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Pathways of Organic Carbon Downward Transport by the Oceanic Biological Carbon Pump

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The oceanic biological carbon pump (BCP) regulates the Earth carbon cycle by transporting part of the photosynthetically fixed CO_2 into the deep ocean. Suppressing this mechanism would result in an important increase of atmospheric CO_2 level. The BCP occurs mainly in the form of (1) organic carbon (OC) particles sinking out the surface ocean, of (2) neutrally buoyant OC (dissolved or particulate) entrained by downward water masses movements and/or mixing, and of (3) active transport of OC by migrating animals such as zooplankton and fishes. These various pools of OC differ in size since their sinking, production and decomposition rates vary spatially and temporally. Moreover, the OC transported to depths via these various export pathways as well as their decomposition pathways all have different ecological origins and therefore may response differently to climate changes. Currently, most ocean biogeochemical models do not resolve these various of OC pathways explicitly; rather, they imply that OC is therein created and destroyed equally. In addition, the organic composition of these various pools is largely unknown, especially at depths below 500 m. Here, known processes of OC export from the surface ocean to the mesopelagic zone (100–1000 m) are briefly reviewed. Three OC export pathways and some of their sub-categories are considered. I refer to published studies of OC fluxes associated with the specific downward export pathways and identify gaps that need to be addressed to better understand the OC fluxes associated with the BCP.

Keywords: plankton, biogeochemical processes, carbon cycle, ecological process, biological carbon pump

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INTRODUCTION

The oceanic biological carbon pump (BCP) is a complex mechanism regulating the Earth carbon (C) cycle by sequestrating part of the photosynthetically fixed CO_2 into the deep ocean and the seafloor. Suppressing this mechanism would increase the current levels of atmospheric CO_2 level by about 50% (Sarmiento et al., 2004; Parekh et al., 2006). Currently, the variability in the proportion of surface primary production (PP) leaving the euphotic zone and the amount of organic carbon (OC) exported to a certain depth via the BCP are challenging to explain. This prevents robust predictions of how C cycle, and hence climate, will change in the future.

Three major forms of the BCP are distinguished: (i) gravitational, (ii) mixing and (iii) migration. The gravitational pump (i) involves downward sinking of the OC contained in various particles

(POC) of planktonic origin from the surface ocean to depth due to their large size and/or high density (Siegel et al., 2016). This sinking POC is termed "marine snow" and can be made of single phytoplankton cells (DiTullio et al., 2000; Rembauville et al., 2016; Leblanc et al., 2018), various types of aggregates resulting from coagulation processes (Alldredge and Jackson, 1995; Riley et al., 2012; Laurenceau-Cornec et al., 2015) and zooplankton fecal pellets (FP) (Turner, 2002; Cavan et al., 2015). The mixing pump (ii) occurs when neutrally buoyant OC is transported to depth by downward-moving water masses and/or mixing. This OC is either dissolved (DOC) or entrained in particles which are too small in size or positively buoyant relative to seawater to sink on their own (Hansell et al., 2009; Le Moigne et al., 2016). The physical mechanisms that transport the OC downward can be either diapycnal with DOC diffusing out of the surface waters, or isopycnal, when water mass movements eddies and/or mixed layer bring DOC and/or suspended particles to depth (Hansell et al., 2009; Omand et al., 2015; Dall'Olmo et al., 2016). (iii) Diurnal vertical migration (DVM) of zooplankton and fish is a common feature in oceanic ecosystems (Longhurst, 1991; Steinberg, 2000; Landry and Calbet, 2004). In order to avoid predation, swimmers feed at night in surface waters and defecate deeper in the mesopelagic during the day. Doing so, they actively transport OC into the ocean's interior.

The presence, absence, and dominance of each of these different export pathways are controlled by biological (Piontek et al., 2014; Agusti et al., 2015; Le Moigne et al., 2016), chemical (Edwards et al., 2015), ecological (Cavan et al., 2015; Guidi et al., 2016), and physical (Levy et al., 2013; Taucher et al., 2014; Dall'Olmo et al., 2016) processes. They all vary in time and space and at depth. Most of these processes, however, are still poorly understood which hinders mechanistic predictions of the magnitude of the downward OC fluxes. At the base of the euphotic zone, the sinking of particles (termed gravitational flux) dominate the amount of OC (Giering et al., 2014). However, in the end of winter, the OC flux is induced by the so-called mixed layer pump which is driven by the seasonal entrainment of surface waters in deeper layers (Gardner et al., 1995) and can supply a substantial amount of OC to the deep ocean. Also, while globally the proportion of OC transported by migrating zooplankton and larger organisms relative to total OC flux is <20%, this active flux can occasionally dominate the total OC flux [(Aumont et al., 2018) and references therein].

These examples demonstrate the need for more systematic and simultaneous knowledge (ecological, biological, and geochemical) of the various pathways of OC export and at a given location and time. As such, the various individual export pathways (Siegel et al., 2016) for POC sinking from the euphotic zone to the mesopelagic and below have to be quantified. This would, for example, improve our understanding of the imbalance between supply and metabolic demand of OC (Steinberg et al., 2008; Burd et al., 2010; Collins et al., 2015) and the discrepancy between observed and modeled O_2 concentration in the mesopelagic zone (Gutknecht and Perruche, 2016). Currently our knowledge of the processes occurring in of the mesopelagic zone is incomplete despite its importance for the air sea carbon balance (Kwon et al., 2009). In this mini-review, I list the OC fluxes associated to the specific downward export pathways published in literature. Missing knowledge in estimates of specific export pathways that need to be addressed to better understand the OC fluxes associated with the BCP are identified.

THE GRAVITATIONAL PUMP FLUX

As stated above, the gravitational flux of OC occurs in the form of various particles of planktonic origin sinking from the surface ocean due to their large size and/or high density. The gravitational pump includes particles that are single phytoplankton cells, various types of aggregates, and zooplankton dejections termed fecal pellets.

Fecal Pellets Flux

Specific OC flux associated with zooplankton fecal pellets is relatively easy to measure. Fecal pellets are compact and have distinctive shapes and thus can easily identified and picked out from samples collected using different types of sediment traps (Refaeli et al., 2008; Turner, 2015). However, some pellets can experience degradation in moored sediment traps cups and are not being counted as such (Wilson et al., 2008). This may result in underestimation of the flux of fecal pellets. The OC flux associated with fecal pellets in the global ocean from 0 to 3500 m depth (n = 374) are shown in **Figure 1** and also compiled in **Supplementary Table S2**. The fluxes classified by depth are presented in **Figures 1A–C**. Note that **Figure 1** only presents the values that were readily available in the literature. I consider that the factors used by the authors to convert fecal pellets count into OC are correct. Counts of fecal pellets observed in various sediment traps if they were not converted to OC fluxes are not reported.

Figure 1A shows the OC flux from 0 to 100 m depth. The OC flux varies from 0–218 mg C m^{-2} d^{-1} with the large OC fecal pellets fluxes recorded in high latitudes [e.g., Kerguelen Island in the Southern Ocean (Ebersbach and Trull, 2008; Laurenceau-Cornec et al., 2015)] and upwelling zones (Le Moigne et al., 2018). Yet, some studies also report absence of fecal pellets in high latitudes regions [e.g., (Cavan et al., 2015)]. Fecal pellets fluxes are significantly lower in mesotrophic and oligotrophic regions (Carroll et al., 1998; Shatova et al., 2012). In the upper mesopelagic zone (100–500 m; **Figure 1B**), the OC flux of fecal pellets ranges from 0 to 71 mg C m^{-2} d^{-1} and on regional scale broadly follows the pattern observed in the upper ocean. At depths below 500 m (**Figure 1C**), fecal pellet fluxes are generally low (0 to 1.5 mg C m^{-2} d^{-1}). No reports of the OC flux below 500 m exist for the high latitude ocean. Fecal pellets sink fast and resist degradation well even under high hydrostatic pressure (Turley and Mackie, 1994; Tamburini et al., 2006; Riou et al., 2017) and thus their flux is expected to be high below 500 m. Coprorhexy (fragmentation of pellets by copepods) and/or coprophagy (ingestion of fecal pellets by copepods) could, however, lower the abundance of fecal pellets and hence the associated OC flux in the lower mesopelagic (Iversen and Poulsen, 2007). Additionally, such a trend could

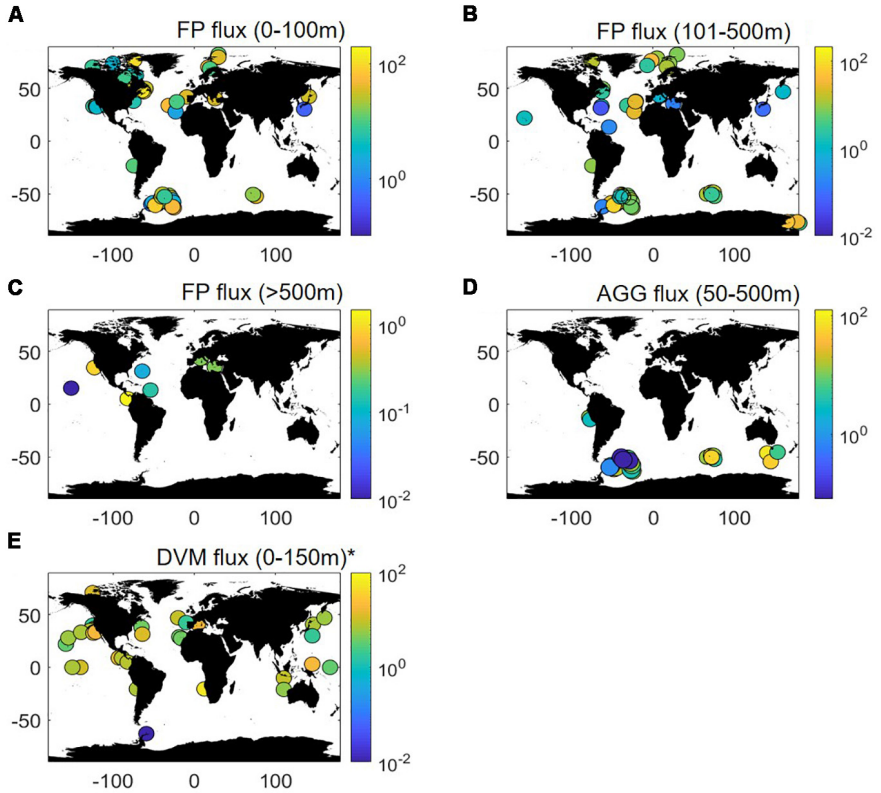

FIGURE 1 | Global distribution of downward flux of organic carbon (OC; units are mg of OC m^{-2} d^{-1}) associated to various export pathways (see main text). Panel **(A)** represents the flux associated to fecal pellets (FP) collected between 0–100 m; **(B)** 101–500 m and **(C)** below 500 m. Panel **(D)** represents the flux of aggregates collected between 50–500 m. Panel **(E)** represents the flux associated to vertically migrating organisms. *Replotted after Aumont et al. (2018). All references/sources are provided in the main text and in **Supplementary Tables S1–S3**.

also result from fish and large zooplankton species (such as siphonophores) feeding on the pellet flux (Proud et al., 2019).

Phytoplankton Cells Flux

Turbulent mixing and buoyancy regulation tend to retain single phytoplankton single cells tend in the surface ocean. However, despite of their small Reynolds number [describes the nature of the surrounding flow and its fall velocity (Stokes, 1851)], some intact cells (not grazed or aggregated) are found in sediment traps. This can happen to single live or dead phytoplankton cells, resting spores or cysts, and colonies.

Phytoplankton cells sink into the ocean's interior as single cells which are live, senescent and/or dead. DiTullio et al. (2000) observed single cells of *Phaeocystis antarctica* in the lower mesopelagic zone (500–600 m) in the Ross sea and concluded that they were exported rapidly and alive following a large *Phaeocystis antarctica* bloom. However, the mechanism delivering these cells down to the mesopelagic zone is unclear. Although physical processes could entrain surface cells to depth (see following sections), the cells observed at 500 m were still photosynthesizing, which suggests that their export to depth was likely too rapid to be induced by a physical process. Phytoplankton cells also sink dead. For example (Salter et al., 2007), observed dead cells of large diatoms *Eucampia antarctica* being selectively exported relative to the surface phytoplankton community in the Southern Ocean. These diatoms were exported rapidly owing to their heavily silicified, and thus dense, frustule (Salter et al., 2007). Phytoplankton resting spores and/or cysts are also exported from the surface ocean down to bathypelagic/abyssal depths (>1000 m). They are formed strategically by some phytoplankton in response to nutrient limitation and contain significant amounts of OC. In sediment traps located within an iron-fertilized bloom in the Southern Ocean near the Kerguelen Islands, Rembauville et al. (2016) measured OC fluxes associated with resting spores of diatoms *Chaetoceros Hyalochaete* or *Thalassiosira Antarctica*. The resting spores of a single species can account for up to 90% of the total gravitational OC flux (Rembauville et al., 2016). Acantharian cysts (unicellular organisms related to Radiolaria producing celestite, the densest biomineral in the ocean) were abundant in deep sediment trap material in the Iceland Basin (Martin et al., 2010) and the Southern Ocean (Belcher et al., 2018). High cyst flux was restricted to only 2 weeks but contributed up to half of the total gravitational OC flux during this period (Martin et al., 2010; Decelle et al., 2013). The Acantarian cysts are made of dense celestite which ensures their fast sedimentation to the bathypelagic depths. Phytoplankton cell colonies and chains are also observed in sediment traps samples. Laurenceau-Cornec

et al. (2015) found chains of the pennate diatoms *Fragilariopsis* sp. in the Southern Ocean, while Pabortsava et al. (2017) collected intact colonies of nitrogen-fixing *Trichodesmium* species in the deep traps (3000 m) collecting in the North Atlantic gyre.

However, all published sediment trap studies do not necessarily report the OC flux associated with phytoplankton cell export. This is because phytoplankton enumeration methods require a substantial amount of cells to be identified in order to provide robust estimates. This is not always possible, and counting is often performed only on a small area imaged under microscopes (Leblanc et al., 2018). Quantification of the cell size (or biovolume) to OC content for a given species is also not straightforward (Gosselain et al., 2000) and varies substantially depending on upper ocean nutrients regime (Davidson and Marchant, 1992). Grouping phytoplankton cell flux in an ecologically meaningful way might be especially advantageous for numerical models as providing the OC flux associated with sinking cells of individual phytoplankton species is computationally inefficient. Future effort may require grouping phytoplankton cell flux functionally based on size, nutrients affinity, and ecological/physiological traits. Therefore, no global maps of the OC flux associated to sinking phytoplankton cells are provided here.

Aggregate Flux

Evaluating OC flux associated with aggregates is challenging as their structure is often fragile and erratic (Alldredge, 1998). In moored sediment traps, marine aggregates lose their shapes. Unlike fecal pellets (see section above), aggregates in the bulk sediment trap material are clumped and thus difficult to pick out individually. The use of polyacrylamide gels as preservative in the sediment traps collection tubes/cups has, however, enabled significant improvements of estimating the aggregates flux (Lundsgaard, 1995; Waite et al., 2000). These highly viscous gels preserve the morphological characteristics of marine particles as they sink through the water column and into collection cups. Gels provide a slow deceleration of sinking particles and isolate particles allowing for quantitative image analysis (Ebersbach and Trull, 2008).

Only few studies quantified aggregate-associated OC flux to date. Most estimates are from the Southern Ocean (Ebersbach and Trull, 2008; Cavan et al., 2015; Laurenceau-Cornec et al., 2015) and upwellings (Le Moigne et al., 2018). Largest OC fluxes (110 mg m^{-2} d^{-1}) were recorded in the Sub-Antarctic zone south of Tasmania (Ebersbach et al., 2011). Large fluxes were also observed in the vicinity of the Kerguelen islands (Laurenceau-Cornec et al., 2015) and in the South Georgia bloom (Cavan et al., 2015) (**Supplementary Table S1**). Vertically, the flux of aggregates rarely shows a clear decrease with depth indicating significant changes in aggregates dynamics with depth. This highlights the importance of disaggregation and aggregation processes. Although overall disaggregation vastly dominates particles dynamics below the surface ocean (Stemmann et al., 2004; Lam and Marchal, 2015), aggregation by differential settling (Lam and Marchal, 2015) does occur in the mesopelagic zone. In addition, while the ratio of disaggregation to aggregation increases with depth, it tends to decrease with increasing PP (Lam and Marchal, 2015). This may partly explain why the vertical fluxes of aggregates presented here show limited decrease with depth.

Quantification of the aggregate-associated OC flux requires the knowledge of the relationship between aggregates biovolume to OC content, which is not straightforward (Alldredge and Crocker, 1995; Alldredge and Jackson, 1995). Laurenceau-Cornec et al. (2015) report particle-specific relationships compiled in the literature from which the OC content of aggregates can be estimated (Alldredge, 1998; Ebersbach and Trull, 2008). However, the database on the aggregates biovolume to OC content has to be significantly expanded to improve the statistical confidence of this relationship and also considering more diverse aggregates types. For example, tools like the Marine Snow Catcher (Riley et al., 2012; Cavan et al., 2015) could be used to collect particles and quantify their size, geochemical content and biological characteristics. The amount of particles collected per deployment can be small with the amount of OC entrained being too low to measure analytically (McDonnell et al., 2015). This device also likely misses the largest particles but pulling particles from multiple deployments or using devices of a larger volume (Cavan et al., 2017) could, however, resolve this issue.

THE MIXING FLUX

Several ocean physical processes transport slow-sinking, neutrally buoyant or dissolved OC (DOC) from the surface where they are produced to the mesopelagic zone. Recently, "mixing fluxes" gained more importance (see following references). This is mainly due the development of semi-automated platforms and devices which enabled high frequency sizing of particles (Picheral et al., 2010; Claustre et al., 2011). Large-scale ocean circulation is also one of the processes transporting particles produced in the surface to ocean's interior. For instance, regions of deep water formation are hotspots for such transport (Levy et al., 2013).

The mixed layer pump is another process that redistributes dissolved OC, neutrally buoyant or slow-sinking organic matter down the water column (Dall'Olmo et al., 2016). This process occurs during transient stratifications at the start of the productive season when suspended POC first accumulates in surface, and then redistributed throughout the water column by deep mixing. Globally, the mixed layer pump is responsible for a flux of 0.5 Gt C yr^{-1}. This process supplies POC mainly to locations with deep winter mixing such as the North Atlantic Ocean or the Southern Ocean (Dall'Olmo et al., 2016).

The water mass subduction induced by eddies also pumps POC into the mesopelagic zone. Omand et al. (2015) quantified the amount of suspended POC sinking following eddy driven subduction in the North Atlantic. In essence, suspended POC produced in surface sink along tilted isopycnals. Globally, eddy-driven subduction of POC is responsible for an export flux of ~1 Gt C yr^{-1} (Omand et al., 2015). Altogether, these processes may export up to 2 Gt of POC yr^{-1}, nearly a third of the gravitational flux (Boyd et al., 2019).

Large-scale circulation, mixing and eddies subduction also transport DOC beneath the surface ocean. Examining large

scale variability of DOC concentrations, Hansell et al. (2009) estimated that DOC export represents 20% that of gravitational POC export flux in the global ocean. However, the amount of DOC transported by processes such as eddy driven subduction and mixed layer pump (see references above) have poor spatial coverage both on local and global scales. Using an artificial neural network, Roshan and DeVries (2017) reconstructed global DOC concentrations distribution. Here, DOC production and export fluxes were estimated by coupling reconstructed DOC concentrations to a global ocean circulation model (DeVries and Primeau, 2011). Large annual DOC export rates were shown in the tropics (50–80 mg of OC m^{-2} d^{-1}) and low in high latitudes (0–40 mg of OC m^{-2} d^{-1}), contrary to findings by Dall'Olmo et al. (2016) and Omand et al. (2015). Their model, however, extrapolated DOC concentrations measured during summer to a global scale. This may have limited the effect of the aforementioned physical processes. More work is required to estimate the annual flux of DOC from the surface ocean.

The global maps of the OC flux associated to the various mixing fluxes are not shown here but are available in the literature cited above.

THE ACTIVE MIGRATION FLUX

The concept of active flux by migrating organisms (also known as "swimmers") in the mesopelagic is based on widespread observations of DVM of zooplankton and fish caught in nets (Longhurst, 1991; Steinberg, 2000; Landry and Calbet, 2004). In essence, to avoid predation swimmers feed at night in surface waters and defecate deeper in the mesopelagic during the day (Steinberg and Landry, 2017). Inverted DVM and desynchronized vertical migration do exist (Neill, 1990; Cohen and Forward, 2016), however, typical DVM as described above are more common in marine systems. This actively supplies OC to depth with minimizing decomposition. To date, estimates of DVM have mostly been focused on mesozooplankton because they are readily caught in multiple opening/closing towed nets (Tarling et al., 2002). DVM is a difficult process to model (Hansen and Visser, 2016), however, this field has made significant progresses recently (Aumont et al., 2018; Archibald et al., 2019; Gorgues et al., 2019).

The active transport of OC by migrating mesozooplankton can contribute up to 40% of the gravitational flux (Stukel et al., 2013) with global estimates ranging from 0.2 to 71 mg m^{-2} d^{-1} (Aumont et al., 2018; **Figure 1E** and **Supplementary Table S3**). Most studies of mesozooplankton associated OC flux were conducted in coastal and upwelling regions, while data from high latitudes and polar waters are scarce (**Figure 1E**). The largest flux is recorded in the Benguela upwelling system while the smallest are observed near the Antarctic peninsula. Large DVM fluxes in upwelling system is counterintuitive given that these waters are productive but often poorly oxygenated below surface. However, some migrating organisms can survive with little oxygen concentrations by adopting adaptive metabolic strategies (Bianchi et al., 2013, 2014; Kiko et al., 2015). Excluding the extreme values of 0.2 and 71 mg m^{-2} d^{-1}, the OC fluxes associated with migratory organisms appear to be relatively homogeneous and in the order of 9.8 ± 7.3 mg C m^{-2} d^{-1}.

The OC flux associated to DVM of both macrozooplankton and fishes are, however, more challenging to estimate. These organisms are not always quantitatively represented in net catchments (Sameoto et al., 2007). Acoustics techniques are promising for estimating these (Lebourges-Dhaussy and Josse, 2008; Lebourges-Dhaussy et al., 2014) and dedicated surveys performed on large scales are starting to emerge (Bianchi et al., 2013; Irigoien et al., 2014). Most of the available observations involve mesozooplankton and/or micronekton. The whole community is, however, represented only by a limited number of datapoints (Aumont et al., 2018). Moreover, these fluxes mostly represent the active flux between the surface and the upper mesopelagic zone. DVM OC fluxes between surface and the lower mesopelagic zone are more rarely estimated. This is despite the presence of migrating species deeper down in the mesopelagic zone (Sutton, 2013; D'Elia et al., 2016).

CONCLUSION AND PERSPECTIVES

In the last decade, numerous studies highlighted the importance and the complexity of the BCP. As our understanding of the BCP advances, new research directions into the functioning of the BCP also emerged building on knowledge about the chemical composition of the bulk export fluxes. For instance, the importance of the types, transport pathways, particles associated communities, and fates of sinking particles have become apparent thanks to technological breakthroughs, and thus need further research. Known processes of OC export from the surface ocean to the mesopelagic zone (100–1000 m) were reviewed. I provided a list of the published OC fluxes associated to the specific downward export pathways involving zooplankton fecal pellets, aggregates, and by vertical migrating organisms. However, while data on phytoplankton cell flux exist, estimates of the OC flux associated to sinking single cells are challenging. Moreover, processes responsible for the sinking of phytoplankton single cells are unclear. I report global estimates of the physically driven processes that supply slow sinking and/or neutrally buoyant and dissolved OC to the dark ocean. However, locally, their contribution relative to the total gravitational flux is often missing, especially in high latitude regions. In addition, most estimates of vertical migration concern only part of the community and organisms migrating deeper are overlooked.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00634/full#supplementary-material

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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