

Length–weight relationships of 216 North Sea benthic invertebrates and fish

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Size-based analyses of marine animals are increasingly used to improve understanding of community structure and function. However, the resources required to record individual body weights for benthic animals, where the number of individuals can reach several thousand in a square metre, are often prohibitive. Here we present morphometric (length–weight) relationships for 216 benthic species from the North Sea to permit weight estimation from length measurements. These relationships were calculated using data collected over two years from 283 stations. For ten abundant and widely dispersed species we tested for significant spatial and temporal differences in morphometric relationships. Some were found, but the magnitude of differences was small in relation to the size-ranges of animals that are usually present and we recommend that the regression relationships given here, based on pooled data, are appropriate for most types of population and community analyses. Our hope is that the availability of these morphometric relationships will encourage the more frequent application of size-based analyses to benthic survey data, and so enhance understanding of the ecology of the benthic/demersal component of marine ecosystems and food webs.

Keywords: length–weight relationships, benthos, demersal fish, size structure, size-based analyses

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INTRODUCTION

In recent years applications of analyses that involve size-classed faunal data to investigate properties and trends in marine communities have increased (Rice & Gislason, 1996; Bianchi *et al.*, 2000; Duplisea *et al.*, 2002; Jennings *et al.*, 2002a; Blanchard *et al.*, 2005; Greenstreet & Rogers, 2006). These analyses are based on the assumption that body size plays a key role in structuring marine communities (Kerr & Dickie, 2001; Jennings & Mackinson, 2003; Jennings *et al.*, 2007), where species have non-deterministic growth and often show ontogenetic changes in life habits (Cushing, 1975; Greenstreet *et al.*, 1998; Cohen *et al.*, 2003). Marine species do not adhere strictly to the classic species-related niche differentiation often observed in terrestrial systems (Persson, 1988), and it is argued that in understanding variability in marine communities, it can be more useful to consider interactions among individuals of similar body size (Cohen *et al.*, 1993; Jennings *et al.*, 2002b, 2007; Jennings & Mackinson, 2003; Brown *et al.*, 2004; Jennings & Blanchard,

2004; Pope *et al.*, 2006). In addition, properties such as community production can be predicted from analyses of body size distributions, but such analyses usually require data on individual body weights (Brey, 1990; Edgar, 1990; Brey *et al.*, 1996).

To carry out analyses based on individual body weight it is necessary to weigh all animals, but this can be prohibitive in terms of the time required for processing samples. In addition to this, many of the animals sampled are killed unnecessarily in the process; to weigh hermit crabs individually, for example, the animals must be removed from their shells. If relationships between a measure of body size (such as total length or longest axis) and body weight can be established, then it is possible to calculate individual body weights based on these size measurements. Size measurements are much quicker and easier to record, destructive handling of specimens can be avoided in many cases, and the need for expensive motion stabilized weighing machines on research cruises is reduced.

Published morphometric (length–weight) relationships are frequently used for size-based analyses of fish communities and routine monitoring of fish stocks. More recently, relationships have also been documented for some common hermit crab species (Paguridae) from the Irish

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and North Seas (Kaiser *et al.*, 1998; Reiss *et al.*, 2005). This study presents length–weight relationships for commonly recorded North Sea epibenthic invertebrates and fish species. Since compilations of length–weight relationships for fish that are caught by the international bottom trawl surveys in the North Sea are already available (Coull *et al.*, 1989; www.fishbase.org), we focused our analysis on those fish species and size-classes that are not regularly recorded on these surveys. The relationships were generated from data collected over two years by an international 2-m beam trawl epifaunal survey. Our hope is that the availability of these data might encourage the more frequent application of size-based analyses to benthic invertebrate survey data, and so enhance understanding of the ecology of the benthic/demersal component of marine ecosystems and food webs.

MATERIALS AND METHODS

Five institutes carried out sampling across the North Sea between July and September in 2003 and 2004. Epifauna was sampled at 283 stations (Figure 1) using a 2-m beam trawl with a cod-end mesh size of 4 mm (Jennings *et al.*, 1999; Callaway *et al.*, 2002a). All samples were washed through a 5-mm sieve to remove the majority of the unwanted sediment material. All but the smallest organisms taken in the net were retained by this mesh size (Callaway *et al.*, 2002a,b). Each sample was sorted first by species, and then individuals of each species were counted, and where possible, measured (to the nearest mm, 0.1 mm, or 0.01 mm depending on measurement taken, see Appendix 1) and weighed (blotted wet weight to the nearest 0.2 g, 0.1 g or 0.01 g) with a motion compensated marine scale. All species that could be separated into

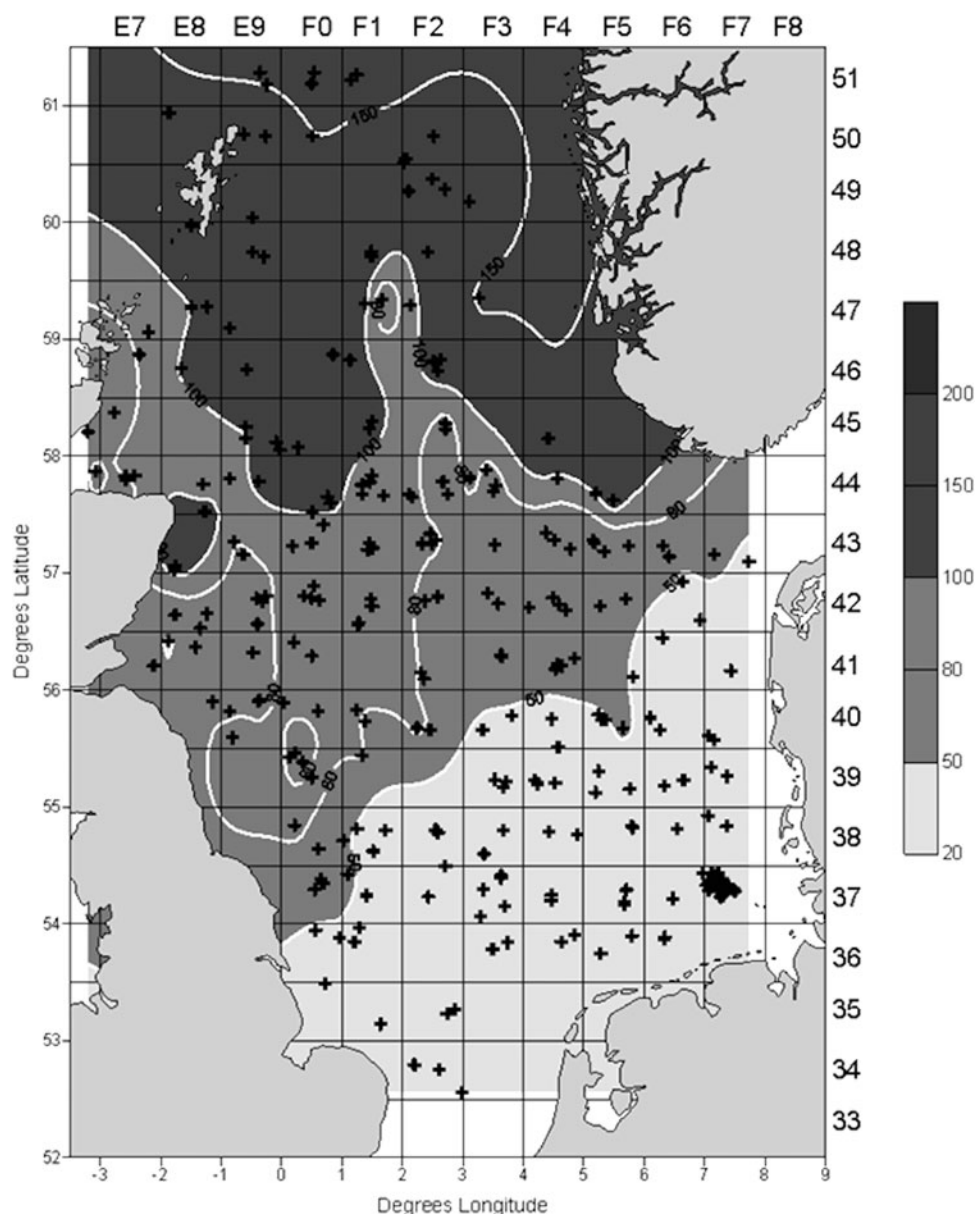


Fig. 1. Map of the North Sea showing the positions of the stations sampled by epifauna surveys in 2003 and 2004.

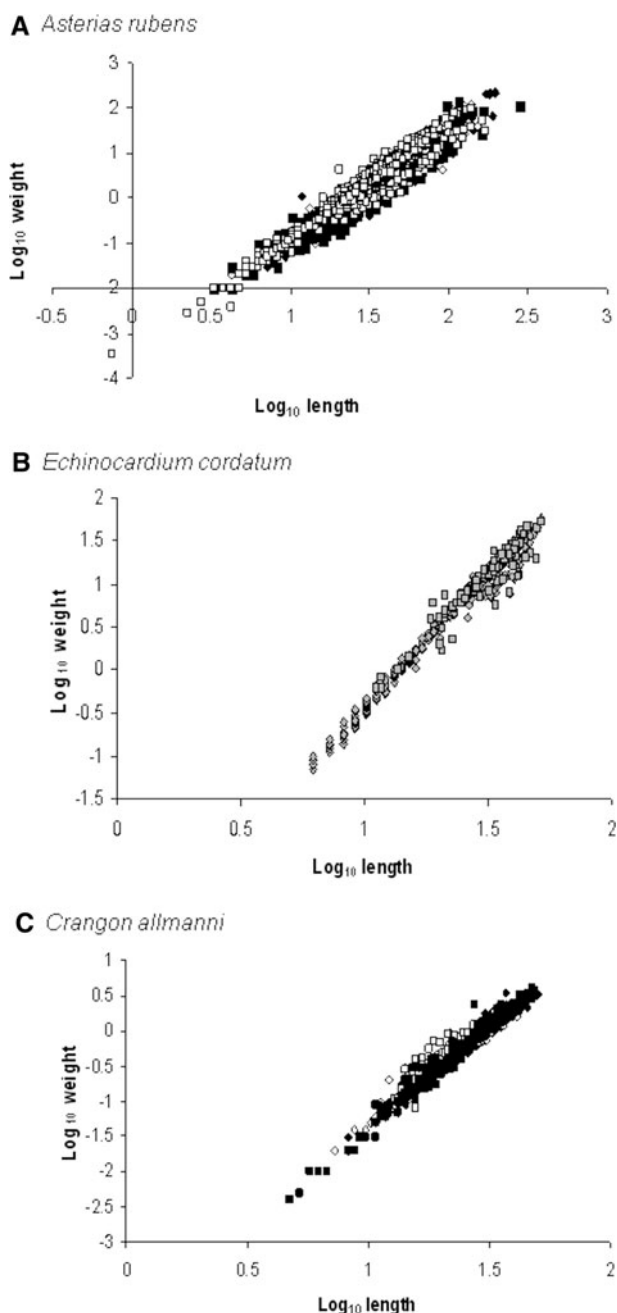


Fig. 2. Variation in weight-length relationships for three epifaunal species among North Sea regions (North, open symbols; South, filled symbols; pooled regions, grey fill) and/or year (2003, diamonds; 2004, squares; pooled years, triangles) that the data were collected in. (A) *Asterias rubens*; (B) *Echinocardium cordatum*; (C) *Crangon allmanni*.

measurable individuals were measured and weighed. A list of the specific size measurements used for each species is given in Appendix 1. In all cases weights were recorded for undamaged individuals only. More details on the sampling methodology are available in Callaway *et al.* (2007).

On completion of the cruises all data were combined and relationships between weight and length were described for all species with more than five individuals recorded, using linear regression on log-transformed data. For a number of species that were both widespread in their distribution and particularly abundant (>500 measurements per species), differences in slopes and intercepts were explored in relation

to spatial (between region) and temporal (between year) effects using analysis of covariance. For the spatial analyses, the North Sea was split into two regions, approximately north and south of the 50 m bathycline that corresponds with the boundary between two major epibenthic assemblages determined by depth, temperature, food availability and substrate type (Frauenheim *et al.*, 1989; Callaway *et al.*, 2002a; Reiss *et al.*, in press).

RESULTS AND DISCUSSION

A total of 497 benthic fish and invertebrate taxa were recorded. Length-weight relationships could not be determined for 213 of these because they were too scarce to meet our abundance threshold for inclusion (>5 individuals), or because it was not possible to take measurements of either their length and/or weight (e.g. bryozoans and hydrozoans). For the 284 fish and invertebrate species that remained, there was a weak or non-significant relationship for 68 (r^2 values were <0.5 and/or $P > 0.05$). Weak relationships were mainly associated with taxa that had extremely variable water contents (e.g. the sea squirt *Polysarpa scuba*) and/or that were difficult to take precise and accurate repeated size measurements from (e.g. the polychaete worms *Lagis koreni* and *Eunoe nodosa*). Appendix 1 lists the regression functions for the specific size and weight measurements recorded for the 216 significant relationships observed.

Ten species met the criteria for wide spatial distribution and high numbers of individuals. For eight of these species there were significant differences in the length-weight relationship among years or regions (Appendix 2). Spatial or temporal differences in intraspecific morphometrics are possible due to the effects of spatial or interannual differences in food availability, life history characteristics or feeding mode. Previous studies on hermit crabs had found neither sex-specific (Kaiser *et al.*, 1998), nor spatial differences in morphometric relationships (Reiss *et al.*, 2005). In contrast, we detected significant differences for eight out of ten species analysed (Figure 2; Appendix 2). However, the absolute differences were small (small coefficients when compared with the effect of length alone—see Appendices 1 and 2) and we conclude that the single regression functions, based on the pooled data (Appendix 1), would be adequate for estimating body weight of the species concerned across the whole North Sea.

Use of the weight at length coefficients supplied here should dramatically reduce the time and costs involved in collecting adequate data for size-based analyses of benthic invertebrates. The availability of such data will enable the more frequent application of size-based analyses to benthic invertebrate survey data, and so improve understanding of the role of benthic animals in food webs and marine ecosystems.

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Appendix 1. Regression coefficients (a, b), r^2 and P values for linear regression of length (L, mm) against blotted wet weight (W, g) of 216 North Sea benthic species. The length measurement taken is given, along with the minimum (Min L) and maximum (Max L) size of the individuals covered by the data, where N = number of individuals sampled. All regression equations are based on the form $\log_{10}(W) = a + b \cdot \log_{10}(L)$.

Species	Phylum	Class	Order	Length	Min L (mm)	Max L (mm)	a	b	r^2	P	N
<i>Aphrodita aculeate</i>	Annelida	Polychaeta	Aphroditoidea	Total length	13.98	112.10	-4.109	2.902	0.966	<0.0001	228
<i>Laetmonice filicornis</i>	Annelida	Polychaeta	Aphroditoidea	Total length	11.88	42.30	-3.216	2.201	0.959	<0.0001	26
<i>Lepidonotus squamatus</i>	Annelida	Polychaeta	Aphroditoidea	Thorax width	1.10	7.54	-1.773	2.058	0.905	<0.0001	12
<i>Eunice norvegica</i>	Annelida	Polychaeta	Eunicida	Thorax width	1.94	5.15	-1.956	2.753	0.677	0.002	11
<i>Nothria conchylega</i>	Annelida	Polychaeta	Eunicida	Thorax width	1.49	4.43	-2.697	4.051	0.816	<0.0001	26
<i>Glycera rouxii</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	0.59	4.40	-1.620	2.414	0.932	<0.0001	16
<i>Goniada maculate</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.56	2.73	-1.309	2.795	0.805	0.039	5
<i>Neanthes fucata</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.21	7.62	-1.832	2.453	0.812	<0.0001	45
<i>Neanthes virens</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.16	3.81	-2.000	3.400	0.834	<0.0001	15
<i>Nephtys hombergii</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.54	3.98	-1.420	1.979	0.935	<0.0001	7
<i>Nephtys kersivalensis</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	0.99	5.57	-1.388	1.913	0.745	<0.0001	25
<i>Nephtys longosetosa</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.32	7.04	-1.867	2.816	0.857	<0.0001	55
<i>Nereis pelagic</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	0.66	4.67	-1.732	2.303	0.993	<0.0001	7
<i>Perinereis cultrifera</i>	Annelida	Polychaeta	Phyllodocida	Thorax width	1.09	4.34	-1.802	2.321	0.874	<0.0001	21
<i>Thelepus cincinnatus</i>	Annelida	Polychaeta	Terebellida	Thorax width	1.43	9.20	-1.821	2.939	0.767	<0.0001	133
<i>Epimeria cornigera</i>	Arthropoda	Crustacea	Amphipoda	Eye to tip of telson	6.04	13.47	-3.426	2.313	0.576	<0.0001	61
<i>Hippomedon denticulatus</i>	Arthropoda	Crustacea	Amphipoda	Eye to tip of telson	10.24	14.72	-4.352	2.615	0.975	0.002	5
<i>Iphimedia obesa</i>	Arthropoda	Crustacea	Amphipoda	Eye to tip of telson	3.67	9.12	-4.333	3.060	0.629	<0.0001	27
<i>Anapagurus chiroacanthus</i>	Arthropoda	Crustacea	Decapoda	Width of chela	0.73	10.89	-1.713	2.475	0.68	<0.0001	26
<i>Anapagurus laevis</i>	Arthropoda	Crustacea	Decapoda	Width of chela	0.69	7.94	-1.879	2.340	0.835	<0.0001	1505
<i>Atelecyclus rotundatus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	11.55	36.73	-3.511	3.107	0.943	<0.0001	108
<i>Calocaris macandreae</i>	Arthropoda	Crustacea	Decapoda	Carapace length	9.67	15.02	-2.587	2.161	0.584	0.002	13
<i>Cancer pagurus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	13.00	176.00	-3.945	3.053	0.998	<0.0001	10
<i>Corystes cassivelaunus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.00	27.47	-3.245	3.150	0.98	<0.0001	476
<i>Crangon allmanni</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	6.72	57.00	-4.823	2.890	0.901	<0.0001	2115
<i>Crangon crangon</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	6.87	80.00	-4.420	2.647	0.97	<0.0001	64
<i>Dichelopandalus bonnieri</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	50.00	91.02	-5.280	3.162	0.823	<0.0001	36
<i>Ebalia cranchii</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	5.00	12.00	-2.916	2.475	0.783	<0.0001	32
<i>Ebalia tuberosa</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.56	15.75	-3.408	2.984	0.957	<0.0001	169
<i>Ebalia tumefacta</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	10.00	12.78	-4.015	3.475	0.863	0.007	6
<i>Eualus gaimardii</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	8.29	35.84	-4.819	2.987	0.969	<0.0001	10
<i>Eurynome aspera</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	6.31	11.80	-3.124	2.914	0.813	<0.0001	24
<i>Galathea dispersa</i>	Arthropoda	Crustacea	Decapoda	Carapace length to base of rostrum	2.91	9.80	-2.592	2.421	0.876	<0.0001	53
<i>Galathea nexa</i>	Arthropoda	Crustacea	Decapoda	Carapace length to base of rostrum	1.60	14.90	-2.978	2.680	0.555	0.001	15
<i>Galathea squamifera</i>	Arthropoda	Crustacea	Decapoda	Carapace length to base of rostrum	2.00	18.00	-2.097	1.721	0.511	<0.0001	317
<i>Galathea strigosa</i>	Arthropoda	Crustacea	Decapoda	Carapace length to base of rostrum	3.55	12.40	-2.733	2.615	0.924	<0.0001	47
<i>Geryon trispinosus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace (in front of spines)	24.00	57.20	-4.242	3.479	0.883	<0.0001	39
<i>Hyas coarctatus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	2.24	48.89	-2.843	2.773	0.955	<0.0001	626
<i>Inachus dorsettensis</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	5.07	25.00	-2.763	2.541	0.839	<0.0001	120
<i>Inachus leptochirus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	5.52	19.73	-2.584	2.389	0.973	0.002	5
<i>Liocarcinus depurator</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.05	52.00	-3.799	3.144	0.982	<0.0001	620
<i>Liocarcinus holsatus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	2.49	62.00	-3.427	2.875	0.986	<0.0001	2988

Continued

Appendix 1. Continued

Species	Phylum	Class	Order	Length	Min L (mm)	Max L (mm)	a	b	r ²	P	N
<i>Liocarcinus marmoreus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.65	30.00	-3.714	3.030	0.993	<0.0001	27
<i>Liocarcinus pusillus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	6.00	21.00	-3.062	2.521	0.926	<0.0001	69
<i>Macropipus tuberculatus</i>	Arthropoda	Crustacea	Decapoda	Width of carapace (in front of spines)	8.70	40.95	-2.890	2.501	0.984	0.001	5
<i>Macropodia rostrata</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.00	14.60	-2.722	2.629	0.763	<0.0001	269
<i>Macropodia tenuirostris</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	4.60	16.07	-2.742	2.601	0.824	<0.0001	203
<i>Munida rugosa</i>	Arthropoda	Crustacea	Decapoda	Carapace length to base of rostrum	5.59	34.47	-3.071	3.073	0.946	<0.0001	148
<i>Necora puber</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	52.00	88.00	-2.767	2.572	0.927	<0.0001	23
<i>Nephrops norvegicus</i>	Arthropoda	Crustacea	Decapoda	Carapace length	3.90	48.00	-3.018	2.883	0.949	<0.0001	99
<i>Pagurus alatus</i>	Arthropoda	Crustacea	Decapoda	Width of chela	1.55	11.32	-2.044	2.718	0.839	<0.0001	27
<i>Pagurus bernhardus</i>	Arthropoda	Crustacea	Decapoda	Width of chela	0.96	28.80	-1.712	2.611	0.966	<0.0001	2038
<i>Pagurus cuanensis</i>	Arthropoda	Crustacea	Decapoda	Width of chela	1.17	12.40	-1.804	2.666	0.965	<0.0001	40
<i>Pagurus forbesii</i>	Arthropoda	Crustacea	Decapoda	Width of chela	4.23	9.48	-2.021	2.771	0.949	<0.0001	8
<i>Pagurus prideaux</i>	Arthropoda	Crustacea	Decapoda	Width of chela	1.36	14.70	-1.934	2.943	0.96	<0.0001	1025
<i>Pagurus pubescens</i>	Arthropoda	Crustacea	Decapoda	Width of chela	1.29	12.67	-1.630	2.573	0.861	<0.0001	557
<i>Pandalina brevisrostris</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	7.69	26.13	-4.750	2.736	0.862	<0.0001	37
<i>Pandalus borealis</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	17.00	68.59	-5.948	3.613	0.905	<0.0001	66
<i>Pandalus montagui</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	8.37	76.53	-4.713	2.844	0.933	<0.0001	719
<i>Philocheras bispinosus</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	5.00	18.60	-3.735	1.896	0.501	<0.0001	190
<i>Philocheras echinulatus</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	26.72	52.41	-5.948	3.640	0.998	<0.0001	6
<i>Philocheras trispinosus</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	12.48	31.00	-4.351	2.684	0.69	<0.0001	25
<i>Pisidia longicornis</i>	Arthropoda	Crustacea	Decapoda	Width of carapace	3.00	6.00	-2.838	2.738	0.713	0.002	10
<i>Pontophilus norvegicus</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	24.51	41.36	-4.419	2.602	0.889	0.005	6
<i>Pontophilus spinosus</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	17.38	54.00	-5.520	3.380	0.851	<0.0001	285
<i>Processa canaliculata</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	10.39	59.76	-4.988	3.011	0.955	<0.0001	198
<i>Processa nouveli holthuisi</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	9.30	44.90	-5.019	3.033	0.965	<0.0001	101
<i>Spirontocaris lilljeborgi</i>	Arthropoda	Crustacea	Decapoda	Eye to tip of telson	8.20	51.20	-4.022	2.513	0.829	<0.0001	358
<i>Astacilla longicornis</i>	Arthropoda	Crustacea	Isopoda	Eye to tip of telson	11.17	46.25	-4.838	2.651	0.817	<0.0001	13
<i>Cirolana borealis</i>	Arthropoda	Crustacea	Isopoda	Eye to tip of telson	10.40	25.76	-2.972	1.924	0.843	<0.0001	24
<i>Janira maculosa</i>	Arthropoda	Crustacea	Isopoda	Eye to tip of telson	2.50	6.50	-3.883	1.874	0.512	0.001	17
<i>Scalpellum scalpellum</i>	Arthropoda	Crustacea	Thoracica	Length of individual capitulum	4.40	18.10	-3.896	2.834	0.919	<0.0001	22
<i>Macandrevia cranium</i>	Brachiopoda	Articulata	Terebratulida	Longest axis	9.70	23.90	-3.349	2.691	0.681	<0.0001	20
<i>Terebratulina retusa</i>	Brachiopoda	Articulata	Terebratulida	Longest axis	11.20	22.10	-4.082	3.297	0.938	<0.0001	14
<i>Gadiculus argenteus</i>	Chordata	Actinopterygii	Gadiformes	Total length	90.00	140.00	-4.813	2.903	0.817	<0.0001	37
<i>Gadus morhua</i>	Chordata	Actinopterygii	Gadiformes	Total length	50.00	550.00	-6.919	3.819	0.814	<0.0001	11
<i>Gaidropsarus vulgaris</i>	Chordata	Actinopterygii	Gadiformes	Total length	26.24	90.61	-4.468	2.547	0.939	<0.0001	14
<i>Merlangius merlangus</i>	Chordata	Actinopterygii	Gadiformes	Total length	33.50	275.00	-4.823	2.863	0.984	<0.0001	92
<i>Micromesistius poutassou</i>	Chordata	Actinopterygii	Gadiformes	Total length	30.00	180.00	-3.755	2.310	0.978	<0.0001	17
<i>Rhinonemus cimbrius</i>	Chordata	Actinopterygii	Gadiformes	Total length	34.00	220.00	-5.356	3.003	0.993	<0.0001	43
<i>Trisopterus esmarkii</i>	Chordata	Actinopterygii	Gadiformes	Total length	40.00	185.00	-5.040	2.956	0.975	<0.0001	59
<i>Trisopterus minutus</i>	Chordata	Actinopterygii	Gadiformes	Total length	52.00	150.00	-4.976	2.970	0.997	<0.0001	12
<i>Diplecogaster bimaculata</i>	Chordata	Actinopterygii	Gobiesociformes	Total length	20.00	35.50	-4.587	2.737	0.906	<0.0001	12
<i>Argentina sphyraena</i>	Chordata	Actinopterygii	Osmeriformes	Total length	27.00	185.00	-5.396	3.059	0.987	<0.0001	13
<i>Ammodytes marinus</i>	Chordata	Actinopterygii	Perciformes	Total length	35.00	160.00	-6.554	3.548	0.932	<0.0001	93
<i>Buenia jeffreysii</i>	Chordata	Actinopterygii	Perciformes	Total length	11.12	42.00	-5.554	3.271	0.936	<0.0001	8
<i>Callionymus lyra</i>	Chordata	Actinopterygii	Perciformes	Total length	26.00	228.00	-4.993	2.927	0.988	<0.0001	256

<i>Callionymus maculatus</i>	Chordata	Actinopterygii	Perciformes	Total length	24.85	165.00	-4.840	2.826	0.98	<0.0001	58
<i>Callionymus reticulatus</i>	Chordata	Actinopterygii	Perciformes	Total length	10.00	170.00	-4.353	2.552	0.946	<0.0001	33
<i>Echiichthys vipera</i>	Chordata	Actinopterygii	Perciformes	Total length	17.00	132.00	-4.836	2.947	0.986	<0.0001	28
<i>Pholis gunnellus</i>	Chordata	Actinopterygii	Perciformes	Total length	115.00	220.00	-5.662	3.097	0.98	<0.0001	11
<i>Pomatoschistus minutus</i>	Chordata	Actinopterygii	Perciformes	Total length	14.00	73.09	-5.379	3.173	0.971	<0.0001	967
<i>Pomatoschistus norvegicus</i>	Chordata	Actinopterygii	Perciformes	Total length	20.00	69.50	-4.988	2.919	0.903	<0.0001	153
<i>Pomatoschistus pictus</i>	Chordata	Actinopterygii	Perciformes	Total length	26.00	58.00	-5.154	3.020	0.931	<0.0001	34
<i>Trachurus trachurus</i>	Chordata	Actinopterygii	Perciformes	Total length	20.00	63.89	-4.618	2.745	0.945	<0.0001	67
<i>Arnoglossus laterna</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	16.00	194.00	-5.283	3.096	0.993	<0.0001	1342
<i>Buglossidium luteum</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	12.00	166.00	-5.235	3.128	0.985	<0.0001	3410
<i>Glyptocephalus cynoglossus</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	39.00	345.00	-5.920	3.310	0.984	<0.0001	16
<i>Hippoglossoides platessoides</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	11.50	250.00	-5.130	2.978	0.986	<0.0001	670
<i>Hippoglossus hippoglossus</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	120.20	238.70	-2.426	1.797	0.673	0.013	8
<i>Lepidorhombus whiffiagonis</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	25.00	315.00	-4.619	2.746	0.997	<0.0001	14
<i>Limanda limanda</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	9.00	265.00	-5.266	3.119	0.993	<0.0001	1174
<i>Microchirus variegatus</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	21.50	155.00	-5.240	3.141	0.994	<0.0001	15
<i>Microstomus kitt</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	125.00	310.00	-5.023	3.014	0.919	<0.0001	58
<i>Phrynorhombus norvegicus</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	40.00	105.00	-5.041	3.054	0.959	<0.0001	14
<i>Pleuronectes platessa</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	11.45	380.00	-5.027	3.009	0.991	<0.0001	112
<i>Solea solea</i>	Chordata	Actinopterygii	Pleuronectiformes	Total length	135.00	310.00	-4.102	2.603	0.984	0.001	5
<i>Agonus cataphractus</i>	Chordata	Actinopterygii	Scorpaeniformes	Total length	21.00	162.00	-4.948	2.905	0.987	<0.0001	130
<i>Eutrigla gurnardus</i>	Chordata	Actinopterygii	Scorpaeniformes	Total length	15.50	225.00	-4.702	2.813	0.991	<0.0001	136
<i>Syngnathus rostellatus</i>	Chordata	Actinopterygii	Syngnathiformes	Total length	52.00	162.00	-7.279	3.414	0.968	<0.0001	26
<i>Ascidia mentula</i>	Chordata	Ascidacea	Enterogona	Longest axis	30.00	59.50	-3.041	2.185	0.693	0.02	7
<i>Ascidia prunum</i>	Chordata	Ascidacea	Enterogona	Longest axis	8.29	17.87	-2.774	1.902	0.839	0.01	6
<i>Ascidia virginea</i>	Chordata	Ascidacea	Enterogona	Longest axis	10.24	44.60	-2.379	1.867	0.614	<0.0001	72
<i>Asidiella aspersa</i>	Chordata	Ascidacea	Enterogona	Longest axis	10.00	45.00	-2.813	2.128	0.876	<0.0001	13
<i>Asidiella scabra</i>	Chordata	Ascidacea	Enterogona	Longest axis	18.73	65.00	-3.580	2.735	0.715	<0.0001	93
<i>Ciona intestinalis</i>	Chordata	Ascidacea	Enterogona	Longest axis	13.88	71.13	-3.292	2.485	0.755	<0.0001	147
<i>Corella parallelogramma</i>	Chordata	Ascidacea	Enterogona	Longest axis	6.00	61.02	-2.948	2.282	0.8	<0.0001	334
<i>Raja radiata</i>	Chordata	Elasmobranchii	Rajiformes	Total length	106.00	450.00	-5.369	3.121	0.98	<0.0001	19
<i>Myxine glutinosa</i>	Chordata	Myxini	Myxiniformes	Total length	92.20	420.00	-5.182	2.699	0.959	<0.0001	162
<i>Pennatula phosphorea</i>	Cnidaria	Octocorallia	Pennatulacea	Total length	14.95	99.00	-5.045	2.816	0.811	<0.0001	567
<i>Asterias rubens</i>	Echinodermata	Asteroidea	Forcipulata	Longest arm to opposite edge of disc	0.98	280.00	-3.445	2.509	0.953	<0.0001	7185
<i>Leptasterias muelleri</i>	Echinodermata	Asteroidea	Forcipulata	Longest arm to opposite edge of disc	6.30	97.00	-3.139	2.193	0.934	<0.0001	132
<i>Stichasterella rosea</i>	Echinodermata	Asteroidea	Forcipulata	Longest arm to opposite edge of disc	14.40	112.40	-3.474	2.437	0.936	<0.0001	17
<i>Astropecten irregularis</i>	Echinodermata	Asteroidea	Phanerozonia	Longest arm to opposite edge of disc	2.56	124.55	-3.768	2.746	0.936	<0.0001	5984
<i>Hippasteria phrygiana</i>	Echinodermata	Asteroidea	Phanerozonia	Longest arm to opposite edge of disc	22.80	145.00	-3.079	2.472	0.96	<0.0001	27
<i>Luidia sarsi</i>	Echinodermata	Asteroidea	Phanerozonia	Diameter of disc	4.29	98.70	-3.958	3.940	0.972	<0.0001	500
<i>Pontaster tenuispinus</i>	Echinodermata	Asteroidea	Phanerozonia	Longest arm to opposite edge of disc	49.15	68.00	-3.455	2.356	0.805	0.006	7
<i>Porania pulvillus</i>	Echinodermata	Asteroidea	Phanerozonia	Longest arm to opposite edge of disc	7.79	101.40	-3.502	2.706	0.986	<0.0001	113
<i>Crossaster papposus</i>	Echinodermata	Asteroidea	Spinulosa	Longest arm to opposite edge of disc	7.63	167.10	-4.545	3.144	0.996	<0.0001	6
<i>Henricia oculata</i>	Echinodermata	Asteroidea	Spinulosa	Longest arm to opposite edge of disc	20.59	47.60	-3.629	2.593	0.917	<0.0001	9
<i>Henricia sanguinolenta</i>	Echinodermata	Asteroidea	Spinulosa	Longest arm to opposite edge of disc	6.92	127.00	-3.399	2.350	0.965	<0.0001	35
<i>Echinocyamus pusillus</i>	Echinodermata	Echinoidea	Clypeastroidea	Longest axis	6.00	21.60	-2.699	2.147	0.867	0.002	7

Continued

Appendix 1. Continued

Species	Phylum	Class	Order	Length	Min L (mm)	Max L (mm)	a	b	r ²	P	N
<i>Echinus acutus</i>	Echinodermata	Echinoidea	Diadematoidea	Longest axis	5.00	78.66	-3.246	2.846	0.963	<0.0001	812
<i>Echinus elegans</i>	Echinodermata	Echinoidea	Diadematoidea	Longest axis	8.00	88.43	-3.258	2.880	0.962	<0.0001	332
<i>Echinus esculentus</i>	Echinodermata	Echinoidea	Diadematoidea	Longest axis	10.00	100.00	-3.460	3.012	0.976	<0.0001	31
<i>Psammechinus miliaris</i>	Echinodermata	Echinoidea	Diadematoidea	Longest axis	4.53	34.74	-3.183	2.877	0.951	<0.0001	328
<i>Strongylocentrotus droebachiensis</i>	Echinodermata	Echinoidea	Diadematoidea	Longest axis	5.73	51.43	-3.452	3.004	0.972	<0.0001	306
<i>Brissopsis lyrifera</i>	Echinodermata	Echinoidea	Spatangoidea	Longest axis	10.00	57.00	-3.240	2.841	0.868	<0.0001	302
<i>Echinocardium cordatum</i>	Echinodermata	Echinoidea	Spatangoidea	Longest axis	6.00	52.39	-3.449	3.011	0.982	<0.0001	507
<i>Echinocardium flavescens</i>	Echinodermata	Echinoidea	Spatangoidea	Longest axis	5.55	50.31	-3.875	3.306	0.965	<0.0001	483
<i>Spatangus purpureus</i>	Echinodermata	Echinoidea	Spatangoidea	Longest axis	17.00	90.00	-3.287	2.887	0.938	<0.0001	233
<i>Psolus phantapus</i>	Echinodermata	Holothuroidea	Dendrochirota	Longest axis	12.10	60.51	-3.557	2.735	0.952	0.005	5
<i>Amphiura chiajei</i>	Echinodermata	Ophiuroidea	Ophiurae	Width of disc	2.16	14.05	-2.795	2.276	0.75	<0.0001	149
<i>Ophiocomina nigra</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	4.92	11.40	-2.242	2.220	0.984	<0.0001	7
<i>Ophiopholis aculeata</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	2.09	15.08	-2.470	2.442	0.939	<0.0001	67
<i>Ophiothrix fragilis</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	1.70	49.28	-2.360	2.337	0.895	<0.0001	437
<i>Ophiura affinis</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	2.77	12.25	-2.981	2.550	0.86	<0.0001	10
<i>Ophiura albida</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	1.85	30.46	-2.895	2.577	0.965	<0.0001	630
<i>Ophiura ophiura</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	3.77	32.90	-2.764	2.507	0.959	<0.0001	599
<i>Ophiura sarsi</i>	Echinodermata	Ophiuroidea	Ophiurae	Diameter of disc	4.00	31.40	-2.345	2.216	0.931	<0.0001	15
<i>Eledone cirrhosa</i>	Mollusca	Cephalopoda	Octopoda	Mantle length	36.70	96.18	-2.711	2.672	0.85	0.003	7
<i>Rossia macrosoma</i>	Mollusca	Cephalopoda	Sepioidea	Mantle length	5.45	59.80	-3.107	2.819	0.979	<0.0001	17
<i>Sepioida atlantica</i>	Mollusca	Cephalopoda	Sepioidea	Mantle length	4.98	26.20	-2.556	2.302	0.831	<0.0001	117
<i>Alloteuthis subulata</i>	Mollusca	Cephalopoda	Teuthoidea	Mantle length	17.00	33.00	-3.106	2.145	0.645	0.003	11
<i>Scaphander lignarius</i>	Mollusca	Gastropoda	Cephalaspidea	Shell length	8.97	30.00	-3.408	2.925	0.846	<0.0001	74
<i>Buccinum undatum</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	10.00	133.59	-3.705	2.840	0.975	<0.0001	383
<i>Colus gracilis</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	20.00	92.00	-3.681	2.708	0.936	<0.0001	357
<i>Colus islandicus</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	12.00	129.10	-3.665	2.641	0.985	<0.0001	41
<i>Colus jeffreysianus</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	10.17	144.42	-3.757	2.750	0.974	<0.0001	122
<i>Hinia reticulata</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	12.00	26.00	-3.323	2.690	0.975	<0.0001	13
<i>Mangelia coarctata</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	13.74	23.46	-3.587	2.502	0.946	0.005	5
<i>Neptunea antiqua</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	13.00	163.00	-3.775	2.834	0.982	<0.0001	325
<i>Trophon muricatus</i>	Mollusca	Gastropoda	Neogastropoda	Longest vertical axis	10.27	31.78	-4.034	2.681	0.896	<0.0001	20
<i>Aporrhais pespelecani</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	17.00	52.16	-4.087	2.993	0.694	<0.0001	112
<i>Aporrhais serresianus</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	15.90	48.00	-2.995	2.169	0.716	<0.0001	40
<i>Euspira catena</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	7.19	29.45	-2.881	2.639	0.931	<0.0001	94
<i>Polinices fusca</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	5.00	24.00	-3.026	2.863	0.991	<0.0001	6
<i>Polinices montagui</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	7.07	30.80	-2.610	2.448	0.936	<0.0001	15
<i>Polinices pulchellus</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	2.49	14.70	-2.629	2.321	0.815	<0.0001	57
<i>Turritella communis</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	4.98	50.38	-4.070	2.755	0.965	<0.0001	1249
<i>Velutina velutina</i>	Mollusca	Gastropoda	Neotaenioglossa	Longest vertical axis	7.00	13.37	-2.975	2.408	0.826	0.002	8
<i>Acanthodoris pilosa</i>	Mollusca	Gastropoda	Nudibranchia	Total length	7.00	25.00	-2.758	2.097	0.903	<0.0001	12
<i>Archidoris pseudoargus</i>	Mollusca	Gastropoda	Nudibranchia	Total length	9.00	53.00	-3.330	2.576	0.936	<0.0001	9
<i>Calliostoma zizyphinum</i>	Mollusca	Gastropoda	Vetigastropoda	Longest vertical axis	8.00	31.00	-3.529	3.015	0.974	<0.0001	32
<i>Gibbula cineraria</i>	Mollusca	Gastropoda	Vetigastropoda	Longest vertical axis	6.00	11.00	-4.183	4.038	0.707	0.001	11
<i>Corbula gibba</i>	Mollusca	Pelecypoda	Myoida	Longest axis	2.59	13.00	-3.844	3.280	0.971	<0.0001	207
<i>Hiattella arctica</i>	Mollusca	Pelecypoda	Myoida	Longest vertical axis	3.00	20.10	-3.915	3.135	0.945	<0.0001	35

<i>Modiolula phaseolina</i>	Mollusca	Pelecypoda	Mytiloida	Longest axis	3.78	29.80	-3.625	2.858	0.971	<0.0001	25
<i>Modiolus modiolus</i>	Mollusca	Pelecypoda	Mytiloida	Longest axis	13.22	165.00	-3.716	2.847	0.996	<0.0001	23
<i>Nucula nitidosa</i>	Mollusca	Pelecypoda	Nuculoida	Longest axis	4.00	14.00	-3.525	2.997	0.936	<0.0001	158
<i>Nucula sulcata</i>	Mollusca	Pelecypoda	Nuculoida	Longest axis	3.45	12.89	-3.756	3.226	0.986	<0.0001	34
<i>Cuspidaria cuspidata</i>	Mollusca	Pelecypoda	Pholadomyoida	Longest axis	8.45	17.00	-4.149	3.306	0.93	<0.0001	18
<i>Aequipecten opercularis</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	5.92	89.00	-3.807	2.986	0.99	<0.0001	110
<i>Anomia ephippium</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	5.33	22.36	-4.241	3.074	0.953	<0.0001	15
<i>Palliolum tigrinum</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	5.09	30.74	-4.295	3.368	0.903	<0.0001	145
<i>Pecten maximus</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	8.60	134.30	-4.018	3.031	0.993	<0.0001	29
<i>Pododesmus patelliformis</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	5.00	41.50	-4.018	2.870	0.872	<0.0001	65
<i>Pseudamussium septemradiatum</i>	Mollusca	Pelecypoda	Pterioidea	Longest axis	8.64	46.22	-3.961	3.084	0.974	<0.0001	99
<i>Abra alba</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	14.00	22.73	-3.754	2.835	0.63	0.001	14
<i>Abra longicallus</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	15.06	27.72	-3.777	3.015	0.841	0.01	6
<i>Abra nitida</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	10.33	22.12	-4.808	3.694	0.94	<0.0001	30
<i>Abra prismatica</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	8.19	23.45	-3.790	2.619	0.772	<0.0001	13
<i>Acanthocardia echinata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	5.00	60.90	-3.493	2.938	0.968	<0.0001	48
<i>Arctica islandica</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	10.70	102.00	-3.009	2.632	0.967	<0.0001	60
<i>Astarte sulcata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	7.74	32.40	-3.338	2.925	0.934	<0.0001	156
<i>Chamelea gallina</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	9.67	29.65	-3.458	2.872	0.933	<0.0001	55
<i>Circomphalus casina</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	30.09	47.30	-5.584	4.360	0.966	<0.0001	7
<i>Clausinella fasciata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	10.85	27.45	-3.733	3.115	0.986	<0.0001	12
<i>Donax vittatus</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	17.71	29.63	-4.416	3.455	0.978	<0.0001	17
<i>Dosinia exoleta</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	23.09	30.44	-4.481	3.664	0.778	0.004	8
<i>Dosinia lupina</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	11.87	29.99	-3.748	3.186	0.99	<0.0001	6
<i>Ensis ensis</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	39.09	78.76	-5.219	3.077	0.994	<0.0001	5
<i>Gari fervensis</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	18.70	46.83	-5.066	3.475	0.84	<0.0001	13
<i>Lucinoma borealis</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	7.46	18.25	-4.144	3.452	0.894	<0.0001	13
<i>Phaxas pellucidus</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	8.80	35.50	-4.759	2.965	0.884	<0.0001	100
<i>Spisula elliptica</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	11.00	31.05	-3.759	3.012	0.853	<0.0001	50
<i>Spisula solida</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	8.70	23.95	-2.816	2.258	0.99	<0.0001	9
<i>Spisula subtruncata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	7.00	29.00	-3.747	3.045	0.972	<0.0001	28
<i>Tapes decussatus</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	9.30	18.55	-4.320	3.605	0.838	<0.0001	42
<i>Timoclea ovata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	6.42	18.00	-3.315	2.745	0.794	<0.0001	79
<i>Tridonta aculeata</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	11.19	26.69	-3.441	2.941	0.916	<0.0001	16
<i>Tridonta elliptica</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	8.70	27.30	-3.833	3.276	0.948	<0.0001	55
<i>Tridonta montagui</i>	Mollusca	Pelecypoda	Veneroida	Longest axis	7.00	27.50	-2.845	2.526	0.908	<0.0001	38
<i>Leptochiton asellus</i>	Mollusca	Polyplacophora	Lepidopleurida	Total length	4.96	9.92	-4.046	3.136	0.913	<0.0001	12
<i>Leptochiton scabridus</i>	Mollusca	Polyplacophora	Lepidopleurida	Total length	4.80	8.45	-4.211	3.358	0.915	0.011	5
<i>Antalis entalis</i>	Mollusca	Schaphopoda	Lepidopleurida	Total length	13.66	42.23	-3.480	2.139	0.714	<0.0001	484

Appendix 2. Significance of differences in length–weight relationships of some key widely distributed benthic invertebrates from the North Sea, with analysis of covariance F values and P values given, where significant effects are found to occur when $P < 0.05$. Coefficients for the interactions are also given to illustrate the amount of variation in the data that is explained by the factor. Factors include the effect of area (samples taken north or south of the 50 m bathycline) and year (data recorded in 2003 or 2004), and the interaction of area and year.

	<i>Asterias rubens</i>	<i>Astropecten irregularis</i>	<i>Crangon allmanni</i>	<i>Echinocardium cordatum</i>	<i>Limanda limanda</i>	<i>Liocarcinus depurator</i>	<i>Ophiura albida</i>	<i>Ophiura ophiura</i>	<i>Pagurus bernhardus</i>	<i>Turritella communis</i>
Total no. measurements	7185	5984	2115	507	1174	620	630	599	2038	1249
Time*log₁₀length										
F value	24.215	9.582		12.945	8.762					14.269
P value	<0.001	0.002	n.s.	<0.001	0.003	n.s.	n.s.	n.s.	n.s.	<0.001
Coefficient	0.033	0.030		0.120	−0.023					−0.065
Area*log₁₀length										
F value	98.721	16.814	13.358				24.273		15.149	14.127
P value	<0.001	<0.001	<0.001	n.s.	n.s.	n.s.	<0.001	n.s.	<0.001	<0.001
Coefficient	−0.065	−0.040	0.088				0.098		0.043	−0.069
Time*area*log₁₀length										
F value	213.370	42.495								57.720
P value	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	<0.001
Coefficient	0.017	0.006								−0.014