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Global distribution of pteropods representing carbonate functional type biomass

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Pteropods are a group of holoplanktonic gastropods for which global biomass distribution patterns remain poorly resolved. The aim of this study was to collect and synthesize existing pteropod (Gymnosomata, Thecosomata and Pseudothecosomata) abundance and biomass data, in order to evaluate the global distribution of pteropod carbon biomass, with a particular emphasis on its seasonal, temporal and vertical patterns. We collected 25 902 data points from several online databases and a number of scientific articles. The biomass data has been gridded onto a $360 \times 180^\circ$ grid, with a vertical resolution of 33 WOA depth levels. Data has been converted to NetCDF format which can be downloaded from PANGAEA, <http://doi.pangaea.de/10.1594/PANGAEA.777387>. Data were collected between 1951–2010, with sampling depths ranging from 0–1000 m. Pteropod biomass data was either extracted directly or derived through converting abundance to biomass with pteropod specific length to weight conversions. In the Northern Hemisphere (NH) the data were distributed evenly throughout the year, whereas sampling in the Southern Hemisphere was biased towards the austral summer months. 86 % of all biomass values were located in the NH, most (42 %) within the latitudinal band of $30\text{--}50^\circ$ N. The range of global biomass values spanned over three orders of magnitude, with a mean and median biomass concentration of 8.2 mg C l^{-1} (SD = 61.4) and 0.25 mg C l^{-1} , respectively for all data points, and with a mean of 9.1 mg C l^{-1} (SD = 64.8) and a median of 0.25 mg C l^{-1} for non-zero biomass values. The highest mean and median biomass concentrations were located in the NH between $40\text{--}50^\circ$ S (mean biomass: 68.8 mg C l^{-1} (SD \times 213.4) median biomass: 2.5 mg C l^{-1}) while, in the SH, they were within the $70\text{--}80^\circ$ S latitudinal band (mean: 10.5 mg C l^{-1} (SD \times 38.8) and median: 0.2 mg C l^{-1}). Biomass values were lowest in the equatorial regions. A broad range of biomass concentrations was observed at all depths, with the biomass peak located in the surface layer (0–25 m) and values generally decreasing with depth. However, biomass peaks were located at different depths in different ocean basins: 0–25 m depth in the N Atlantic, 50–100 m in the Pacific, 100–200 m in the Arctic,

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200–500 m in the Brazilian region and >500 m in the Indo-Pacific region. Biomass in the NH was relatively invariant over the seasonal cycle, but more seasonally variable in the SH. The collected database provides a valuable tool for modellers for the study of ecosystem processes and global biogeochemical cycles.

5 1 Introduction

The phylum Mollusca comprises at least 100 000 species, of which only 4000 species inhabit the upper ocean, principally those in the class Gastropoda. Of those, around 140 species are holoplanktonic, meaning that they do not inhabit the seabed at any phase of their lifecycle. This lifestyle is facilitated by particular adaptations, such as the development of swimming appendages and the reduction or total disappearance of the calcareous shell. The pteropods are holoplanktonic gastropods that are widespread and abundant (Lalli and Gilmer, 1989). They consist of two orders: the Thecosomata (shelled pteropods) and the Gymnosomata (naked pteropods). The two orders are taxonomically separated not only by their morphology and behaviour, but also by their trophic position, with the former consisting of mainly herbivores and detritivores (Hopkins, 1987; Harbison and Gilmer, 1992) and the latter, carnivores (Lalli, 1970). A further systematic detail divides order Thecosomata into two suborders, Euthecosomes and Pseudothecosomes. The two suborders have similar lifestyles, but are set apart by their anatomical characteristics, most notably a gelatinous internal pseudoconch in Pseudothecosomes that replaces the external shell present in Euthecosomes (Lalli and Gilmer, 1989).

Pteropods have high ingestion rates that are in the upper range for mesozooplankton (Perissinotto, 1992; Pakhomov and Perissinotto, 1997). Even though pteropods constitute on average only 6.5 % of the total abundance density of grazers, in areas such as the Southern Ocean they contribute on average 25 % of the grazing impact and consume up to 19 % of daily primary production (Hunt et al., 2008). Pteropods are also an

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important dietary food item for many predators, such as larger zooplankton as well as herring, salmon, whales and birds (Hunt et al., 2008; Karnovsky et al., 2008).

Pteropods are involved in numerous pathways of organic carbon export. As is common to most zooplankton, they contribute to the downward flux of carbon through the production of negatively buoyant faecal pellets. A number of pteropods also produce pseudo-faeces, i.e. accumulations of rejected particles expelled in mucous strings (Gilmer, 1990). Pteropods feed using feeding webs that trap fine particles and small faecal pellets, which form fast sinking colloids when abandoned (Jackson, 1993; Gilmer and Harbison, 1991). Pteropods actively transport carbon downwards during the descent phase of nycthemeral migrations, mostly from the shallow euphotic zone into the deeper twilight zone, where they respire and defecate.

In terms of inorganic carbon, pteropods are one of only a few taxa that make their shells out of aragonite as opposed to the calcite form of calcium carbonate. The biogeochemical importance of aragonite production by pteropods has been shown in a number of studies (Berner and Honjo, 1981; Acker and Byrne, 1989). Their aragonite shell not only contributes to the transfer of inorganic material into the deep ocean (Tréguer et al., 2003) but also increases the weight of pteropods as settling particles and, hence their sinking speed (Lochte and Pfannkuche, 2003). Ontogenetic (or seasonal) migration, often followed by mass mortality, transports both organic and inorganic carbon to depth (Tréguer et al., 2003). On a global scale, aragonite production by pteropods might constitute at least 12 % of the total carbonate flux worldwide (Berner and Honjo, 1981).

Although the ecological and biogeochemical importance of pteropods has been well recognised, essential details on their global biomass distribution remain poorly resolved. Such information is required to allow this group to be accurately incorporated as a functional type within ecosystem models and to allow a further assessment and simulation of their contribution to carbon export in biogeochemical models.

The Marine Ecosystem Model Inter-comparison Project (MAREMIP) has been launched as an initiative to construct a database for ten major plankton functional types

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(PTFs) currently represented in marine ecosystem models. Field measurement-based data on abundance and/or biomass has been collected for the purposes of compiling biomass data sets, called the “MARine Ecosystem Data” (MAREDAT) project, which includes ten major plankton functional types (PFT): diatoms (silicifiers), Phaeocystis (DMS producers), coccolithophores (calcifying phytoplankton), diazotrophs (nitrogen fixers), picophytoplankton, bacterioplankton, mesozooplankton, macrozooplankton and pteropods and foraminifera (calcifying zooplankton). All MAREDAT data sets of global biomass distribution will become publicly available and will serve marine ecosystem modellers for model evaluation, development and future model inter-comparison studies. This study will present and evaluate the seasonal and temporal distribution of pteropod carbon biomass, with a particular emphasis on the seasonal and vertical biomass patterns.

2 Data

2.1 Origin of data

The sources of the data were several online databases (PANGEA, ZooDB, NMFS-COPEPOD) and scientific articles (Table 1). The full dataset is comprised of 25 902 data points, from 39 projects (Table 1). Each data point includes the following information: Year, Month, Day, Longitude, Latitude, Sampling Depth (m), Abundance (ind m^{-3}) or Biomass ($mg m^{-3}$) and the data source. All data points presenting abundance measurements were later converted to biomass values. Zero biomass values were included as biologically valid data points in the dataset. However, some datasets included multiple samples at several stations, which would bias the global biomass estimates if not suitably treated. Thus, when repeat sampling of the same station location was conducted in a single day (for instance through sampling both night and day or with different mesh-sized nets), a mean biomass at that station was calculated and used in subsequent processing. Where different pteropod species or life stages were included

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in the sampling, the biomass of these data points was summed. This procedure led to a final number of 15 194 data points.

The database encompassed both Gymnosomata and Thecosomata (including the suborder of Pseudothecosomata) with data sorted to the level of species. Further sub-species levels (or formae) were not resolved within the database.

2.2 Quality control

Stations with abundance of $>20\,000$ individual m^{-2} and where life-stage was not recorded were assumed to be juveniles and a conversion to biomass carried out accordingly (see below). The identification and rejection of statistical outliers in the summarised biomass dataset was performed using Chauvenet's criterion (Glover et al., 2011; Buitenhuis et al., 2012). Based on this statistical analysis, none of the stations were excluded as outliers (two sided z-score: $z_c = 4.0462$).

2.3 Methodology behind biomass conversion

The majority of studies reported abundance values ($ind\ m^{-3}$) while only a small proportion reported biomass values ($mg\ m^{-3}$). We extracted the abundance value where reported and converted to biomass using a length to weight algorithm. For consistency, the same algorithm was used when biomass values was reported in the literature.

Three studies have reported such algorithms, all on the pteropod species *Limacina helicina*, as follows:

$$DW = 0.257L^{2.141}, \text{ Gannefors (1995)} \quad (1)$$

$$\log DW = 0.685L - 2.222, \text{ Fabry (1989)} \quad (2)$$

$$DW = 0.1365L^{1.501}, \text{ Bednaršek et al. (2011)} \quad (3)$$

where DW is dry weight in mg and L is shell diameter in mm.

The algorithms were fitted to differing size ranges of pteropods, so we compared their performance across a uniform size range to consider their suitability for more broad

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scale application (Fig. B1). The functional form of Fabry (1989), although optimum for a size range between 1 and 4 mm, became exponentially large at shell diameters above this range so was considered unsuitable for the present analysis. The Gannefors et al. (2005) and Bednaršek et al. (2011) functional forms performed similarly and realistically across the shell diameter size ranges encountered by the present study (0.01 to 50 mm). We chose the Bednaršek et al. (2011) function given that its estimate of dry weight between 1 and 4 mm shell diameter fell midway between the estimates of the Fabry (1989) and Gannefors et al. (2005) algorithms combined with the fact that its behaviour remained realistic at larger size categories. It is to be noted that applying this algorithm across all shelled pteropod species has its limitations and is likely to work better for species with a similar shape to coiled, moderately spired shell of *Limacina helicina ant.* than for uncoiled, needle-like, triangular, or pyramidally shaped species. Nevertheless, we consider it to provide a suitably reasonable first order approximation of individual shell biomass for the purpose of the present analysis.

For some data records, only the species and abundance was recorded without any indication of individual size or weight. In these instances, we had to make assumptions with regard to the individual shell diameter in order to calculate biomass. Our first step was to determine approximate adult size for each species using information from the Marine species identification portal (<http://species-identification.org/>). We then categorised species as either being small (0–1.2 mm shell diameter), medium (1.2 to 4 mm shell diameter) or large (>4 mm shell diameter). The corresponding mean individual dry weights of these three categories were estimated from Bednaršek et al. (2011), where a studied population of *Limacina helicina antarctica* spanned all 3 of the above size categories (Table 2). Dry weight was subsequently transformed to carbon using a conversion factor of 0.25, following Larson (1986).

This conversion process would benefit from further refinement, as dry weights for other pteropod species become available in the future, in which case biomass can be calculated through the application of species specific algorithms to the datasets compiled by this study.

3 Results

3.1 Global data distribution of biomass data

Altogether, there were 25902 data entries across all oceanic regions (Fig. 1). Of these, 1579 were reported as zero values (10.4 % of all values). 86 % of non-zero entries were located in the Northern Hemisphere (NH), with the remaining 14 % in the Southern Hemisphere (SH, Table 4). With respect to latitude, most entries (42 %) came from within the latitudinal band of 30–60° N (Fig. 2), while 9 % of entries were between 60 and 90° N. Comparatively less samples were collected in the SH, with the equivalent latitudes of 30 to 90° S accounting for just 3 % of all entries.

Net samples were taken down to a maximum depth of 1000 m, with 80 % being taken within the top 200 m (Table 5). 87 % of all biomass occurred within the top 25 m, with the remaining biomass being relatively evenly distributed down to 500 m. The deepest occurrence of pteropods in our database was 915 m, located at 18° N/21° E. The highest biomass (3214 mg C l⁻¹) was recorded at the surface (25 m) in the NH temperate region, at 42° N/70° W.

3.2 Temporal distribution of data

The data was collected between 1951–2010, with two sampling peaks in the late 1950s and early 1960s and then in the late 1990s and early 2000s. There was a disproportionate number of samples take in 1958, when 21 % of all data points were obtained (Fig. 3). The sampling period between 1980 and 1990 was the period with the lowest number of samples, contributing just 11 % of all database entries. From the 1990s onwards, there was a more consistent sampling effort.

To check for seasonal biases, the data was divided into four seasons for each hemisphere. While in the NH, the data was distributed evenly across the four seasons (24 % in spring, 30 % in summer, 23 % in autumn and 23 % in winter), sampling in the SH was biased towards summer values (42 %, Table 6).

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3.3 Global biomass characteristics

The range of global biomass concentrations was wide, spanning over three orders of magnitude (Fig. 5a), with a mean biomass of 8.2 mg C l^{-1} (SD = 61.4) for all data points and 9.1 mg C l^{-1} (SD = 64.8) for non-zero biomass values. In the NH, mean biomass was $10.37 \text{ mg C l}^{-1}$ (SD = 69.7) and the median biomass, 0.3 mg C l^{-1} . In the SH, mean biomass was 1.73 mg C l^{-1} (SD = 10.1) and the median biomass, 0.02 mg C l^{-1} (Table 3).

3.3.1 Latitudinal biomass distribution

Pteropods were found at all latitudes in which samples were taken (Table 6, Fig. 1). The highest mean and median biomass values were within the NH between 40 and 50° N (North Atlantic; mean biomass of 68.8 mg C l^{-1} (SD = 213.4), median biomass of 2.5 mg C l^{-1}). The highest mean and median biomass values in the SH were between 70 and 80° S (10.5 (SD = 38.8) and 0.2 mg C l^{-1} , respectively, Table 3). Biomass values were lowest in the equatorial regions.

There was a difference in latitudinal trends between hemispheres (Fig. 5a), with highest biomass values in the NH being at mid-latitudes decreasing towards the equator and the poles while, in the SH, highest biomass values were seen at the poles, steadily decreasing through the mid-latitudes towards the equator. Biomass values at both poles were approximately similar.

3.3.2 Depth distribution

A broad range of biomass values has been observed at all depths down to 1000 m (Fig. 5b), although the funnel-shaped curve from the surface indicates a decrease in the range of biomass values with increasing depth. The highest values were recorded at the surface, with a mean biomass of 44.9 mg C l^{-1} (SD = 147.3) and median biomass

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of 2.5 mg Cl⁻¹. Biomass decreased from the surface to depth by around 2 orders of magnitude.

The global distribution of pteropod biomass at six different depth ranges revealed some interesting patterns (Fig. 4). There are clear geographic differences in the depth zones at which biomass peaked: in the North Atlantic, highest biomass values were recorded between 0 and 25 m, in the Pacific 50 to 100 m, in the Arctic 100 to 200 m, in the Brazilian regions (7–8° N/30–33° W) 200 to 500 m and in the Indo-Pacific region below 500 m. This indicates that tropical species concentrate at greater depths than temperate and high-latitude species. For instance, *Limacina helicina*, which is common at higher latitudes, is most commonly found in the surface layers while *Styliola* spp. and *Clio pyramidata* occur mainly at depth in tropical waters. These findings are consistent with Solis and von Westernhagen (1978), who reported that most records of *Clio pyramidata* were from greater depths. *Styliola* spp. are also regarded as deep-mesopelagic species (Wormuth, 1981; Almogi-Labin et al., 1998).

3.3.3 Seasonal distribution

Seasonal variation in biomass values were much more extreme in the SH compared to the NH, which probably reflects the larger contribution of samples from higher latitudes in the SH (Table 5). This is also apparent in the biomass contributions of both hemispheres to the global biomass across seasons. Taking into account the median biomass values, the NH contributes ten times to the global biomass in all seasons apart from the spring, where the ratio between NH and SH biomass is reduced to the factor of three. In the case when mean biomass is being examined, the NH:SH contribution to global biomass contribution is the highest (40:1) within the half year period between autumn and winter, but decreases to 6:1 during the spring and summer time (Table 7).

In both hemispheres, there was a spring-summer peak in biomass, which is likely to have originated from spring spawning episodes. In the NH, the first spring–summer

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peak is more pronounced in comparison with a subsequent autumn peak. However, it is the spring peak that is more evident in the SH, with another less marked peak in the summer (Table 7). The time and the extent of spawning is in the agreement with the results of previous studies (Bednaršek et al., 2011; Hunt et al., 2008) and indicates a life-style which depends on seasonal pulses of productivity.

Although there were peaks and troughs in the amount of biomass over the course of a year, a residual biomass level was always present (Fig. 6). This indicates that there is likely to be an overlap of generations (Bednaršek et al., 2011). In the higher latitudes, where there is likely to be just a single recruitment event per year, this means that the pteropods must have a life-cycle that extends into a second year. In the Southern Ocean, Bednaršek et al. (2011) proposed that some *Limacina helicina ant.* live for more than 2 yr and, although small in number, these individuals may be vital for future recruitment. Strong seasonality increases the vulnerability of early life-stages of pteropods that rely on pulses of production to thrive (Bernard et al., 2009; Seibel and Dierssen, 2003). Such an overlap of generations gives a greater stability to population recruitment processes.

4 Discussion and conclusions

The aim of this study was to collect and synthesize available existing abundance and biomass data in the first global pteropod biomass database. Studies mostly reported abundance data rather than biomass values. In so doing, it was necessary to estimate carbon biomass using length to weight conversion equation. This was also done in the cases of reported biomass values to retain consistency and facilitate further intercomparison between various studies. Uncertainties in the biomass estimates in this study will result from sampling errors, the variation in size classes between different pteropod species and their generations, the use of length to weight conversions and biases due to selective sampling, both seasonally and spatially. These uncertainties are discussed below, although it is only possible to give qualitative estimates of these potential errors.

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With regards to the sampling error, the use of different nets for different pteropod size classes generates some uncertainty, as the capture and filtering efficiencies differ between nets. Furthermore, one needs to consider sampling issues such as net-avoidance behaviour, extrusion of animals through mesh and clogging of the net (Harris et al., 2000). In addition, there is generally an insufficient use of smaller meshed nets to estimate population size. Wells (1973) proposed that there was a clear underestimation of the fraction of the pteropod population smaller than 100 μm . As they constitute by far the largest part of the natural population (Fabry, 1989), there is a clear underrepresentation of this cohort in the scientific literature and thus of their importance within the microzooplankton community (Dadon and Masello, 1999). When sampling with small vertical nets, which preferentially catch small or sluggish taxa, additional sampling biases arise as the nets can be avoided by larger plankton. On the other hand, nets with larger mesh size can miss the mesozooplankton size fractions including pteropods (Boysen-Ennen et al., 1991).

The uncertainty introduced due to the conversion of abundance to biomass can be considered at several different levels. Primarily, some studies within the database did not contain information on life stages. In these cases, the length of an adult animal for that particular species was used. This will probably result in an overestimation of the biomass, given that at least part of the sampled population could consist of smaller juvenile stages. Additionally, some studies did not provide a specific name of the pteropod group but only a broad group name description (e.g. pteropoda, pteropods, thecosomes, euthecosomes). Where a more detailed classification was missing, a sub-adult length was assumed for the biomass calculations. This subsequently resulted in either an underestimation (if the pteropods investigated in the study were adults) or an overestimation (if the studied animals were juveniles). Applying just a single length to weight conversion algorithm across all species, is likely to introduce error particularly when applied to shell shapes that differ from that of *Limacina helicina*, on which the algorithm was fitted (Bednaršek et al., 2011). Finally, as biomass is a product of abundance and weight, there will be a multiplication of the errors from these two separate terms.

Another uncertainty within the database is the bias introduced through sampling mainly in the austral summer in the SH. This means that our ability to describe biomass patterns in other seasons in the SH is limited. Furthermore, the SH is consistently undersampled compared to the NH, making comparisons difficult.

Nevertheless, this study has now enabled estimates of global pteropod biomass across a number of spatial and temporal scales. Furthermore, it has revealed some global patterns of pteropod biomass, only possible due to the wealth of data available in our datasets. We hope that the database will be a valuable tool for future modelling work, both of ecosystem processes, as pteropods constitute a key marine plankton functional group, and for the study of global biogeochemical cycles, since pteropods are a major contributor to organic and inorganic carbon fluxes. Finally, this database can also make a timely contribution to the assessment of the effects of ocean acidification, particularly in terms of the vulnerability of calcifying species, since it provides a benchmark against which model projections and future sampling efforts can be compared.

Appendix A

A1

A full data set containing all abundance/biomass data points can be downloaded from the data archive PANGAEA (<http://doi.pangaea.de/10.1594/PANGAEA.777387>). The data file contains longitude, latitude, sampling depth (m), date (Year, Month, Day in ISO format), taxon/species/body size, abundance (ind m^{-3}), biomass (C mg l^{-1}), and full data reference list ([doi/journal/database](http://doi.org/10.1002/journal/database)).

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A2 Gridded NetCDFbiomass product

The biomass data has been gridded onto a $360 \times 180^\circ$ grid, with a vertical resolution of 33 WOA depth levels. Data has been converted to NetCDF format for easy use in model evaluation exercises. The NetCDF file can be downloaded from PANGAEA, <http://doi.pangaea.de/10.1594/PANGAEA.777387>. It contains data on longitude, latitude, sampling depth (m), month, abundance (ind m^{-3}) and biomass (mg Cl^{-1}).

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Table 1. The list of data contributors in alphabetical order, with the two major online databases listed at the end of the list.

Entry No.	Principal Investigator	Database	Year (data collection)	Region
1	Andersen (1997)	PANGEA	1991–1992	NE tropical Atlantic
2	Bednaršek et al. (2011)	–	1996–2010	Southern Ocean (Scotia Sea)
3	Bernard and Froneman (2005)	–	2004	Southern Ocean (west-Indian sector of the Polar Frontal Zone)
4	Blachowiak-Samolyk et al. (2008)	–	2003	Arctic (N Svalbard waters)
5	Boysen-Ennen et al. (1991)	–	1983	Antarctica (Weddell Sea)
6	Broughton and Lough (2006)	–	1997	North Atlantic (Georges Bank)
7	Clarke and Roff (1990)	–	1986	Caribbean Sea (Lime Cay)
8	Daase and Eiane (2007)	–	2002–2004	Arctic (N Svalbard waters)
9	Dvoretzky and Dvoretzky (2009)	–	2006	E Barents Sea (Novaya Zemlya)
10	Elliot et al. (2009)	–	2006–2007	Antarctica (McMurdo Sound)
11	Flores et al. (2011)	–	2004–2008	Southern Ocean (Lazarev Sea)
12	Foster (1987)	–	1985	Antarctica (McMurdo Sound)
13	Froneman et al. (2009)	–	1998	Southern Ocean (Prince Edward Archipelago)
14	Hunt and Hosie (2006)	–	2001–2002	Southern Ocean (south of Australia)
15	Koppelman et al. (2004)	PANGEA	1999	Eastern Mediterranean Sea
16	Marrari et al. (2011)	–	2001/2002	W Antarctic (Marguerite Bay)
17	Mazzocchi (1997)	PANGEA	1991–2002	Eastern Mediterranean Sea
18	Mileikovsky (1970)	–	1966	North Atlantic, Subarctic and North Pacific Ocean
19	Moraitou-Apostolopoulou et al. (2008)	PANGEA	1994	Eastern Mediterranean Sea
20	Mousseau et al. (1998)	–	1991–1992	NW Atlantic (Scotian Shelf)
21	Nishikawa (2007)	–	2000–2002	Pacific Ocean (Sulu Sea, Celebes Sea, South China Sea)
22	Pakhomov and Perissinotto (1997)	–	1993	Southern Ocean (Subtropical Convergence)
23	Pane et al. (2004)	–	1995	Antarctica (Ross Sea)
24	Fernandez de Puelles et al. (2007)	–	1994–2003	Western Mediterranean
25	Ramfos et al. (2008)	PANGEA	2000	Eastern Mediterranean
26	Rogachev et al. (2008)	–	2004	W Pacific Ocean (Academy Bay, Sea of Okhotsk)
27	Schalh (1990)	–	1984–1999	Indo-Pacific waters (E Banda Sea, W Arafura Sea)
28	Schnack-Schiel and Cornils (2009)	PANGEA	2005	Pacific Ocean (Java Sea)
29	Siokou-Frangou et al. (2008)	PANGEA	1987–1997	Eastern Mediterranean
30	Solis and von Westernhagen (1978)	–	1972	Philippines (Hilutangan Channel)
31	Swadling et al. (2011)	–	2004–2008	E Antarctica (Dumont d'Urville Sea)
32	Volkov (2008)	–	1984–2006	Okhotsk Sea, Bering Sea, NWP
33	Ward et al. (2007)	–	2004–2005	Southern Ocean (S&W of Georgia)
34	Wells Jr. (1973)	–	1972	N Atlantic Ocean (Barbados)
35	Werner (2005)	–	2003	Arctic (W Barents Sea)
36	Wormuth (1985)	–	1975–1977	N Atlantic Ocean (NW Sargasso Sea)
37	Zervoudaki et al. (2008)	PANGEA	1997–2000	Eastern Mediterranean
38	NOAA (National Oceanic and Atmospheric Administration), (2011)	COPEPOD – The global plankton database	1953–2001	Global dataset
39	Ohman (2011)	ZooDB – Zooplankton database	1951–1999	Pacific Ocean (Southern and Central California)



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Table 2. Length and weight of different life stages corresponding to the category based on which the biomass conversions were determined based on Bednaršek et al. (2011).

Life stage	Length (mm)	Weight (mg)	Category
Juvenile (G2)	0–1.2	0.025	1
Sub-adult (G1)	1.2–4	0.06	2
Adult (G)	4–onwards	2	3

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Table 3. Mean, median, maximum and minimum with standard deviation (std) of pteropod biomass concentrations in mg C l^{-1} on a global scale and separately for the Southern and Northern Hemispheres.

summed biomass data	mean	median	max	min	std
all data	8.20	0.18	3213.80	0.00	61.37
non-zero data	9.15	0.25	3213.80	1.00×10^{-6}	64.76
for the NH non-zero data	10.37	0.30	3213.80	1.88×10^{-6}	69.69
for the SH non-zero data	1.73	0.02	281.40	1.00×10^{-6}	10.06

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Table 4. Latitudinal distribution of abundance data in ten degree latitudinal bands (90° to 90°), mean, maximum (max), median and standard deviation (stdev) of biomass per each latitudinal band are calculated from non-zero entries. All biomass concentrations are given in mg C l⁻¹.

Latitude	Entries	Mean (mg C l ⁻¹)	St dev	Max (mg C l ⁻¹)	Median (mg C l ⁻¹)
90 to 80° S	0	–	–	–	–
80 to 70° S	72	10.5	38.8	281.4	0.2
70 to 60° S	59	0.9	4.9	36	0
60 to 50° S	90	5.7	16.4	85	0.1
50 to 40° S	90	0.8	4.9	10.9	0.1
40 to 30° S	127	0.2	1.4	9.7	0
30 to 20° S	167	0	0.1	1.3	0
20 to 10° S	310	0.1	0.3	2.6	0
10° N to 0°	1007	1.8	6.9	87.1	0
0° to 10° N	1078	2.1	10.6	222.4	0.2
10° to 20° N	2044	1.8	15.4	364.5	0
20° to 30° N	1725	1.9	17.2	338.6	0.1
30° to 40° N	2958	16.6	74.9	753.2	0.2
40° to 50° N	756	68.8	213.4	3213.8	2.5
50° to 60° N	1958	2.8	17	400	0.6
60° to 70° N	896	0.7	4	64	0.3
70° to 80° N	85	14.8	33.3	127.7	0.5

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Table 5. Depth distribution of non-zero biomass values. mean, maximum (max), median and standard deviation (stdev) per depth range are calculated from non-zero entries. All biomass concentrations are given in mg C l^{-1} .

depth range (m)	entries	Mean (mg C L^{-1})	Max (mg C l^{-1})	Median (mg C l^{-1})	std
0–25	2266	44.9	3213.8	2.5	147.3
25–50	676	1.4	220.3	0.1	9.6
50–100	1245	2.1	400	0.3	16.1
100–200	3478	1.4	127.7	0.1	10
200–500	1894	1.1	330	0	9.6
500–1000	45	0.5	100.5	0	6

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Table 6. Monthly distribution of non-zero biomass values for the Northern (NH) and Southern (SH) Hemispheres. The entries contain all the biomass non-zero values and the representative percentage (%) of each month and for each month in the NH and SH.

months	entries	NH season	SH season	%	% NH non-zero data	% SH non zero data
January	1185	winter	summer	8.7	8.3	11.9
February	1457	winter	summer	10.7	9.3	20.4
March	998	spring	autumn	7.3	7.5	6.7
April	1298	spring	autumn	9.5	9.7	8.9
May	876	spring	autumn	6.4	6.9	3.7
June	802	summer	winter	5.9	6.3	4
July	1352	summer	winter	9.9	10.5	7
August	1790	summer	winter	13.1	13.2	13.6
September	1143	autumn	spring	8.4	8.3	9.1
October	1049	autumn	spring	7.7	8.4	3.6
November	859	autumn	spring	6.3	6.7	3.7
December	806	winter	summer	5.9	5.3	10.1

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Table 7. Values for the seasonal distribution of non-zero biomass values for the Northern (NH) and Southern (SH) Hemispheres with calculated mean, standard deviation (std), median, minimum (min) and maximum (max). All biomass concentrations are given in mg C l^{-1} .

	NH mean	NH std	NH median	NH min	NH max	SH mean	SH std	SH median	SH min	SH max
winter	10.5	62.5	0.2	3.8×10^{-5}	1362.5	0.3	1.4	0.02	1.7×10^{-4}	16.9
spring	19.2	111.9	0.2	3.0×10^{-5}	3213.8	3.0	7.2	0.05	3.0×10^{-4}	70.2
summer	12.8	69.7	0.3	1.9×10^{-6}	1606.9	2.8	15.5	0.03	1.4×10^{-4}	281.4
autumn	15.3	79.5	0.2	2.9×10^{-4}	1446.2	0.4	1.4	0.03	7.5×10^{-5}	10.5

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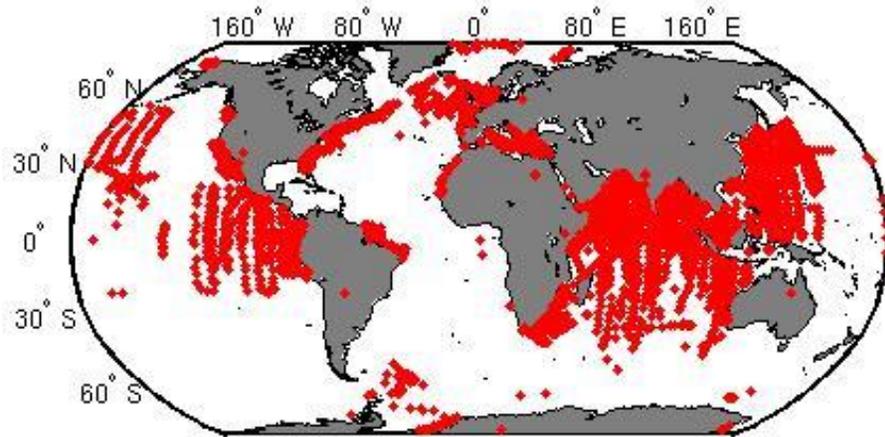


Fig. 1. Global distribution of quality controlled data where pteropod biomass counts were available. The stations are ubiquitous in all coastal basins.

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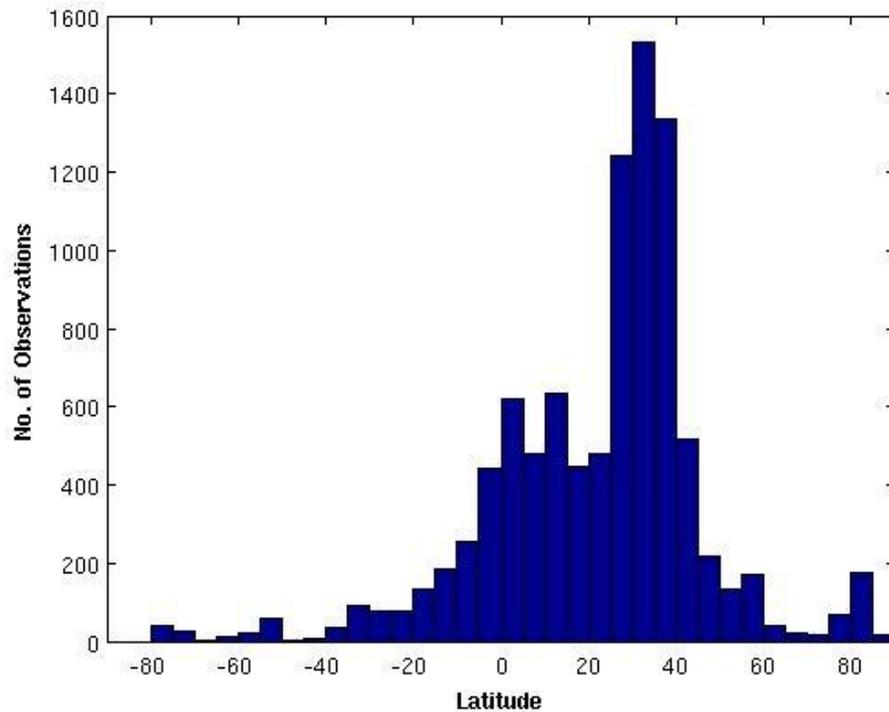


Fig. 2. Number of pteropod observations as a function of latitude for the period from 1951–2010. The majority of observations are located in the latitudinal band between 30–50° N.

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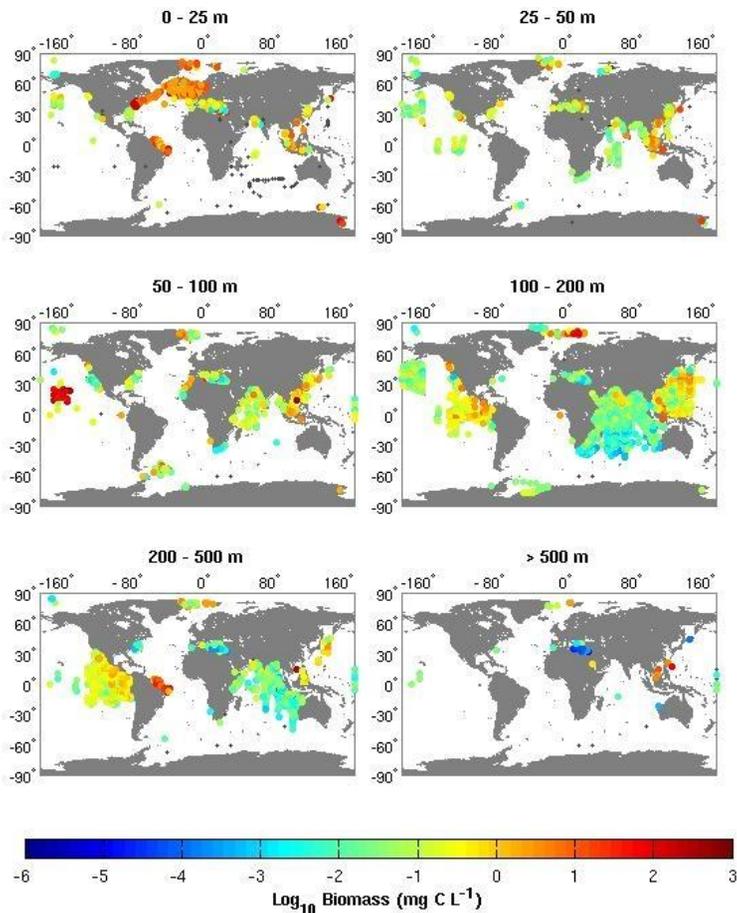


Fig. 4. Log-transformed/normalized pteropod carbon biomass (original units mg C L^{-1}) for six depth bands: **(a)** surface (0–25 m), **(b)** 25–50 m, **(c)** 50–100 m, **(d)** 100–200 m, **(e)** 200–500 m, **(f)** ≥ 500 m.

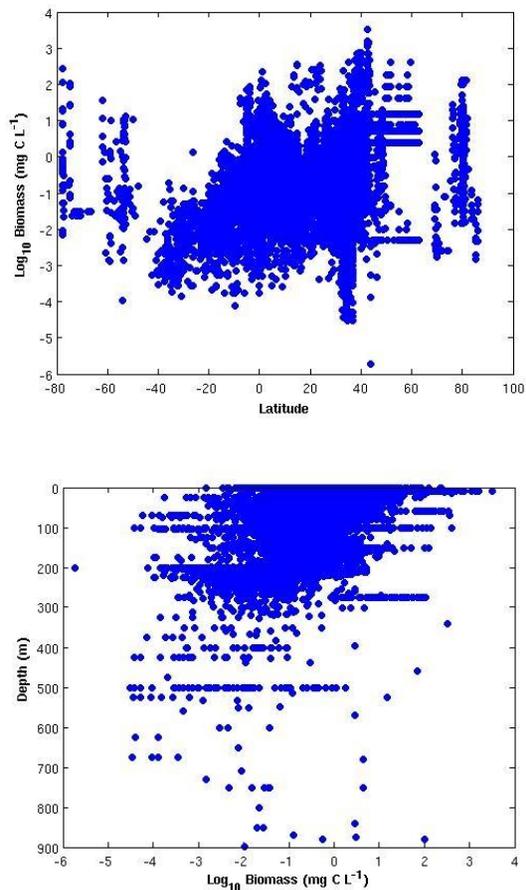


Fig. 5. Distribution of log-normalized biomass (mg C l^{-1}) of the individual pteropods **(a)** as a function of latitude and **(b)** as a function of depth.

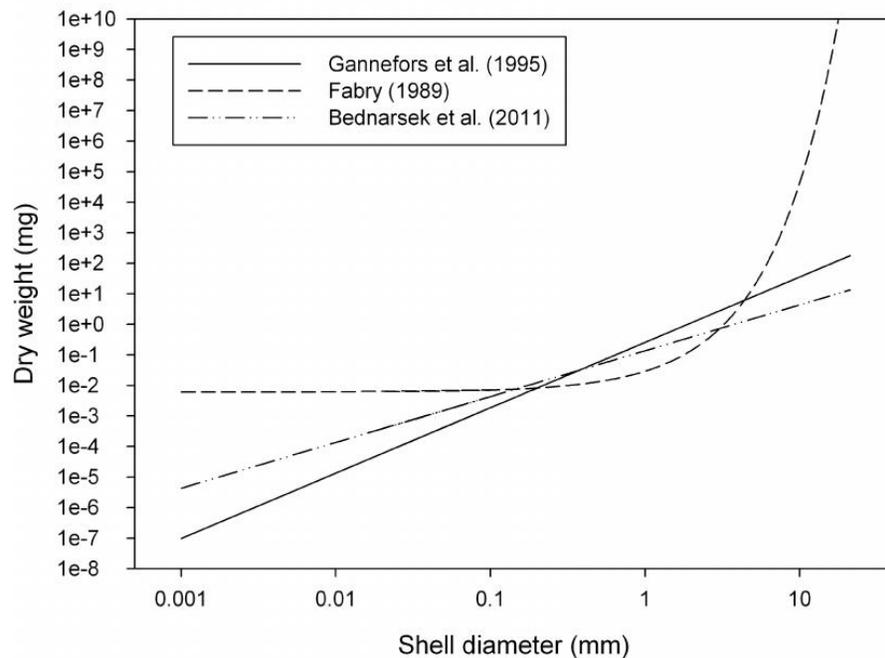


Fig. B1. Comparison of shell diameter to dry weights for three different studies based on which the conversion equation was determined.

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