are presented in Table 1, and preserved wet weights of a further 6 taxa for which dimensions could not be measured are given in Table 2. Published size and preserved wet weight data are scarce for many deep-sea taxa, so we have included values for as many groups as possible. The number of specimens available per taxon ranged from 6 to 44 630, with 24 of the conversions based on at least 50 specimens. The goodness of fit of the conversions derived from the trawl catch data (R^2) varied between taxa, with 24 conversions having values of at least 0.75. Conversions computed from small numbers of specimens should of course be treated with caution.

For some taxa, the trawled specimens represented a wide range of dimensions and preserved wet weights (e.g. Fig. 2A,B), likely encompassing much of the sea-
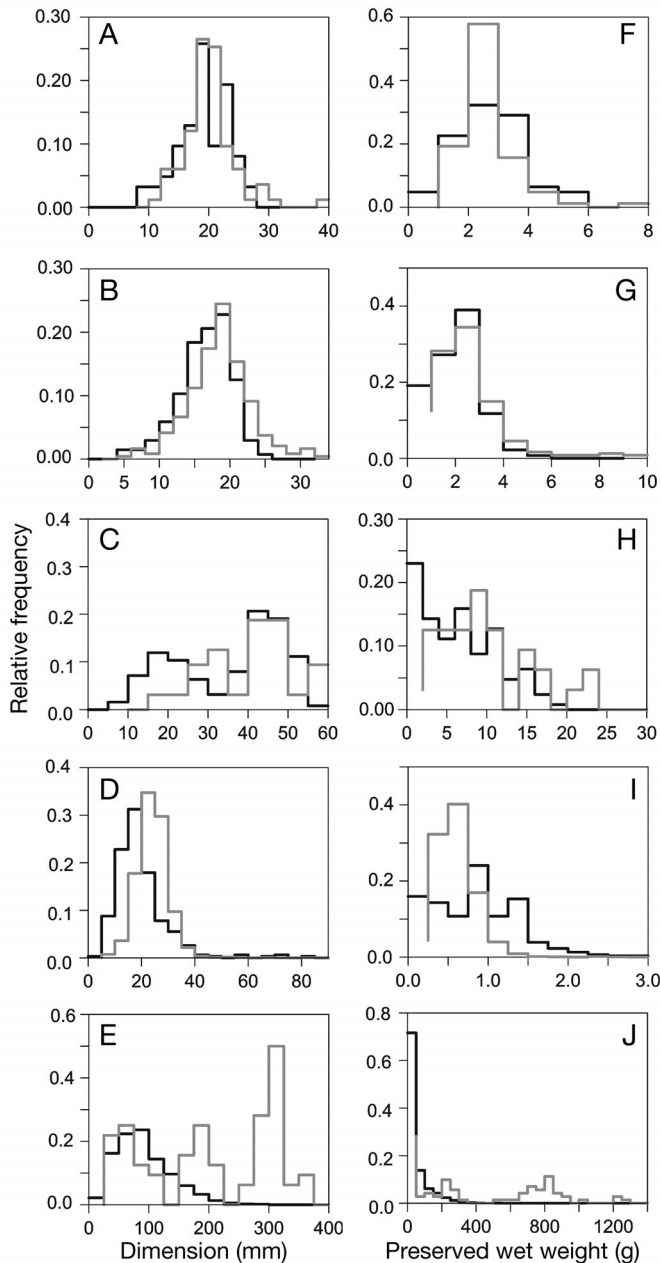
Fig. 2. Distributions of dimension and preserved wet weight from trawl-caught specimens (black) and estimated from photographs (grey) for: (A,F) *Daontesia porcupina* (diameter); (B,G) *Amphianthus bathybium* (diameter); (C,H) *Styracaster* spp. (radius); (D,I) Ophiuroidea (radius), and (E,J) *Psychropotes longicauda* (length)

sonal and inter-annual variations in individual size. However, the trawl-caught specimens did not always include the full range of dimensions determined from the photographs. The size classes of taxa in photographs overlapped those from the trawls, but for some taxa, smaller or larger individuals were measured in the photographs (e.g. Fig. 2E). This comparison pro-

vides an indirect validation of the dimensions measured in photographs, as there was no drastic difference in sizes, and indicates the broad equivalency of sizes between trawled and photographed specimens, suggesting that the application of our conversions was appropriate. However, extrapolation of conversions beyond the size ranges of the trawl-caught specimens may not be appropriate.

The use of the oral disk to column diameter conversion in the 4 actiniarian taxa resulted in a substantial improvement in the correspondence of size classes between photographs and trawls. For example, of 86 individuals of *Daontesia porcupina* (Riemann-Zürneck 1997a) identified in photographs, 72 were larger than the range of trawled specimens without the conversion; this was reduced to 2 after the conversion was applied. Similarly, of 259 photographed individuals of *Amphianthus bathybium* (Hertwig & Herdman 1882), 234 were larger than the trawl-measured size range, reduced to only 8 after conversion. Further improvements to this method for anemones, and other taxa that retract or shrink substantially upon collection, could be made by photographing and collecting specific individuals *in situ*, given sufficient ROV time.

Published conversions between preserved and fresh wet weights in deep-sea taxa are also scarce. Here we have included conversions for as many taxa as possible (Table 4), even where sample numbers were low. Nevertheless, the goodness of fit was generally high ($R^2 = 0.93$–0.998).

Taxa with substantial proportions of soft tissues, such as some holothurians, tunicates, sipunculids, and cephalopods, appear to lose 35 to 60% of their fresh wet mass on preservation. This is similar to the loss estimated generally for holothurians (40%) by Billett et al. (2001) from data on shallow-water species given by Conand (1989). Taxa with greater proportions of hard/structural tissues, such as asteroids, some arthropods, and gastropods, lose 10 to 20% of their fresh wet weight on preservation. Our estimates do not consider changes in preserved wet weights with time, which have been studied in shallow-water polychaetes and amphipods (Gaston et al. 1996, Wetzel et al. 2005). For example, Mills et al. (1982) found that wet weight increased immediately after fixation in formalin, followed by a reduction in wet weight over time. As our specimens were preserved for at least 2 months prior to measurement, their wet weights may have largely stabilised, as potentially suggested by the high R^2 values (Table 4).

The development of wet weight conversions from photographic dimensions for a wide range of taxa will facilitate the improved estimation of deep-sea

Table 4. Fresh wet weight to preserved wet weight conversions in the form: preserved wet weight (g) = J × fresh wet weight (g) (see Eq. 3), where J is a factor determined by linear regression with zero intercept

Taxon	J	R^2	n
ANNELIDA			
Polynoidae	0.812	0.995	6
ARTHROPODA			
Cirripedia	0.751	0.98	11
Pycnogonida	0.838	0.98	9
Cerataspis spp.	0.781	0.97	4
Stereomastis spp.	0.822	0.99	8
Munida spp./*Munidopsis* spp.	0.780	0.98	7
CNIDARIA			
Actiniaria			
Iosactis vagabunda	0.887	0.99	13
Parasicyonis biotrans	0.784	0.998	7
Daontesia porcupina	0.818	0.99	8
Actinauge abyssorum	0.722	0.99	13
Amphianthus bathybium	0.664	0.95	13
Segonzactis platypus	0.681	0.98	9
Sicyopus commensalis	0.966	0.96	9
Zoanthidea	0.755	0.99	5
Umbellula spp.	0.656	0.98	9
ECHINODERMATA			
Asteroidea			
Pythonaster atlantidis	0.845	0.999	3
Styracaster chuni/ *Styracaster horridus*	0.873	0.999	10
Dytaster grandis grandis	0.820	0.998	11
Hyphalaster inermis	0.873	0.99	8
Freyella spp./*Freyastera* spp.	0.886	0.99	12
Pterasteridae	0.820	NA	1
Holothuroidea			
Amperima rosea	0.627	0.995	13
Benthodytes spp.	0.470	0.99	8
Deima validum validum	0.648	0.98	12
Ellipinion spp./*Kolga* spp.	0.460	0.99	10
Zygothuria candelabri	0.604	0.96	12
Oneirophanta mutabilis	0.539	0.99	6
Paroriza prouhoi	0.527	0.96	10
Peniagone spp.	0.684	0.93	11
Pseudostichopus aemulatus/ *Molpadiodemas villosus/* *Pseudostichopus* spp.	0.413	0.93	11
Psychropotes longicauda/ *Psychropotes semperiana* (Théel 1882)	0.505	0.96	6
Molpadia spp.	0.576	0.98	9
Crinoidea	0.680	0.94	8
Echinoidea	0.570	NA	1
Ophiuroidea	0.835	0.996	10
ECHIURA	0.670	0.99	6
MOLLUSCA			
Cephalopoda	0.415	0.99	7
Gastropoda	0.861	0.99	13
Bivalvia	0.715	0.97	8
TUNICATA	0.657	0.99	8
SIPUNCULA	0.649	0.99	5
PORIFERA	0.791	0.97	8

megafaunal biomass from the large numbers of seabed photographs now being routinely captured in many studies (e.g. Morris et al. 2014, Wynn et al. 2014). The improved quantification of benthic megafaunal biomass using photographs (see e.g. Christiansen & Thiel 1992, and expanded upon here) can be illustrated with key taxa from the PAP. Holothurians dominate the biomass at the PAP and their temporal variation has long been the focus of research (Billett et al. 2001, 2010), while the dominance of cnidarians has only recently been appreciated (Durden et al. 2015b). Billett et al. (2010) estimated mean holothurian biomass across all trawls over the years 1989–2005 at 1903 (95% CI = 1693–2138) g wet weight ha^{-1}, cnidarian biomass at 44 (38–51) g wet weight ha^{-1}, and that of total invertebrates at 2111 (1888–2359) g wet weight ha^{-1}. Durden et al. (2015a) employed a towed camera survey and preliminary conversions to wet weight from photographs, and estimated total invertebrate biomass at the PAP at 24 200 g wet weight ha^{-1}, 8 times the highest value reported by Billett et al. (2010). Holothurian and cnidarian biomass were estimated at 18 500 and 5400 g preserved wet weight ha^{-1}, respectively, 10 and 125 times the values reported by Billett et al. (2010). Using the conversions presented here, and the photographic survey reported by Morris et al. (2014) at the PAP site, holothurian biomass was estimated at 36 200 g fresh wet weight ha^{-1}, and cnidarian biomass at 9200 g fresh wet weight ha^{-1}. These estimates are each twice those given by Durden et al. (2015a), and 19 and 214 times the estimates by Billett et al. (2010). The sum of holothurian and cnidarian biomass is ~20 times the Billett et al. (2010) value for total invertebrate biomass. Given these dramatic uplifts in megabenthic biomass over trawled estimates from the PAP, it is clear that biomass estimation by this method will have a profound effect on studies of standing stocks, community metabolism, and the numerical modelling of carbon flows (e.g. van Oevelen et al. 2012).

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