



## The Biomass Composition of the Oceans

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## The biomass composition of the oceans - a blueprint of our blue planet

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Obtaining a quantitative global picture of life in the great expanses of the oceans is a challenging task. By integrating data from across the literature, we provide a comprehensive view of the distribution of marine biomass between taxonomic groups, modes of life, and habitats.

Main text:

The marine environment covers about 70% of Earth's surface and is responsible for around half of its total primary production (Falkowski and Raven, 2013). Over a century of intense research has been invested in characterizing the organisms inhabiting our oceans, culminating in influential syntheses such as the work by (Whittaker and Likens, 1973), which, while not encompassing all taxa, has had a profound scientific impact. New sampling techniques and global expeditions have improved our ability to make quantitative observations of marine organisms and have increased both our taxonomic and geographical coverage. Gaining a comprehensive, quantitative view of the current state of biomass in the oceans is becoming increasingly important as human activities and climate change inflict ever-mounting pressures on marine ecosystems and shift their unknown baseline biomass composition (Jackson, 1997).

Here we compile estimates for global marine biomass and use it to provide a holistic view (see Summary box) of the absolute and relative abundance of different marine taxa. Our results integrate data from several decades and represent, to a first approximation, the current state of ocean biomass. We relied on and augmented data from our recent synthesis of measurements of the global biomass of different groups of organisms (Bar-On et al., 2018). We filtered the data to include only marine organisms and used these measurements to estimate the total biomass of each kingdom (namely, bacteria, archaea, animals, protists, plants, and viruses). We excluded mangroves and salt marshes from our analysis as they are coastal and not continuously submerged in water. See [github.com/milo-lab/ocean\\_biomass](https://github.com/milo-lab/ocean_biomass) for detailed methods and source data.

As shown in Figure 1, the biomass in the oceans is dominated by three kingdoms: animals (mainly crustaceans and fish) and protists (containing mostly non-photosynthetic unicellular eukaryotes and a minority of photosynthetic eukaryotic microalgae), followed by bacteria (including heterotrophic bacteria and photosynthetic cyanobacteria). Plants (green algae and seagrasses), fungi and archaea each account for less than 10% of the global marine biomass. Although viruses dominate the ocean in terms of sheer number, they represent only  $\approx 1\%$  of the total biomass, as we elaborate on below. We further observe that in the marine environment, animals, protists and bacteria together account for  $\approx 80\%$  of total marine biomass, whereas in the terrestrial environment they represent a mere  $\approx 2\%$  of the total biomass (Bar-On et al., 2018).

What might cause such a stark contrast between the relative contribution of bacteria, protists and animals in the ocean and on land? One reason is the difference in biomass and identity of land and marine primary producers. Plants are the dominant primary producers in terrestrial ecosystems, accounting for  $\approx 95\%$  of the total terrestrial biomass (Bar-On et al., 2018). In the ocean, primary producers account for  $\approx 20\%$  of total biomass, distributed almost equally across several kingdoms. The immediate explanation for the disparity between the biomass of primary producers on land and in the ocean is the huge mass of supportive woody tissues in land plants. Considering only leaf mass would reduce the total plant biomass by  $\approx 30$ -fold (Bar-On and Milo, 2019). There are several plausible reasons that recalcitrant supportive tissues are common on land and not in oceans (Shurin et al., 2006). Here, we focus on those mechanisms that have a direct connection to basic physical constraints. One such mechanism is competition for light-energy. On land, being taller gives greater access to light and makes a plant a better competitor (Falster and Westoby, 2003). So accumulating biomass in supportive structures such as tree trunks might produce a selective advantage. In the ocean, it is not necessary to grow tall to reach the light. Rather, organisms can adjust their buoyancy to float to the light or, alternatively, build a small body so that they sink very slowly. Other physical constraints also select for smaller-sized primary producers in aquatic environments (Andersen et al., 2016). Most primary producers in the ocean acquire their supply of inorganic nutrients by diffusion. Smaller organisms benefit from a higher rate of diffusion per unit volume. On land, plants collect a sufficient amount of nutrients by increasing their surface-to-volume ratio, first by constructing a vast root network, and second through symbiotic relationships with fungi and nitrogen-fixing bacteria, which supply inorganic nutrients from the soil. This fundamental difference between primary producers on land and in the ocean also impacts the flow of energy and the distribution of biomass between producers and consumers.

Our analysis shows that marine biomass is composed of  $\approx 1$  Gt C of producers, roughly equally spread across bacteria, protists, and plants, and  $\approx 5$  Gt C of consumers, dominated by animals, protists and bacteria. This analysis is broadly consistent with earlier reports (Sheldon et al., 1972). This result might seem paradoxical at first glance. How can a small mass of producers sustain a larger biomass of consumers? The answer lies in the relative turnover rate of producer and consumer biomass. In the ocean, producer turnover occurs over fast timescales of days, whereas larger consumers like fish or crustaceans have much longer turnover times, on the order of months to years (Sheldon et al., 1972). The flux of energy, which is proportional to biomass and inversely proportional to turnover time, is still higher in producers than in consumers, as dictated by the conservation of energy. That is, even though producer biomass is small, it turns over much more rapidly, and thus producer productivity is higher than consumer productivity.

We proceed to analyze the dominant marine taxa within each kingdom. For the animal kingdom, the main groups are fish and crustaceans, far outweighing the biomass of bigger organisms

such as whales and squids. Crustaceans are dominated by small planktonic forms such as copepods, shrimp and krill. Fish biomass is mostly dominated by small (few-cm-long) mesopelagic fish, which hide at depths up to  $\approx 1000$  m during the day and migrate up the water column at night to feed on zooplankton, often eating the highly-abundant copepods (Battaglia et al., 2014).

Similar in abundance to animals is the protist kingdom. Protists are commonly defined as eukaryotes that are not animals, plants or fungi. Even though this definition is problematic, because this is not a monophyletic group, we use it here as is common in the literature. A significant portion (tentative rough estimate of about a quarter) of the global biomass of protists are photosynthetic, both microscopic algae (e.g. diatoms, coccolithophores and dinoflagellates) and macroscopic algae (e.g. kelp and other brown algae) (S11). The remaining protist clades, which are not obligately photosynthetic, often employ different types of mixed phototrophy and heterotrophy. For example, while Rhizaria, which contribute around 20% of the total biomass of protists, are heterotrophs, they are commonly associated with photosynthetic symbionts (Leles et al., 2017). Some protists can also utilize the chloroplasts of their prey as a source of organic carbon (Leles et al., 2017).

As stated above, the biomass of primary producers in the ocean is distributed across diverse groups of organisms. Marine primary producers can be divided into distinct categories based on different traits, including taxonomy, size, and habitats. Marine primary producers are often referred to as “algae”, even though this term is vague and includes a polyphyletic group of photoautotrophs. We can look at the biomass of marine primary producers and compare its distribution across different traits. From a taxonomic perspective, marine primary producers are composed of three main kingdoms: plants in the broad sense (archaeplastida, including green and red algae as well as flowering plants such as seagrasses), protists (including macroalgae such as kelp and other brown algae) and bacteria (such as cyanobacteria). We estimate that out of the total biomass of marine primary producers, protists and plants in the broad sense each account for  $\approx 40\%$ , with bacteria forming the remaining  $\approx 20\%$  (S11). In terms of size, marine primary producers include both unicellular (such as microalgae) and multicellular (such as macroalgae and seagrasses) organisms. We estimate that the biomass of marine primary producers is split roughly equally between unicellular and multicellular organisms (S11). In terms of habitat, most marine primary producers are either planktonic (phytoplankton) or benthic (living on the seafloor, such as seagrasses and most macroalgae). The vast majority of primary production in the ocean is carried out by planktonic organisms (Falkowski and Raven, 2013). In terms of total biomass, however, benthic primary producers account for a similar fraction as planktonic primary producers (S11).

Within the bacteria, we find two groups that are abundant and geographically widespread. The first is the SAR11 clade, composed of small heterotrophic bacteria with highly streamlined genomes of merely  $\approx 1$  million base-pairs, whose estimated biomass represents  $\approx 10\%$  of the total biomass of marine bacteria (White et al., 2019). The second group consists of *Prochlorococcus* and *Synechococcus*, two ubiquitous cyanobacteria genera. The combined biomass of *Prochlorococcus* and *Synechococcus* is estimated at  $\approx 15\%$  of marine bacterial biomass. An interesting feature of the SAR11 clade, among many other abundant marine bacterial clades such as the gammaproteobacteria clade SAR86, is the fact that they harbor proteorhodopsin. Proteorhodopsin is a light-driven proton pump whose activity might be sufficient to sustain the basal metabolism of SAR11 (Gómez-Consarnau et al., 2019), blurring the lines between trophic modes.

Marine viruses are numerous and play an important role in elemental cycling in the ocean through cell lysis and the consequent release of nutrients (Jover et al., 2014). While marine viruses outnumber bacteria and archaea by about an order of magnitude across diverse habitats (Wigington et al., 2016), in terms of biomass in the ocean, they constitute but a miniscule fraction. The characteristic diameter of marine viruses (dominated by phages) is  $\approx 50$  nm (S11), making the carbon content of a single marine virus about two and a half orders of magnitude smaller than that of a single bacterial or archaeal cell. Thus, even though they are more numerous, the global biomass of marine viruses is about one and a half orders of magnitude smaller than that of bacteria.

Our integrated dataset enables us to address basic questions such as: Is marine biomass mostly unicellular or multicellular, and where does it reside? Our analysis reveals that unicellular organisms, mostly protists and bacteria, contribute  $\approx 2/3$  of the total biomass of marine organisms (S11). In terms of habitat, we looked at the distribution of biomass between seafloor dwelling (benthic) organisms, plankton (carried by ocean currents), nekton (which can move independently of ocean currents), and particle-attached organisms (attached to micro- or macro-aggregates in the open ocean). At the risk of not giving enough emphasis to the large uncertainties that still exist and are detailed in the SI, our current integrated dataset suggests that the majority of marine biomass is planktonic, followed by similar contributions from nekton, particle-attached and benthic organisms ( $\approx 10\%$  each). Benthic biomass does not include contributions from seafloor hotspots such as seamounts and submarine canyons, the global biomass of which is still largely unknown (see S11 for further discussion). This overall depiction varies between kingdoms. For example, most plant biomass is benthic, not planktonic (S11).

Our statements about the distribution of biomass across kingdoms and between lifestyles should be taken with caution due to significant uncertainties, as shown in Figure 1B, but can also serve to focus future data collection efforts to better constrain the estimates. Specifically, our analysis should motivate deeper study of macroalgae, marine fungi, and the deep ocean and seafloor environments, since these estimates are especially uncertain.

Overall, the picture that arises from our compilation and analysis is consistent with general patterns observed in the marine macroecology literature. We believe that using an all-encompassing and consistent quantitative approach to estimate global biomass across marine taxa will advance us towards a much needed holistic view of the marine ecosystem. Monitoring the global biomass of marine biota will be key for gauging our society's impact on the oceans through overfishing, ocean acidification, microplastic, temperature rise and many other anthropogenic effects. As such, the integrative view described here could serve as a basis for future investigations that integrate new data to revisit the changing biomass composition of the ocean.

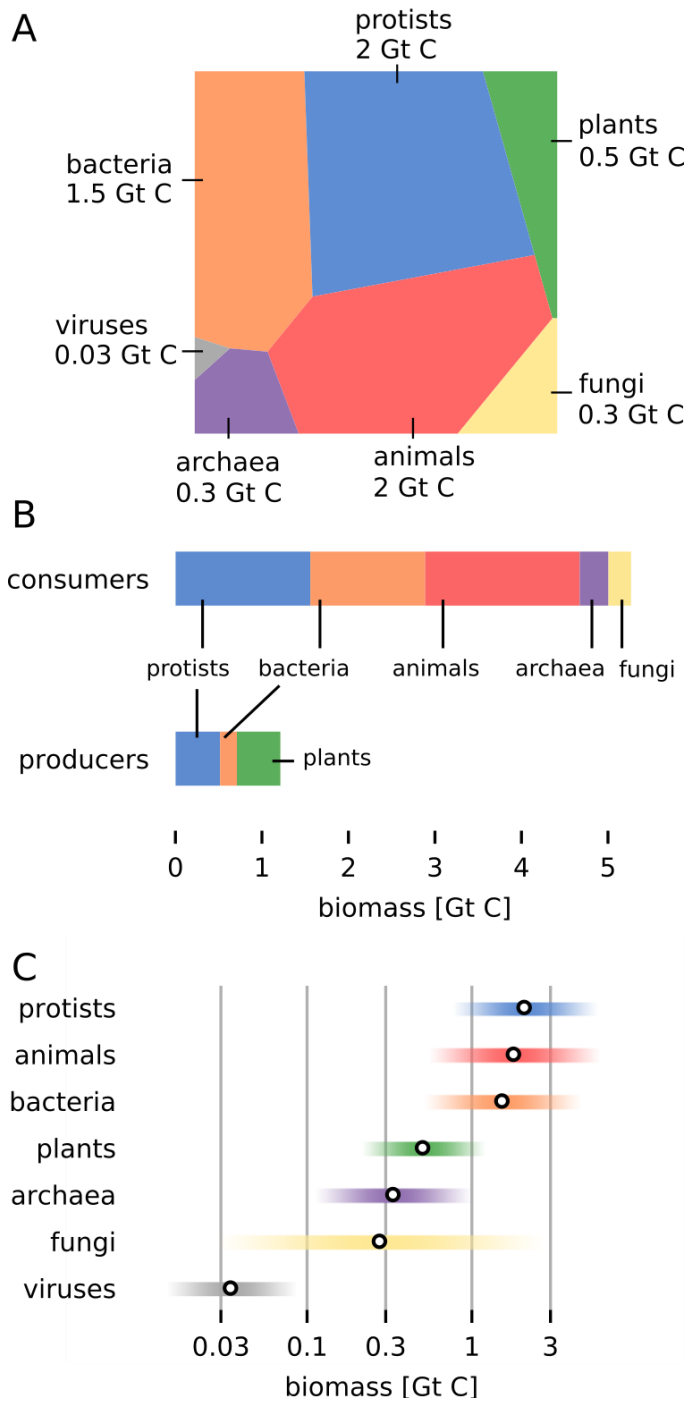


Figure 1. The composition of marine biomass. A. The absolute biomasses of different taxa are represented using a Voronoi treemap. Algae are counted as either protists or plants following their taxonomy. Values are based on the analysis detailed in the [SI1](#) with uncertainties as depicted in panel C as a color gradient around each estimate. The strength of the gradient at each point represents the probability that the total biomass of a specific kingdom has the specific value. The distribution is not well constrained by the data and was assumed to be log-normal, truncated at 2.5% and 97.5%. Our uncertainty projections may underestimate the true uncertainty due to factors such as systematic biases in sampling methods. B. Dissection of the global marine biomass by trophic mode and taxonomy. We consider these estimates as a rough global view, which should serve as motivation for more accurate and constrained values in the future.

### Summary box:

1. In contrast to their domination on land, plants (green algae and seagrasses) account for less than 10% of the total biomass in the ocean.
2. Viruses dominate the ocean in terms of number but constitute only  $\approx 1\%$  of the total biomass.
3. Animals, protists, and bacteria together account for  $\approx 80\%$  of the marine biomass, whereas in the terrestrial environment they comprise only  $\approx 2\%$ .
4. Marine animals are dominated by small mesopelagic fish and crustaceans, mostly copepods, shrimp and krill.
5. The oceans contain much more consumer biomass ( $\approx 5$  Gt C) than producer biomass ( $\approx 1$  Gt C).
6. Unicellular organisms contribute  $\approx 2/3$  of the total biomass of marine organisms.

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