

ESTIMATION OF GLOBAL MEIOFAUNA AND MACROFAUNA BIOMASS*

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Abstract

Global distribution models of benthic biomass were generated for meiobenthos (0.1-1 mm) and macrobenthos (1 mm - 1 cm) based on general linear models linking benthos biomass with depth, sea surface and bottom temperature, and surface chlorophyll-*a*. The source of the data points (n=184 and n=140, respectively), and environmental variables used for the calculations are presented, along with the most important sources of uncertainty. The models for meiofauna and macrofauna accounted for 27% and 42% of the variation in measured biomass values, respectively ($p < 0.0001$). The model predicts a total of 2.34×10^9 teragrams of meiofauna biomass and 1.07×10^7 teragrams macrofauna biomass across the world ocean for an estimated total of 1.3×10^{10} teragrams benthic invertebrate meiofauna and macrofauna biomass worldwide. This study, performed about 12 years ago, but not published then, yielded result roughly similar to the more detailed contribution by Wei *et al.* (2010, PLoS ONE 5(12): e 15323; doi: 10:1371/journal.pone.0015323), though it is based on far less input data and variables.

Introduction

Invertebrate species buried in or living on the sea bottom and jointly forming the benthos occur in all oceans. Understanding the spatial distribution of benthic invertebrate biomass can provide valuable information about regional variability in biogeochemical processes (Marcus 1998; Wei *et al.* 2010), and allow for the more complete construction of mass-balance models of oceanic systems (Vasconcellos 2004). Estimates of benthic biomass can also serve as a time averaged proxy for the flux of carbon to the deep ocean (Rex *et al.* 2006). The continental shelves, which receive organic input from terrestrial sources, and upwelling regions are considered to have the greatest abundance of benthic biomass, but primary production from chemoautotrophic bacteria in communities at great depths surrounding cold seeps (Gatehouse 1998) and hydrothermal vent (Van Dover 2000) can also support high levels of biomass.

In general, with increasing distance from land, benthic communities, especially those in the deep sea, depend on a small amount of organic input from animal and plant remains and marine snow—macroscopic aggregations of detritus, inorganic matter and living organisms that fall to the ocean floor from the euphotic zone (Alldredge and Silver 1988). While it is widely accepted that benthic biomass for all size classes falls steadily with depth (Rowe 1984; Thiel 1975), spatial variation in a variety of physical, chemical and biological factors may also play a significant role in determining biomass distribution and abundance (Gooday and Turley 1990; Galeron *et al.* 2000).

The input of organic matter varies temporally and spatially throughout the world's oceans. Miller (2004) credits greater benthic biomass in high latitudes to seasonal blooms in primary productivity. Unlike higher latitudes, primary production at low latitudes is utilized year-round by pelagic communities, which reduces food availability for benthic communities. Lateral transfer by currents at the surface and at depth is important in the distribution of organic material (Kroncke 2000; Soltwedel 1997). Additional biotic and abiotic factors, such as nutrient (silicate, nitrate, phosphate) and oxygen availability, local sedimentation and substrate composition

* Cite as Szumylo, A. and Pauly, D. (2018) "Estimation of Global Meiofauna and Macrofauna Biomass," Pp. 44-52. In Pauly D. and V. Ruiz-Leotaud (eds.) Marine and Freshwater Miscellanea. Fisheries Centre Research Reports 26(2). Institute for the Oceans and Fisheries, University of British Columbia.

(Lovell and Trengo 2003) and inter- and intra- species interaction may also influence the spatial distribution of benthic biomass (Alongi 1992).

The spatial variation of the biotic and abiotic environmental characteristics outlined above suggests that the accepted assumption that benthic biomass decreases with depth may not be valid for some regions of the world's oceans and that prediction of biomass distribution must take these variables into account. While benthic biomass measurements have been recorded for all ocean basins, the vast majority of measurements have been taken in the Atlantic and Arctic Oceans by long-established European and American oceanographic institutions (Rex 2006). The scarcity of measurements from the Indian, Pacific, and Southern Oceans, makes modeling benthic biomass for these regions difficult. Further, a number of the factors speculated to be important in influencing benthic biomass distribution are complicated, if not impossible, to estimate on any scale.

Because of these factors, global accounts of benthos distribution are rare (see Rex *et al.*, 2006), and no estimation exists that attempts to deal simultaneously with the major factors affecting benthos distribution for the world ocean. This contribution represents such an attempt, and is based on multivariate analysis of two datasets summarizing biomass measurements for meiobenthos and macrobenthos combined with GIS mapping.

Our aim is not to replace measurements for site-specific purposes, such as environmental impact assessment, but to produce broadly patterned global maps, thereby fulfilling three goals:

- 1) Providing a global benchmark for benthic biomass, enabling comparisons of local studies, i.e. providing a standard for low or high biomasses;
- 2) Providing a first estimate of benthic biomass for large-scale trophic models of ecosystems;
- 3) Providing the first step of an exercise to identify additional factors impacting the distribution of benthos on a global scale.

Methods

Data Used

Table 1 summarizes the key features of the two datasets assembled here from 28 publications which reported to geographic coordinates for their benthos biomass measurements (listed with location and size class in References; see also Figure 1). As in Rex *et al.* (2006), taxonomic groups of marine benthic invertebrates are segregated by size in this study. Metazoan meiofauna, invertebrate groups retained on sieves of 30 to 74 μm mesh size, include foraminiferans, nematodes, harpacticoid copepods among others. Metazoan macrofauna included those organisms retained on sieves between 250 and 1000 μm mesh size such as polychaete worms, crustaceans and mollusks. Because of the limited number of publications presenting samples of metazoan megafauna, which comprises cnidarians, crustaceans and echinoderms visible on the sediment, global estimates for this size class are not presented in this analysis. Figure 1 shows the geographic distribution of observed data points for meiofauna and macrofauna.

Table 1. Size classes used to categorize benthos, associated mesh sizes and number of cases available for the empirical equations. The data originated from peer-reviewed journal articles published between 1962 and 1998).			
Class	Size	Lower sieve mesh size (μm)	Number of data points
Meiofauna	0.1-1 mm	30 – 74	184
Macrofauna	1 mm – 1 cm	250 – 1000	140

The spatial and temporal resolution for environmental parameters used to estimate global distribution of benthic meiofauna and macrofauna biomass are summarized in Table 2. ETOPO2 bathymetry data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Geophysical Data Center (NGDC). This dataset was constructed by combining available depth soundings with high-resolution marine gravity information from the Geosat and ERS-1 spacecraft. Spatial resolution of ETOPO2 bathymetry is 2-minute (13.7 km² at the equator) (Smith and Sandwell, 1997).

Table 2. Spatial and temporal scale of environmental variables used to estimate benthic biomass distribution and abundance. Meiofauna and macrofauna range refer to the minimum and maximum value for each environmental variable that occurs for all observed data points, as used to generate the global estimate presented here.

Environmental variable (unit); source	Spatial	Temporal	Meiofauna range	Macrofauna range
Bathymetry (m); Smith and Sandwell (1997)	2 min.	None	3 - 8232	2 - 5721
Sea Surface Temperature (°C); NASA/GSFC MODIS; Feldman (2006)	4.7 km	Annual mean (2002-2005)	-0.98 - 28.7	-0.98 - 28.7°
Bottom temperature (°C); 2001 World Ocean Atlas; Conkright (2002)	1 °C	Annual mean	-0.81 - 27.8	-1.9 - 27.3
Bottom salinity (PSU); 2001 World Ocean Atlas; Conkright (2002)	1 deg	Annual mean	32.8 - 38.9	33.5 - 35.8
Surface Chlorophyll-<i>a</i> concentration (m·mg³); NASA/GSFC MODIS; Feldman (2006)	4.7 km	Annual mean (2002-2005)	0.06 - 17.4	0.07 to 17.4
Nutrients (μmol L⁻¹); 2001 World Ocean Atlas; Conkright (2002)	1 deg	Annual mean	--	--
Bottom silicate	--	--	1.5 - 150.4	2.4 - 154.3
Bottom phosphate	--	--	0.09 - 2.7	0.22 - 0 3.2
Bottom nitrate	--		0.13 - 37.1	0.36 - 44.2
Bottom oxygen; 2001 World Ocean Atlas; Conkright (2002)	1 deg	Annual mean	--	--
Apparent oxygen utilization (mL·L⁻¹)			-0.41 - 4.9	-0.23 - 6.5
Dissolved Oxygen (mL·L⁻¹)			1.4 7.4	0.26 - 7.4
Oxygen saturation (%)			24.5 - 108.7	3.1 - 105.4

Bottom temperature, bottom salinity, bottom phosphate, bottom nitrate, bottom silicate, bottom dissolved oxygen, apparent bottom oxygen utilization (oxygen saturation concentration minus measured dissolved oxygen concentration), and percent bottom oxygen saturation (the amount of dissolved oxygen as a percentage of maximum potential oxygen amount that could be present for the given temperature and salinity at standard atmospheric pressure), are annual mean measurements of these variables (Conkright, 2002) taken at standard intervals down to 5500 meters. The native resolution of WOA01 data is 1-degree, but this was resampled by the Kansas Geological Survey (KGS) at ETOPO2 resolution and depth. There were several regions of the world's oceans that did not have values for these grids. These areas were interpolated by the KGS using the ESRI ArcGIS Nibble Algorithm, which replaces missing values with the value of the nearest neighbor.

Sea surface temperature and chlorophyll-*a* data were obtained from NASA's Goddard Space Flight Center. Both data sets were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS), a key instrument aboard the Aqua Earth Observing System PM satellite (Feldman, 2006). Annual averaged grids from 2002 to 2005 were averaged together to produce a single composite grid. Spatial resolution was resampled from 4.7 km resolution to 2-minute resolution using ESRI's resampling algorithm.

Inconsistencies in the yearly average grids for sea surface temperature and chlorophyll-*a* were found for areas presumably covered by ice for a significant portion (more than six months) of the year. These areas not used in the analysis.

Analyses

Selection of environmental variables

We investigated seven variables for their relationship to benthic biomass. Depth, surface and bottom temperature and chlorophyll-*a* concentration were included to represent spatial variation in food availability. Other variables, such as bottom nutrient concentrations (silicate, nitrate and phosphate), salinity and several expressions of oxygen content were tested to determine if they might have an effect. The correlation matrices (Table 3) evaluate the degree of global covariation of the environmental variables. The strongest correlation was found between the bottom nutrient concentrations and the variants of bottom water oxygen content.

Table 3. Correlation matrix of variables for the data points associated with meiofauna (in gray) and macrofauna biomass samples (1: depth; 2: average annual sea surface temperature; 3: bottom temperature; 4: bottom salinity; 5: average annual chlorophyll-*a* concentration; 6A: bottom silicate; 6B: bottom phosphate; 6C: bottom nitrate; 7A: apparent bottom oxygen utilization; 7B: bottom dissolved oxygen; 7C: percent bottom oxygen saturation).

	1	2	3	4	5	6A	6B	6C	7A	7B	7C
1	-	0.208	0.457	0.235	0.078	0.600	0.500	0.495	0.324	0.095	0.206
2	-0.105	-	0.389	0.142	0.338	0.135	0.237	0.241	0.381	0.602	-0.431
3	0.356	0.509	-	0.564	0.249	0.404	-0.545	-0.565	-0.227	0.538	0.055
4	0.243	0.067	0.147	-	-0.141	-0.310	-0.595	-0.563	-0.261	-0.255	0.139
5	0.349	0.528	-0.375	0.152	-	0.030	0.025	0.012	0.045	0.264	0.084
6A	-0.451	0.401	0.043	0.006	0.067	-	0.763	0.711	0.618	0.204	0.486
6B	0.344	0.545	0.024	0.124	-0.123	0.876	-	0.976	0.846	0.292	-0.729
6C	0.407	0.480	0.066	0.185	0.082	0.882	0.977	-	0.861	-0.301	-0.749
7A	-0.259	0.506	0.115	0.204	-0.081	0.796	0.956	0.935	-	0.682	-0.973
7B	0.050	0.636	0.478	0.224	0.258	-0.676	0.845	-0.793	0.920	-	0.796
7C	0.181	-0.533	-0.201	0.232	0.118	-0.726	-0.925	0.894	0.990	0.948	-

Modeling benthic biomass distribution

The ArcGIS sample algorithm was used to link values from the bathymetry, bottom temperature, sea surface temperature, chlorophyll-*a*, silicate, nitrate, phosphate and oxygen grids to the log biomass values associated with the points shown in Figure 1. Again, data points from areas that appeared to be covered in ice for a significant portion of the year were not included in the final analysis. Multiple linear regression analysis was performed in STATA™ to develop a model for predicting log meiofauna and macrofauna biomass using a number of combinations of environmental variables (Table 4). Because the addition of environmental variables

aside from those that proxy spatial variation in food availability did not significantly strengthen models across size classes, the final model chosen only included depth, surface and bottom temperature and chlorophyll-*a* concentration. The resulting regression equations were used with the variable grids to create an estimate of global benthic log biomass for each size class.

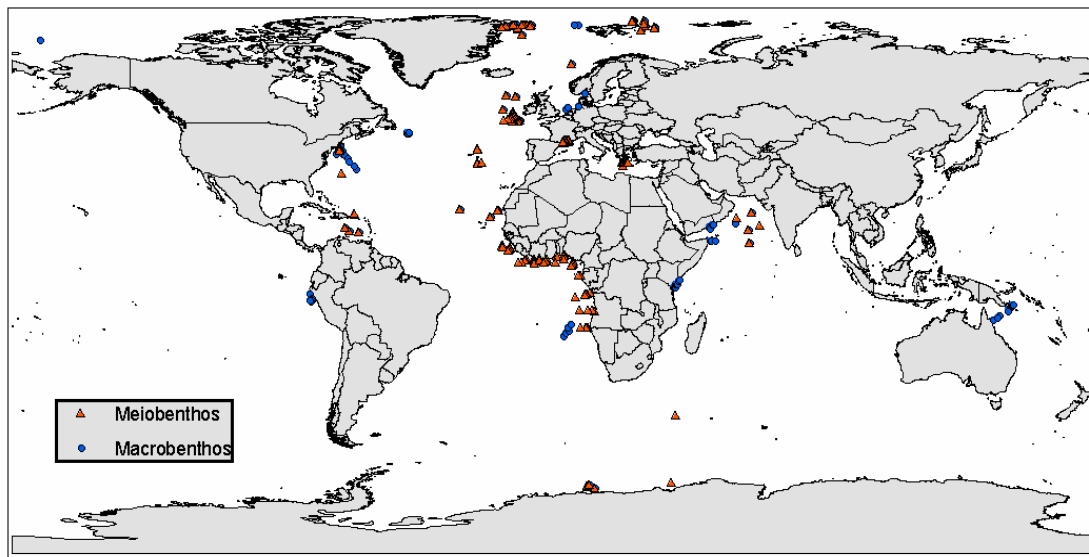


Figure 1. Global distribution of the sample benthos measurements used to estimate biomass abundance.

Results and Discussion*

Regression coefficients are shown in Table 5. The models for meiofauna and macrofauna accounted for 27% and 42% of the variation in measured biomass values, respectively ($p < 0.0001$). Bathymetry and sea surface temperature had significant influence in both models ($p < 0.05$), and bottom temperature had a significant influence on the macrofauna model ($p < 0.01$). The resulting maps are shown in Figure 2, whose basic features are roughly similar to those in Figure 7 of Wei *et al.* (2010); the main difference between these maps is that mid-ocean ridges are prominent in Figure 2, if only because they are predicted to have the higher benthic biomass associated with their elevation (as also occurs in reality, see, e.g., Haymon *et al.* 1991 and Mortensen *et al.* 2008). In contrast, Figure 7 of Wei *et al.* (2010) shows no mid-ocean ridge effect.

Table 6 presents estimated total values of meio- and macrobenthos biomass summarized by ocean basin from maps presented in Figures 2a and 2b. The model predicts a total of 2.34×10^9 teragrams of meiofauna biomass and 1.07×10^7 teragrams macrofauna biomass across the world ocean for an estimated total of 1.3×10^{10} teragrams benthic invertebrate meiofauna and macrofauna biomass worldwide.

This study represents a method for predicting benthic biomass on the global scale using depth, temperature, and chlorophyll-*a* concentration. The maps derived from the regression analysis presented in Table 2 resemble bathymetric maps (Figure 2). This is to be expected, as depth has the most predominant effect on biomass distribution. While sampling coverage is limited (there was very little data available for the Pacific Ocean basin) and measurements of biomass used in this projection were recorded over a course of more than 30 years using a number of different collection, sorting and preservation methods (Gage *et al.*, 2002), the analysis presented here is a step towards quantifying the environmental variables that influence the distribution of benthic biomass between and within ocean basins.

* When this report was issued, it was overlooked that tables 5 and 6 were omitted. These tables also appear to have been lost; and thus the maps (Figure 2a & 2b) have to be taken at face value, i.e., cannot be reproduced. The editors apologize for this. (Note added on March 15, 2021)

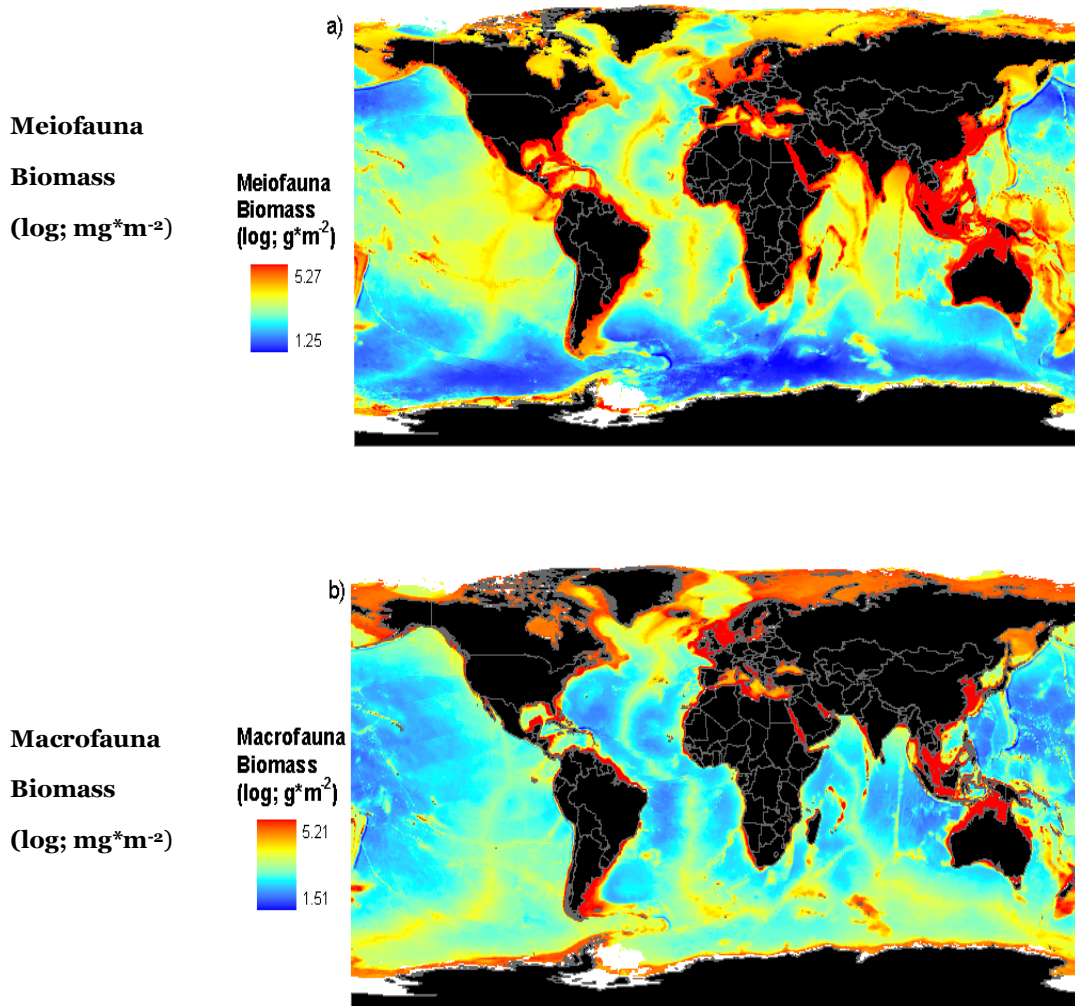


Figure 2. Maps detailing log benthic biomass for meiofauna (a) and macrofauna. White areas of the map are covered by ice for more than six months of the year.

Several additional considerations, experimental investigation of the importance of other environmental variables, the variable response of different taxa to food availability, physical oceanography and an expanded distribution of field measurements, should be taken into account in future permutations of this study. In investigating variations in benthic community structure and size class in the tropical North East Atlantic, Galeron *et al.* (2000) demonstrated that within a single geographic location, both different size class and different taxa within size classes responded differently to variations in food availability. This suggests that other environmental variables, such as those used in this analysis, may play a part in governing benthic biomass distribution.

Food availability has been shown to determine the relative abundance of benthic size classes in the Eurasian Arctic Ocean (Kroncke, 1998). The findings of Galeron *et al.* (2000) and Kroncke *et al.* (2000) suggest that in the presence of an abundant food supply, larger benthic organisms compete directly for organic material. On the other hand, in food-limited locations, smaller benthic organisms and bacteria convert organic matter into a form usable by higher trophic levels. Thus, the distribution and abundance of bacteria should also be considered in future models.

The investigation of ocean movement and physical disturbances may also be helpful in estimating biomass distribution. Kroncke *et al.* (2000) suggested that currents may actually assist in the lateral transport of organic material which may sustain life in areas with low food supply from the overlying waters. At greater velocities,

however, currents inhibit the growth of benthic communities by re-suspending sediment (Rhoads and Young, 1970). There may also be areas in polar regions where the contact of glacial ice with the ocean floor may prevent growth of benthic organisms.

Benthic biomass estimates of the Arctic and Antarctic were not included in this analysis because environmental data for these regions, specifically remotely sensed data for sea surface temperature and chlorophyll-*a* concentrations, were unavailable. Because the polar regions tend to have higher than average benthic biomass (Brey and Gerdes, 1997) and intermediate species richness (Piepenburg, 2005), improvements of sea surface temperature and chlorophyll-*a* grids generated from satellite imagery can be used to improve benthos biomass estimations.

Acknowledgements

We express our thanks to Drs. Elliott Norse, John Guinotte and Lance Morgan of the Marine Conservation Biology Institute and Gilbert Rowe of Texas A&M University for their assistance in analysis of the data presented therein.

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* With region and type of benthic fauna in bold characters when appropriate.

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