



## Jellyfish biomass in the biological pump

# Expanding the oceanic carbon cycle

With atmospheric CO<sub>2</sub> concentrations increasing, it is vital to improve our understanding of the processes that sequester carbon, the most important being the biological pump of the world's oceans. Jellyfish might not spring to mind as major players in the global carbon cycle but the evidence of large jelly-falls on the world's deep seabeds suggests that gelatinous zooplankton have a greater role in the biological pump than we thought previously. Jellyfish blooms may be increasing and dead jellyfish may offer a rapidly accessible food source as they sink. We have developed a model to explore the remineralization of gelatinous carcasses as they sink, which is allowing us to predict the effects of jelly-falls on carbon transfer around the world.

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### The oceans and the biological pump

The oceans cover the majority of the Earth's surface (~70%), playing a major role in regulating climate patterns, temperature and atmospheric gases. They harbour a large portion of the world's biodiversity. The average depth is roughly 4 km; however, the majority of the biological and chemical processes that we study take place in the top 1 km. The deep ocean remains largely unexplored, thus it represents for us the last frontier in terms of adventure and discovery. Over the last 40 years, we have studied in detail the biogeochemical processes occurring in these first 1000 m, and especially in the so-called euphotic zone (~200 m), where the waters are exposed to sunlight that can support photosynthesis. This photochemical process mediates primary production by forming organic material using dissolved carbon dioxide (CO<sub>2</sub>) as a substrate (Figure 1). The majority of life in the oceans directly or indirectly depends on primary production, which forms the base of trophic webs.

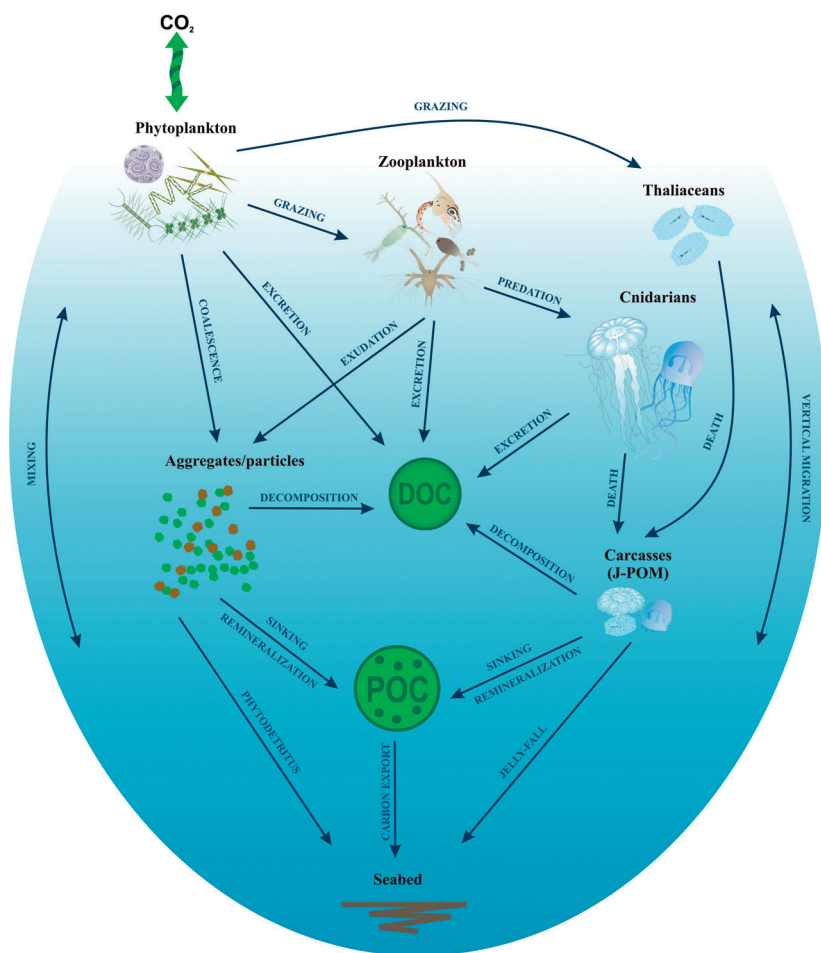
Particulate organic matter (POM) is traditionally linked to primary production as sinking particles, aggregates and biogenic remains produced in the euphotic zone (Figure 1), including phytodetritus (detrital material after the demise of phytoplankton blooms), marine snow (a mixture of dead organisms and particle remains), zooplankton mucous sheets

(shed continuously), zooplankton faecal pellets and the carcasses of organisms themselves (fish, whales, jellyfish). POM is extremely important in regulating chemical gradients in the water column during remineralization<sup>1</sup> and providing food to fuel benthic communities<sup>2</sup>. The 'biological pump' thus includes the continuous downward flux of autochthonous particles (those found at their site of formation, e.g. dead cells, as opposed to wind-blown dust, for example) from the euphotic zone to the ocean's interior. The associated biogeochemical changes taking place during sinking (e.g. decomposition/remineralization), eventually regulate CO<sub>2</sub> levels, providing a feedback to the atmosphere.

### Gelatinous biomass and its fate

Marine gelatinous organisms are commonly termed 'gelatinous zooplankton', avoiding taxonomic terminology, but highlighting convergent evolutionary traits such as planktonic life history, a transparent structure, and a fragile body mainly composed of water<sup>3</sup>. The term 'gelata' has also been coined to describe other planktonic gelatinous organisms beyond jellyfish (Cnidaria) and pelagic tunicates (Thaliacea), such as siphonophores, ctenophores, pelagic worms and molluscs. For the purpose of this article, we refer to 'gelatinous biomass' (J-POM, Figure 1) as dead and sink-

**Key words:** biological pump, carbon sequestration, euphotic zone, jelly-falls, zooplankton.



**Figure 1.** A representation of the biological pump and the biogeochemical processes that remove elements from the surface ocean by sinking biogenic particles. The diagram is adapted from a JGOFS U.S. cartoon to accommodate the J-POM and jelly-falls. Symbols are courtesy of the Integration and Application Network (<http://ian.umces.edu/symbols/>).

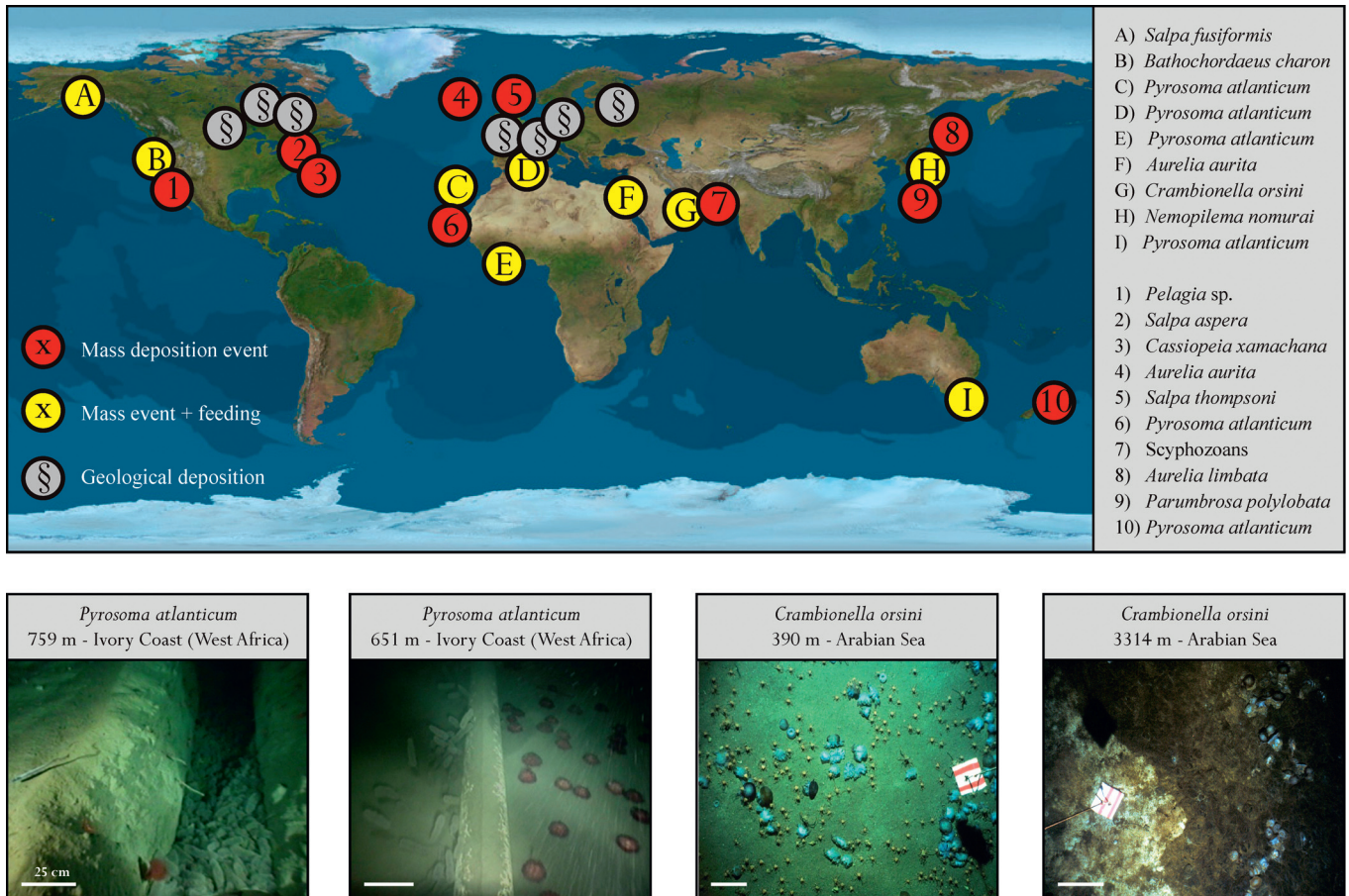
ing biomass (as carcasses/bodies) originating in Cnidaria, Thaliacea and Ctenophora. Blooms of these organisms occur periodically in the oceans, and can extend for thousands of square kilometres. The complex spatiotemporal distribution of the biomass, and the existence of large deep sea populations (beyond 1000 m), makes it difficult to understand the fate of the gelatinous biomass after blooms crash and die. The biomass cannot just vanish, and the most reasonable assumption is that it sinks, while remineralizing, and, in some cases, it sediments out at the seabed in so-called ‘jelly-falls’ (Figures 1 and 2).

### Jelly-falls: evidence and associated processes

Jelly-falls not only are a feature of the present ocean, but also have left behind evidence in rocks and sediments as fossil depositions (see <sup>4</sup> for a review) (Figure 2). Jelly-falls are known from the Cambrian (~500 million years ago) as circular impressions (Cnidaria-like) found in sedimentary layers and specimens accumulated in sedimentary horizons<sup>5</sup>. The majority of these depositions are attributed to very shallow oceans, thus they differ from our present concept of gelatinous biomass sinking in the open ocean. In the present era, since the late 1950s there are field

reports of jelly-falls occurring at the seabed (Figure 2). Jelly-falls of thaliaceans (pyrosomids and salps) have been found in New England (USA), New Zealand, Tasman Sea, Australia, Madeira, Mediterranean Sea and Gulf of Guinea. Other jelly-falls associated with scyphozoans (Cnidaria) have also been observed in the Japan Sea, Red Sea, Pakistan Margin, Chesapeake Bay (USA) and the Arabian Sea. The jelly-fall in the Gulf of Guinea (Ivory Coast) was studied in detail by Lebrato and Jones 2009<sup>6</sup> (Figure 2). Decomposing *Pyrosoma atlanticum* carcasses were observed from the continental shelf (<200 m) to the deep slope (>1000 m) using remotely operated vehicle (ROV) surveys in collaboration with the oil industry (SERPENT project; [www.serpentproject.com](http://www.serpentproject.com)). Carcasses were observed in large patches at the seabed, accumulating in channels and also being transported by the bottom current. Organic carbon contribution was estimated to be near one order of magnitude above sediment trap data in the area. Benthic animals were observed periodically feeding on the decomposing material, thus indicating that jelly-falls have an active role in benthic food webs. This means that, apart from bacterial decomposition<sup>7</sup>, large organisms (mega- and macro-fauna) also play an important role in regenerating gelatinous biomass. A jelly-fall in the Arabian Sea was also studied in detail<sup>8</sup> (Figure 2). Thousands of *Crambionella orsini* carcasses were surveyed with a towed camera and found to form large patches at the seabed on the continental shelf (~300 m), canyons and the continental rise (~3000 m). Organic carbon was estimated to be several orders of magnitude above sediment trap data. In many cases, the patches were so densely packed that they completely carpeted the seabed with a ‘fluffy’ material.

The baseline information we obtain from jelly-falls is a sudden large pulse of organic carbon (J-POM) reaching the seabed. Yet their origin in time and space is unclear. Current oceanographic techniques (sediment traps, remote sensing, acoustic backscatter) do not accurately assess the flux of J-POM. A jelly-fall can start at any point in the water column from the euphotic zone (0–200 m) to near the seabed (>1000 m) depending on the life history and the vertical migration patterns of the organisms involved. We call this starting point a ‘death depth’ or an exiting depth ( $E_z$ ), similar to other pelagic particles (small size) exiting the euphotic zone<sup>1</sup>. Gelatinous biomass sinks by density changes and as it sinks it starts decomposing (also being consumed by planktonic scavengers). Dissolved organic carbon (DOC) components leach and contribute to the total carbon pool (the so-called jelly-pump<sup>9</sup>), thus fuelling the pelagic microbial loop (Figure 1). A combination of material lability (the ease



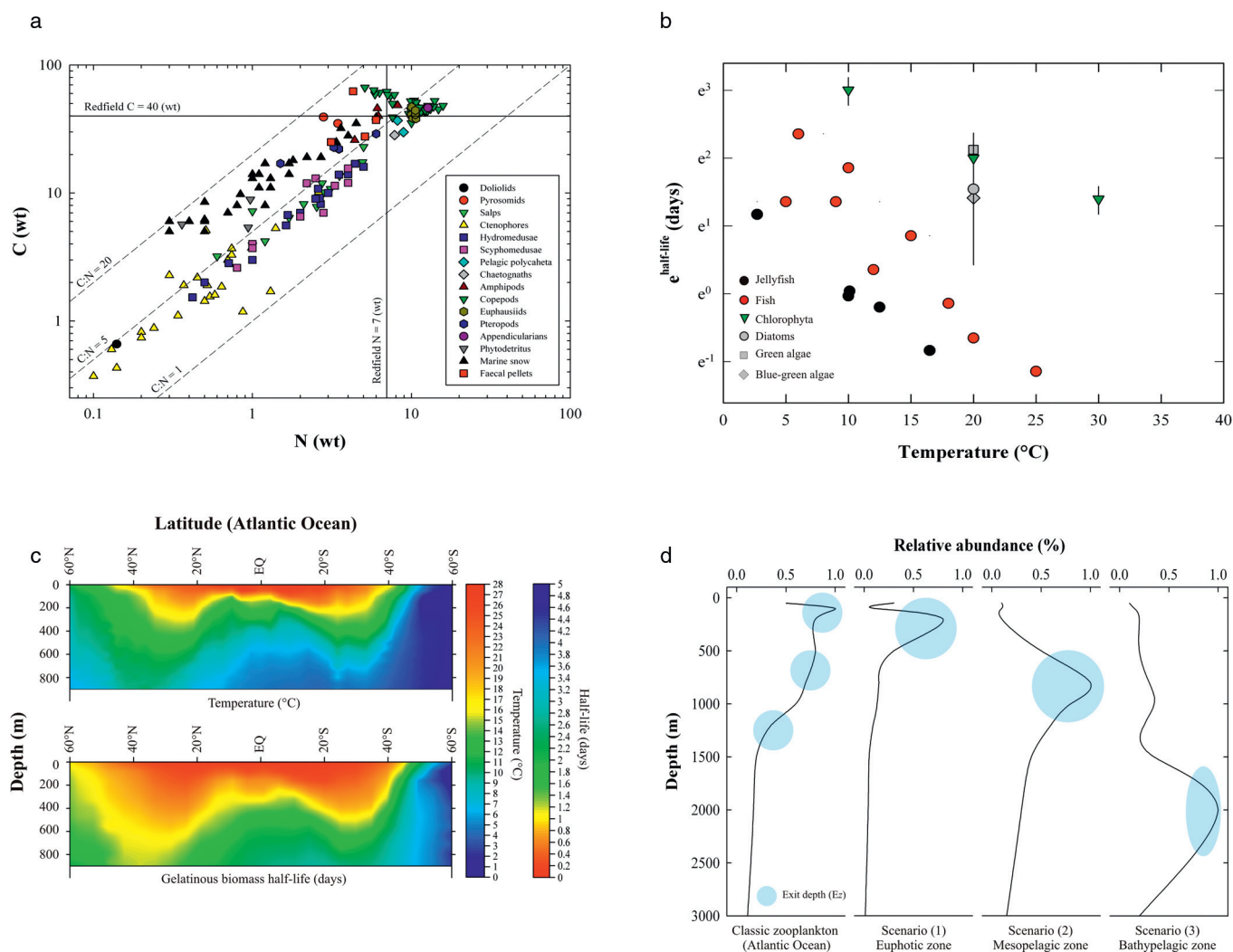
**Figure 2.** Map of the global distribution of jelly-falls at the seabed monitored to date. Colours differentiate between a jelly-fall with megafaunal scavenging activity (and none), and geological depositions. Images show jelly-falls in the Gulf of Guinea<sup>6</sup> and in the Arabian Sea<sup>7</sup>. Scale bar refers in all cases to 25 cm.

of assimilation, e.g. stoichiometric ratios), sinking rate,  $E_z$  and remineralization rates determinate the extent of recycling in the water column compared with at the seabed. At the seafloor, J-POM is a source of labile food for benthic communities (as with phytodetritus). J-POM is widely known to be an important component in the diet of scavengers (Figure 2), and at certain times of the year when gelatinous biomass is available, it could be the dominant resource.

### Gelatinous biomass stoichiometry and half-life

Jelly-falls constitute a biomass flux from the water to the sediment that can alter elemental cycling. The nutrient regeneration depends on the stoichiometry (the quantitative [mass] relationships among elements in compounds, e.g. carbon/nitrogen ratio, C/N) of the organisms involved. In phytoplankton, biomass stoichiometry is more variable than in zooplankton, being mainly driven by taxonomic composition, growth rate and nutrient limitation. Zooplankton maintain a more constant stoichiometry over time, although in many gelatinous species, the C/N and overall carbohydrate content oscillate during the year. The variability reflects changes in the food community (phytoplankton) available, as well as a succession of primary and secondary producers associated with the food resource. The C/N of sinking POM tends to show an initial increase in the ratio over time owing to a preferential remineralization of nitrogen with respect to carbon (Fig-

ure 3a). The same happens with J-POM, where remineralization (in laboratory experiments) is initially rapid as the more labile nitrogen-rich compounds (e.g. amino acids), are hydrolysed faster than the carbon-rich compounds (e.g. polysaccharides). This preferential hydrolysis of nitrogen compounds has been empirically determined for scyphomedusae<sup>10</sup>. The large C/N increase is observed in material that has undergone degradation for long periods (phytodetritus, marine snow and faecal pellets) (Figure 3a). The C/N of gelatinous biomass remains below the traditional Redfield stoichiometry (the usually constant molecular ratio of carbon, nitrogen and phosphorus in plankton; the term is named after the American oceanographer Alfred C. Redfield) of 40:7 (by weight; as in zooplankton and bacteria), with the exception of pyrosomids, some salps and scyphomedusae. The C/N is extremely dependent on the taxonomic group/type of material (Figure 3a). The gelatinous biomass C/N is relatively low owing to a high nitrogen and low carbon content in the majority of the



**Figure 3.** Gelatinous biomass stoichiometry, half-life, and exit depth ( $E_z$ ) considerations. (a) The relationship between carbon and nitrogen (by weight) on gelatinous biomass (thaliaceans [doliolids, pyrosomids, and salps], ctenophores, hydromedusae and scyphomedusae), on zooplankton (pelagic polychaetes, chaetognaths, amphipods, copepods, euphausiids, pteropods and appendicularians), and on sinking biogenic material found in the ocean (phytodetritus, marine snow and faecal pellets). The Redfield ratio by weight is also included ( $C/N=40:7=5.71$ ). Data were compiled from the literature. (b) The relationship between half-life in days (expressed in e) and temperature for gelatinous biomass (jellyfish), fish and phytoplankton (chlorophytes, diatoms, green algae, and blue-green algae). Data were compiled from the literature as the original decay rates ( $k$ ) empirically determined, and then transformed to half-life ( $t_{1/2} = -\ln(0.5)/k$ ). (c) Vertical profiles of gelatinous biomass half-life in the Atlantic Ocean from 60°S to 60°N calculated from the  $t_{1/2}$ -temperature relationship in (b). The temperature fields used as input data were obtained from the World Ocean Circulation Experiment (WOCE) dataset, accessed at the CLIVAR & Carbon Hydrographic Data office (CCHDO). (d) An abstract representation of relative abundance (%) of gelatinous biomass in the water column to exemplify the different scenarios considered when using an exit depth ( $E_z$ ).

groups ( $C/N$  almost 20% lower than in other zooplankton groups, and overall it is between 10 and 20% lower than for phytoplankton and phytodetritus/marine snow/faecal pellets).

A low  $C/N$  implies a higher organic matter lability<sup>11</sup>, as remineralization occurs faster when nitrogen-rich compounds are present. Thus nutrient regeneration should proceed faster in gelatinous biomass in comparison with other POM. We can explore this stoichiometric prediction by empirically evaluating the half-life of dif-

ferent dead organisms (Figure 3b). The half-life ( $t_{1/2}$ ) of biogenic material is the time required for biomass to fall to half of its original value, and it is normally expressed as a function of a decay constant ( $k$ ). Decay rate data are empirically determined from exponential decay series, where a 'quantity' decreases at a constant rate over time. We model this by using the differential equation  $dM/dt = -kM$ , where  $M$  is the original mass (quantity), and  $k$  is the decay rate (constant). The solution is  $M_t = M_0 e^{-k\Delta t}$ , where  $M_t$  is the mass after a period of time  $t$ ,  $M_0$  is the mass at  $t=0$ , and  $\Delta t = t_1 - t_0$ . We use the  $k$  exponent from decay series belonging to different dead organisms at different temperatures to estimate the half-life,  $t_{1/2} = -\ln(0.5)/k$ .

When we compare  $t_{1/2}$  data from gelatinous zooplankton, fish and phytoplank-

ton, we find an exponential decrease with increasing temperature in the three groups (Figure 3b). Jellyfish decay faster than the rest at any temperature, and above 15°C,  $t_{1/2}$  approaches half a day. Fish decay slower than jellyfish, and only above 20°C,  $t_{1/2}$  approaches 1 day. Phytoplankton decay much slower than the other groups, and even at 30°C,  $t_{1/2}$  remains above 4 days. The low  $t_{1/2}$  of jellyfish indicates that gelatinous biomass turnover proceeds faster than for other POM (Figure 3b). It also means that with higher temperatures (e.g. tropical latitudes), regeneration will be faster than in colder waters towards the poles (Figure 3c). When we model jellyfish  $t_{1/2}$  in the water column (e.g. Atlantic Ocean from 60°S to 60°N) using natural temperature gradients (Figure 3c), we find low  $t_{1/2}$  values in the tropics below 1 day in the euphotic zone (< 200 m), whereas  $t_{1/2}$  gets larger with depth (between 1 and 2.5 days from 200 to 1000 m). In temperate latitudes,  $t_{1/2}$  is similar to the tropics in the euphotic zone (1–3 days), but can go above 3 days in the transit to 1000 m. In sub-polar latitudes,  $t_{1/2}$  is more constant in the water column, changing from 1.6 to 3 days (northern hemisphere), and from 2.8 to 5 days (southern hemisphere) from 0 to 1000 m (Figure 3c).

A problem we encounter when assessing jellyfish  $t_{1/2}$  is that we ignore at which point in the water column the biomass starts sinking (exit depth,  $E_z$ ). The temperature-dependence of J-POM  $t_{1/2}$  is much higher than for other organisms (Figure 3b), therefore gelatinous material temperature sensitivity and the  $E_z$  must play an important role in the formation of seabed jelly-falls compared with regeneration in the water column. Classic zooplankton profiles in the open ocean<sup>12</sup> show peak abundances in the first 1000–1500 m (Figure 3d), thus, in reality, we can consider a ‘continuum’ of  $E_z$  from many different depths. Yet, to understand jelly-falls, we need to classify where individual species are more abundant to estimate the most likely  $E_z$ . The next problem appears with vertical migration, which changes the depth of peak biomass during day and night. In brief,  $E_z$  seems to be extremely complex in time and space, and in modelling studies, we need to provide a range to target the separation of biological niches from different species. Thus we tend to consider three general scenarios of  $E_z$  for gelatinous biomass: (i) a euphotic zone living mode with a shallow  $E_z$  between 0 and 200 m, (ii) a mesopelagic living mode with a  $E_z$  between 500 and 1200 m, and (iii) a special case for organisms living in the bathypelagic zone with a  $E_z$  below 1500 m and/or near the seabed. The most likely material to form jelly-falls at the seabed must originate from cases (ii) and (iii), whereas material originating in (i) will probably be regenerated in the water column. An  $E_z$  below the thermocline guarantees a large  $t_{1/2}$ , allowing time for the material to sink and settle at the seabed.

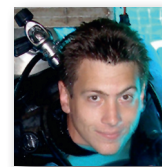
## Conclusions and research directions

Jelly-falls occur after populations of gelatinous zooplankton crash and die. These post-bloom processes are poorly explored in oceanography. We do not even have good understanding of what triggers death. Much research has focused on life cycle and the biology surrounding the start of blooms, and now is the time to move on to

assess processes at the end of the bloom and explore the fate of the biomass. Quantification of the regional and global gelatinous biomass [e.g. Jellyfish Database Initiative, JEDI ([www.jellywatch.org/blooms](http://www.jellywatch.org/blooms))] is a key step towards integrating these elemental fluxes into models and thus broadening the understanding of the biological pump. It would seem likely that we are missing an important vector for carbon to be transferred quickly from the atmosphere into deep waters. This is particularly important in the context of environmental change. In the coming decades, synergistic effects of CO<sub>2</sub> and temperature may trigger marine ecosystem shifts: even if jellyfish do not have the predicted population increases in the future ocean, gelatinous organisms will certainly play a preponderant role in channelling of carbon away from the atmosphere to the deep sea. ■



Mario Lebrato is completing a PhD at the Leibniz Institute of Marine Science (IFM-GEOMAR) in Germany, under the ‘European Project on Ocean Acidification’ (EPOCA, grant agreement number 211384) and also funded by the Kiel Cluster of Excellence ‘The Future Ocean’ (D1067/87). His research focuses on biogeochemical modelling, carbonate geochemistry and ecosystem processes in the carbon cycle. Previously, he was doing a masters at the National Oceanography Center (Southampton, UK), working on gelatinous zooplankton carbon export and ocean acidification. He also does consulting work at Atmocean, Inc. (USA) on alternative energies, geo-engineering and oceanography. email: [mlebrato@ifm-geomar.de](mailto:mlebrato@ifm-geomar.de)



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