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The importance of jellyfish–microbe interactions for biogeochemical cycles in the ocean

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Abstract

Jellyfish blooms can represent a significant but largely overlooked source of organic matter (OM), in particular at the local and regional scale. We provide an overview of the current state of knowledge on the bloom-forming jellyfish as sink and source of OM for microorganisms. In particularly, we compare the composition, concentration, and release rates of the OM excreted by living jellyfish with the OM stored within jellyfish biomass, which becomes available to the ocean's interior only once jellyfish decay. We discuss how these two stoichiometrically different jelly-OM pools might influence the dynamics of microbial community and the surrounding ecosystem. We conceptualize routes of jelly-OM in the ocean, focusing on different envisioned fates of detrital jelly-OM. In this conceptual framework, we revise possible interactions between different jelly-OM pools and microbes and highlight major knowledge gaps to be addressed in the future.

Bloom-forming gelatinous zooplankton, including *jellyfish* (hereinafter cnidarian subphylum *Medusozoa* and phylum *Ctenophora*) and pelagic tunicates (*Thaliaceans*), can represent a major perturbation to the marine ecosystem with their *boom and bust* population dynamics. Understanding the response of marine ecosystems to this natural and/or anthropogenic perturbation is crucial, particularly, since the adaptive features of jellyfish will probably allow them to flourish under projected future changes of the oceanic habitats, that is, warming, acidification, oxygen loss, and the increasing human exploitation of the ocean's services, that is, overfishing, maritime transport, increase of marine-based infrastructures (Richardson et al. 2009; Purcell 2012; Steinberg and Landry 2017). Despite the debate on the accuracy and the cause of recently observed jellyfish fluctuations, most likely a consequence of the combined effect of natural oscillations of populations, multiple anthropogenic stressors and climate change, the increase in their population size can have important socioeconomic and serious ecological consequences (Richardson et al. 2009; Purcell 2012; Condon et al. 2012, 2013; Sanz-Martín et al. 2016).

In the aftermath, jellyfish blooms can represent a significant but largely overlooked source of organic matter (OM), in particular at the local and regional scale. In this context, jellyfish were recently recognized as important agents of carbon export to the ocean's interior, highlighting the necessity of including jellyfish into ocean biogeochemical models as an important component of the biological soft-tissue pump (Steinberg and Landry 2017; Lebrato et al. 2019). Ultimately, jellyfish (and carbon transformations conducted by jellyfish) could represent one of the missing puzzles in the riddle of the mismatch between surface-ocean supply exported to the ocean's interior via sinking POC and dissolved organic carbon (DOC) advection and the carbon demand by mesopelagic and bathypelagic zooplankton and heterotrophic microbes (Burd et al. 2010; Steinberg and Landry 2017).

To constrain and balance deep-ocean carbon budgets, the relationships and interactions between microbes, jellyfish and jellyfish-derived OM have yet to be fully characterized and need to be taken into account, as stressed by Steinberg and Landry (2017). This implies also a more comprehensive determination of the release rates and the biochemical composition of different jellyfish OM pools. The complex pool of dissolved organic matter (DOM) is almost exclusively accessible to marine microorganisms, the most abundant, diverse, and productive organisms in the food web. Diverse members of the microbial community employ different types of

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metabolisms to interact with the broad spectrum of compounds present in the oceanic DOM pool and thereby, affect the biogeochemical state of the ocean and thus the global climate (Azam and Malfatti 2007). Knowledge on the interactions between individual constituents of the DOM pool and the microbial consortia is still in its infancy and needs to be refined to obtain a mechanistic understanding on the relation between the OM field and the metabolic network operated by the microbial community (Kujawinski 2010; Arrieta et al. 2015; Moran et al. 2016). Only when we arrive at this mechanistic understanding, we will be able to predict the response of the marine ecosystem to natural and anthropogenic perturbations.

Thus, elucidating the interactions between jellyfish-derived OM (at the individual compound level) and microbes will allow us to more accurately incorporate jellyfish into global carbon budgets. This is required to understand the implications of jellyfish blooms for the biogeochemical state and functioning of marine ecosystems (Steinberg and Landry 2017). Yet, the link between jellyfish, jelly-OM, and microbes has been investigated by only few studies (Titelman et al. 2006; Condon et al. 2011; Dinasquet et al. 2013; Blanchet et al. 2015; Tinta et al. 2016, 2019, 2020).

Here, we provide an overview of the current state of knowledge on the composition, concentration, and release rates of different jelly-OM pools, ranging from OM captured and stored/encapsulated within the jellyfish biomass to the OM released by jellyfish throughout their life span. We conceptualize routes of jelly-OM in the ocean, focusing on different envisioned fates of detrital jelly-OM. In this conceptual framework, we revise possible interactions between different jelly-OM pools and microbes, highlighting knowledge gaps and future challenges to be addressed to better understand the implications of jellyfish blooms for biogeochemical cycles and ecosystem functioning.

Jellyfish as sink and source of OM

Jellyfish are ubiquitous and important players in various estuarine, coastal, and open-water ecosystems around the world and can cope with a large spectrum of environmental conditions (Richardson et al. 2009; Purcell 2012; Schnedler-Meyer et al. 2018; Goldstein and Steiner 2020). One of the key factors for their widespread distribution in diverse ecosystems and their abundance is their simple body plan with a high water (> 95%) and low carbon content (< 1% of we weight) resulting in a low maintenance metabolism (Acuña et al. 2011; Pitt et al. 2013). These features allow jellyfish to reach a considerably larger size than nongelatinous zooplankton of equivalent carbon content at the expense of a relatively short life span (from weeks up to ~ 1 yr depending on the species; Ceh et al. 2015 and reference therein). The inflated body size increases the probability for jellyfish to encounter prey. This results in higher clearance rates than in nongelatinous zooplankton if normalized to carbon biomass (Sørnes and Aksnes 2004; Kiørboe 2011; Acuña et al. 2011; Anderson et al. 2017). Jellyfish efficiently graze on phytoplankton and prey on micro- and meso-zooplankton, fish larvae and even other species of gelatinous zooplankton (Richardson et al., 2009 and references therein) (Fig. 1). In scyphozoans, respiration consumes up to 66% of the assimilated organic carbon, while production reaches 34%, with a net growth efficiency ranging from 35% to 37% (Fraser 1969; Olesen et al. 1994; Ikeda 2014; Lebrato et al. 2019). Recently, it was estimated that globally gelatinous zooplankton consume

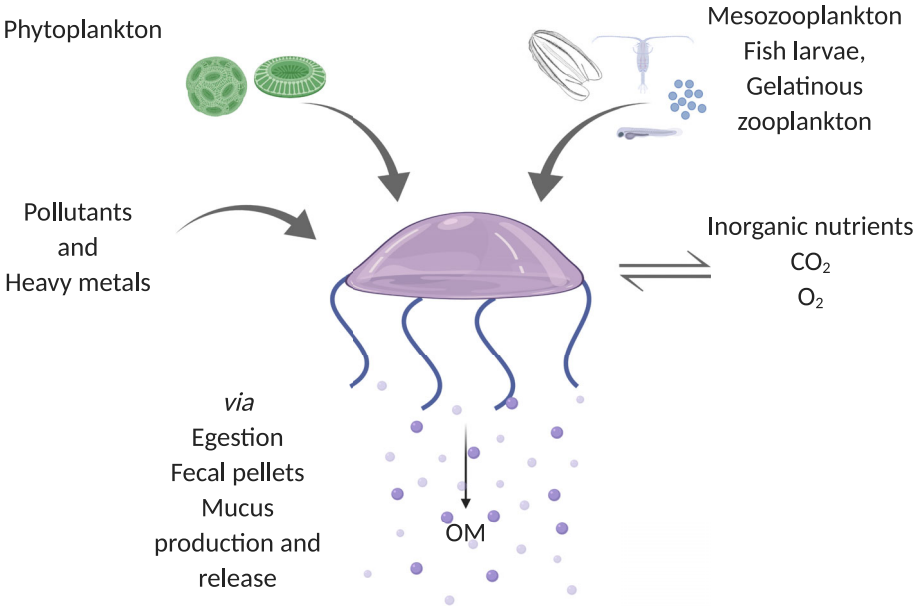

Fig. 1. Visualization of a living jellyfish as sink and source of organic matter (OM) in the ocean.

7.9–13 Pg C yr^{-1} of phytoplankton and zooplankton, resulting in a net gelatinous zooplankton production of 3.9–5.8 Pg C yr^{-1} in the epipelagic ocean (Luo et al. 2020). However, the authors of this study also recognized that they did not consider all the factors in their model (e.g., life history, Henschke et al. 2018) and that there are many unknowns with respect to gelatinous zooplankton predation that needs to be elucidate in the future (Luo et al. 2020). This estimate corresponds to 7.8–11.6% of the global marine primary production (about 50 Pg C yr^{-1}, Field et al. 1998).

Due to their low metabolic requirements compared to their high growth rates, complex life history, and large reproductive output, some jellyfish species (primarily *Scyphozoa*) are capable of generating large blooms within a short period of time if conditions are favorable (Condon et al. 2013; Pitt et al. 2013). The biomass of jellyfish blooms regularly exceeds 10 t of wet weight 100 m^{-3} covering areas of many square kilometers (Lilley et al. 2011; Condon et al. 2013). It was recently estimated that the global mean gelatinous zooplankton biomass standing stock represents ~ 510 Tg C in the epipelagic ocean (Luo et al. 2020), which is about 13 times higher than previous estimate of ~ 38 Tg C (Lucas et al. 2014), due to the modified methodology and updated data set supplemented with some additional time series data. The discrepancy between the two estimates is discussed in detail by Luo et al. (2020). This new estimate translates to ~ 8 mg C m^{-3} of global gelatinous zooplankton in the epipelagic ocean, with ~ 57% attributed to "true jellyfish" (phylum Cnidaria, class *Scyphozoa*, and ~ 40% to Ctenophora; Luo et al. 2020). This represents 14% of the global phytoplankton biomass (56 mg C m^{-3}, Boyce et al. 2010). However, jellyfish biomass also exhibits high variability both, in space and time (based on the calculated variance of the long-term mean by Condon et al. 2013), with highest spatial variability and highest biomass values in the coastal realm (> 10 g C m^{-3}) largely due to cnidarian jellyfish (Lucas et al. 2014; Luo et al. 2020).

Global jellyfish biomass estimates are based on the global gelatinous zooplankton database *JeDI* (Condon et al. 2013; Lucas et al. 2014). This database served as baseline for several publications that, together with citizen-science projects and platforms (e.g., https://www.jellywatch.org), substantially improved our knowledge on the global abundance and distribution of gelatinous zooplankton in the ocean (Lucas et al. 2014; Lebrato et al. 2019). However, due to the lack of monitoring campaigns, sampling difficulties (e.g., temporal and spatial patchiness of jellyfish populations, their transparency and fragility) and the lack of the standard sampling approaches, the monitoring of jellyfish populations is not consistent, nor is it trivial (Lebrato et al. 2012; Brodeur et al. 2016; Lebrato et al. 2019; Luo et al. 2020). Consequently, the *JeDI* database currently covers less than 50% of the global ocean, is biased toward certain regions and ocean depths, provides only limited insight into jellyfish diversity and is biased toward bloom-forming species. Also, it lacks important parameters, such as the biochemical composition of different jellyfish species (Lucas et al. 2014; Lebrato et al. 2019).

Yet, in order to accurately incorporate jellyfish biomass and jellyfish-derived OM into global biogeochemical models and budgets, the estimation of global jellyfish biomass needs to be better constrained. This could be achieved via implementing globally consistent monitoring programs and standardized sampling techniques, which would provide more accurate information on the temporal and spatial distribution of jellyfish abundance (Lebrato et al. 2012; Brodeur et al. 2016). New nondestructive approaches should be implemented for in situ monitoring of jellyfish populations, such as ROVs (e.g., Zooglider, an autonomous vehicle for optical and acoustic sensing of zooplankton (Ohman et al. 2019), or ROV-deployable laser-sheet imaging device DeepPIV recently developed and applied to provide high-resolution visualization of giant larvacean houses (Katija et al. 2020), camera systems to perform vertical profiling, acoustic and/or electronic tagging systems and physical models (Fossette et al. 2016; Vodopivec et al. 2017; Fannjiang et al. 2019), as reviewed in detail by Lebrato et al. (2012).

Taken together, jellyfish inhabit a wide range of ecosystems, encapsulate a substantial amount of pelagic production and occasionally form large blooms with high biomass. Thus, we argue that they represent a largely overlooked, but significant, temporarily available source of OM for marine microorganisms.

Biochemical characteristics of jellyfish OM

Hereby, we revise and discuss the release rates and the biochemical composition of different jelly-OM pools. Understanding the quality and quantity of jelly-OM that is available to microbes is crucial for understanding the associated microbial metabolic processes and rates. Generally, the biochemical composition of substrate defines how rapidly it is incorporated into new microbial biomass or respired (del Giorgio and Cole 2000; Williams 2000). A high growth yield of heterotrophic microbes utilizing jelly-OM results ultimately in a larger fraction of particulate OM in the form of newly generated biomass retained within the food web (del Giorgio and Cole 2000).

Characteristics of DOM produced and released by living jellyfish

Jellyfish biomass is characterized by a low C : N molar ratio (~ 4.5 : 1; Anninsky 2009; Pitt et al. 2009; Lucas et al. 2011; Kogovšek et al. 2014; Molina-Ramírez et al. 2015; Merquiol et al. 2019), as discussed in details in the next section on *OM encapsulated within jellyfish biomass*. By feeding on a food source of higher C : N ratios (~ 6.6 for phytoplankton and ~ 4.8–6.2 for crustacean zooplankton, Redfield et al. 1963; Ventura 2006) jellyfish assimilate more C than required to meet their N demand (Pitt et al. 2013). It has been suggested

that via the release of organic and inorganic compounds, jellyfish maintain a nutrient balance between ingested food and body requirements (Kremer 1975, 1977). Carbon is lost via respiration, egestion of dissolved digestive products and leaching from fecal pellets (Kremer 1977; Caron et al. 1989; Hansson and Norrman 1995; Costello et al. 1999; Pitt et al. 2009; Condon et al. 2010; Iversen et al. 2017) (Fig. 1). Another possible route for jellyfish to remove excess C is via production and excretion of colloidal DOM (Wells 2002) rich in carbon, for example, as mucus (C : N = 25.6 ± 31.6 : 1; Condon et al. 2011) (Fig. 1). While having a higher C : N molar ratio than the canonical Redfield ratio (6.6 : 1), the jellyfish excreta and mucus have lower molar N : P ratios (6.9–11.4) than the Redfield ratio (16 : 1) (Pitt et al. 2009; Condon et al. 2010; Liu et al. 2018). Jellyfish mucus and excreta are composed of dissolved organic nitrogen (DON), dissolved free amino acids (AAs) and dissolved organic phosphorus, nucleosides, and purine compounds as well as inorganic nutrients, mainly ammonia (but not urea, as in the case of crustaceous zooplankton) and phosphate (Pitt et al. 2009). Although jellyfish release substantial amounts of inorganic N and P along with DOC it has been suggested that the organic C : N : P stoichiometry and biochemical quality makes the released OM only moderately accessible for microbes (Condon et al. 2011).

The release of jellyfish mucus might be weight specific and species specific and the stoichiometry of the released mucus might also depend on the physiology of the individual organism and on ambient conditions such as feeding history, prey availability, and temperature (reviewed by Pitt et al. 2009). For example, a mucus release rate of 0.012 mg C per g wet weight d^{-1} was estimated for *Aurelia aurita* (Hansson and Norrman 1995) and 0.006 mg C per g dry weight d^{-1} for *Mnemiopsis leidyi* (Condon et al. 2010). A release of 21.2 ± 9.4 mg POC and 2.3 ± 1.1 mg PN m^{-2} jellyfish surface area hr^{-1} was measured for *Cassiopea* sp., which exceeds release rates reported for hermatypic corals by a factor of 2–15 (Niggl et al. 2010). When stressed (i.e., during reproduction, digestion, senescence, surface cleaning and defense against predators), jellyfish can release mucus in large quantities from gland cells present in the epidermis and gastrodermis (Heeger and Möller 1987; Patwa et al. 2015). Mucus production is a form of chemical defense as indicated by the presence of nematocysts and toxins in the mucus (Shanks and Graham 1988). Mucus has unique properties to trap pathogens as reflected by its high elasticity, adaptive rheology and self-repairing capabilities (reviewed in Bakshani et al. 2018). In addition, mucus has numerous other functions such as holding moisture, has antimicrobial properties and acting as adsorbent and surfactant (Bakshani et al. 2018). Besides, large quantities of the neurotransmitter/neuromodulator tryptamine were found in mucus considered an indicator of stress (Liu et al. 2018). In contrast to the biochemical composition of coral mucus, jellyfish mucus is largely unexplored. However, it has been suggested to resemble that of other cnidarians and thus is composed mostly of proteins, carbohydrates, and to a lesser extent of lipids (Ducklow and Mitchell 1979; Manzari et al. 2015; Stabili et al. 2015). A detailed proteomics and metabolomics study of jellyfish mucus identified more than 1000 proteins ranging from 37 to 250 kDa (Liu et al. 2018). A self-protective function of mucus proteins was related to the degradation of toxic compounds and/or pathogens (Liu et al. 2018). The main component of mucus is mucin, a glycoprotein consisting of a single protein chain connected to oligosaccharide branches through serine or threonine residues by O-glycoside bonds (Masuda et al. 2007). Threonine, serine, alanine, and proline are the main building blocks of the protein part (Uzawa et al. 2009), while the oligosaccharide part is mainly composed of *N*-acetyl-galactosamine, arabinose, and galactose (Masuda et al. 2007). However, the release rates and the composition of the OM pool produced and excreted by living jellyfish are largely unknown.

OM encapsulated within jellyfish biomass

Recent analysis of the OM of one of the most cosmopolitan bloom-forming scyphozoan jellyfish *A. aurita* s.l. revealed that about half is present in the form of DOM, with most of the jelly-DOM composed of complex polymeric compounds (Tinta et al. 2020). This study also reported that from 100 mg of jellyfish detritus L^{-1} approximately 44 μmol L^{-1} is DOC, 13 μmol L^{-1} total dissolved nitrogen (TDN, mainly DOM), 11 μmol L^{-1} total dissolved hydrolysable AAs (of which 55% free AAs with a considerable amount of free glycine and taurine) and 0.6 μmol L^{-1} PO_4^{3-} (Tinta et al. 2020). All these components can be rapidly released. This has important implications for the cycling and fate of this OM pool in the ocean and implies that a large fraction of jelly-OM, its dissolved part, is exclusively and readily accessible to microbes. Understanding the quantity and quality of DOM stored within biomass of the vast diversity of jellyfish species occupying different ecosystems is crucial to understand how much of jelly-OM can be instantly released and processed by microbes.

While jellyfish have similar carbon requirements as other metazoans, their nitrogen demand exceeds that of other metazoans (Pitt et al. 2013). It has been suggested that this is due to their high protein (72% ± 14% of total jelly-OM; Anninsky 2009; Pitt et al. 2009) and low lipid content (22% ± 12% of total jelly-OM; Pitt et al. 2009; Merquiol et al. 2019). Carbohydrates represent only a small fraction of total jelly-OM (7% ± 12%; Pitt et al. 2009; Merquiol et al. 2019). This composition is reflected in the low C : N molar ratio of jellyfish biomass (~ 4.5 : 1; Anninsky 2009; Pitt et al. 2009; Lucas et al. 2011; Kogovšek et al. 2014; Molina-Ramírez et al. 2015; Merquiol et al. 2019). Thus, the characteristics of jellyfish biomass differ substantially from that of the phytoplankton and crustacean zooplankton. OM of phytoplankton origin has a C : N ratio of ~ 6.6 (Redfield et al. 1963) and is composed of 40% ± 7% proteins, 26% ± 14% carbohydrates, and 15% ± 8% of lipids (Rios et al. 1998). In contrast,

the C : N ratio of crustacean zooplankton is 4.8–6.2 (but for calanoid copepods ~ 3; Båmstedt 1986), with proteins accounting for 20% to 70%, lipids from 0.5% to 74% and free AAs, chitin, and carbohydrates between 2% and 10% of dry weight (Ventura 2006). In contrast to the crustacean zooplankton, jellyfish lack a chitinous exoskeleton, contain ~ 50% less lipids and thus, exhibit a ratio of proteins to lipids of ~ 3.3 or up to twice that of the nongelatinous zooplankton (Pitt et al. 2013). Thus, with no hard exoskeleton and the proteinaceous character and low C : N ratio, the OM contained within the jellyfish body represents a high-quality and easily degradable substrate for heterotrophic marine bacteria (Benner 2002). Yet, information on release rates and the detailed biochemical composition of the OM of different jellyfish taxa is scarce and needs to be further investigated.

There is literature available on the protein, lipid, and carbohydrate content of jellyfish as reviewed by Pitt et al. (2009) for Cnidaria and Ctenophora and recently by Merquiol et al. (2019) for Scyphomedusae. However, so far only a few jellyfish species were analyzed, most commonly Scyphomedusae occurring in the Mediterranean Sea and edible or invasive jellyfish species (such as *M. leiydi*). In addition, the existing data are difficult to compare due to methodological differences, and all three classes of macromolecular compounds were rarely quantified in the same species. The majority of studies lacks information on the carbohydrate content (as emphasized by Merquiol et al. 2019). However, recently available data on transcriptome and proteome profiles of several jellyfish and ctenophore represent a largely unexplored, but valuable source of information on the complexity of the jellyfish OM (Brekhman et al. 2015; Brinkman et al. 2015; Liu et al. 2015; Frazão and Antunes 2016; Lewis Ames et al. 2016; Ge et al. 2018; Liang et al. 2019). These studies indicate that some genes and corresponding proteins are preserved in different jellyfish species, while some seem to be species specific, suggesting that not all the jellyfish OM is the same. A simple example is the lack of toxins in ctenophores, which could have important implications for interacting microbes.

The core of the jellyfish body is the mesoglea, an extracellular matrix composed of water, collagen, and salts (Verde and McCloskey 1998; Pitt et al. 2013). The most abundant transcripts and proteins of scyphozoan jellyfish *A. aurita* and *Rhopilema esculentum* are associated with extracellular matrix constituents and the synthesis of proteins ensuring tissue elasticity and enabling rapid muscle contractions (e.g., fibrillar collagens, hemicentin-like and folistatin-like proteins, myosin heavy and light chains) (Brekhman et al. 2015; Tinta et al. 2020). It was estimated that collagen represents ~ 50% of the total protein content of some edible jellyfish (Khong et al. 2016) and that jellyfish, in particular rhizostome Scyphomedusae, have a higher content of collagen than other organisms such as sponges (Addad et al. 2011; Merquiol et al. 2019).

The AA composition is only available of a few jellyfish species and was recently reviewed for Scyphomedusae (Merquiol et al. 2019). The existing data are difficult to compare, since some studies analyzed the AA content of the entire jellyfish biomass (Kogovšek et al. 2014; Leone et al. 2015; Wakabayashi et al. 2016). Other studies focused, however, only on specific components such as collagen (Calejo et al. 2009; Barzideh et al. 2014; Cheng et al. 2017) as reviewed in Merquiol et al. (2019). In addition, most published data are derived from a limited number of individuals and systems. Likewise, fatty acid (FA) profiles of jellyfish are scarce in the literature, available only for a limited number of species. The available data indicate that polyunsaturated FA are more abundant than monounsaturated and saturated FA in Scyphomedusae, but considerably lower than in crustacean zooplankton (Merquiol et al. 2019). Recent analysis of the nutritional value of *A. aurita* revealed a low FA content characterized by essential FAs, exhibiting seasonal and life stage variability, with mature medusae having the highest FA content (Stenvers et al. 2020).

As revealed by jellyfish transcriptome profiling, transcriptional expressions are altered along with major morphological changes taking place throughout the life cycle of jellyfish. The differences in the biochemical composition of different jellyfish life stages are important since most of the OM that becomes available in the ocean's interior once jellyfish decay originates from moribund individuals. The amount of proteins, carbohydrates, free AAs, and OM as a whole gradually decreases with increasing size of the jellyfish and thus, likely with maturity of individuals (Lucas 1994; Anninsky 2009). However, there is a lack of data on the relationship between the C : N ratio, biochemical composition and health condition of mature medusae (e.g., healthy individuals vs. moribund).

Jellyfish also represent a major sink and reservoir for nanoparticles and microplastic debris in the ocean (Patwa et al. 2015; Macali et al. 2018) and accumulate heavy metals and pollutants (Caurant et al. 1999) (Fig. 1). These aspects of jellyfish are largely unexplored and should be addressed more intensively in future studies. These types of compounds and pollutants can evoke specific type of metabolic pathways in microbes with important implications for ecosystem functioning (Dombrowski et al. 2016; Li et al. 2019; Pinto et al. 2020). Since jellyfish blooms likely increase in the future in several anthropogenically impacted coastal zones, where also higher concentrations of pollutants can be expected than in open waters, jellyfish might be substantially biomagnifying heavy metals and pollutants (Caurant et al. 1999; Sun et al. 2017; Macali et al. 2018; Iliff et al. 2020). Importantly, as the medusa stage drifts with ocean currents over long distances, they could serve as transmission vectors of pollutants to otherwise not impacted environments. Knowing the level of potential contaminants and pollutants present in jellyfish biomass is important since jellyfish have been considering to be used as food, fertilizers, medicine, cosmetics and waste water

treatment applications (i.e., GoJelly project; Emadodin et al. 2020; Freeman et al. 2020).

To summarize, jellyfish are an important source of OM and inorganic nutrients for the ocean's interior. The composition and stoichiometry of jellyfish mucus and excreta differ substantially from OM encapsulated within jellyfish biomass. These two jellyfish-derived OM pools might be utilized by different organisms, carrying out different metabolic processes and thus, influence the surrounding system differently. In addition, the biochemical composition of different jellyfish species, different compartments, different life stage, age, and health conditions most likely differ and therefore, affect the composition, dynamics, and metabolism of microbial community interacting with these types of OM sources.

Links between jellyfish and microbes

Microorganisms interact with jellyfish throughout their life span (Fig. 2). Different life stages of jellyfish can serve as host for microorganisms, with specific microbiota associated with different jellyfish body parts (Fig. 2). Jellyfish can also exert top-down control over the microbial populations from the surrounding ecosystem. Via production and release of DOM and inorganic nutrients living jellyfish can induce bottom-up effects on the microbial community of the ambient water (Fig. 2). Finally, at the end of their life span, jellyfish detritus can represent a source of OM for pelagic and/or benthic microbial communities (Fig. 2). Below, we revise different possible relationships between jellyfish and microbes, focusing on interactions between microbes and different jelly-OM pools characterized by different composition and stoichiometry as discussed above.

Jellyfish as host and vector for allochthonous microbes

Due to their ubiquitous distribution, simple anatomy, evolutionary age and alteration between different life stages, jellyfish might harbor and interact with taxonomically and metabolically diverse microorganisms throughout their life (Fig. 2). Basic characteristics of the jellyfish-associated microbiome have been recently reviewed (Tinta et al. 2019). The few available studies reveal the importance of the ambient microbial community for recruiting members of the jellyfish-microbiome and a certain degree of microbiome specialization with some preferences for specific jellyfish taxa and populations, life stages, and body parts (Basso et al. 2019; Kos Kramar et al. 2019; Tinta et al. 2019). The role of the microbiota associated with jellyfish was related to food digestion and defense mechanisms against hostile microorganisms and larger organisms in their surroundings (Basso et al. 2019 and references therein). Moreover, Weiland-Bräuer et al. (2020) highlight the importance and function of the microbiome for asexual reproduction, health, and fitness in *A. aurita*. At the

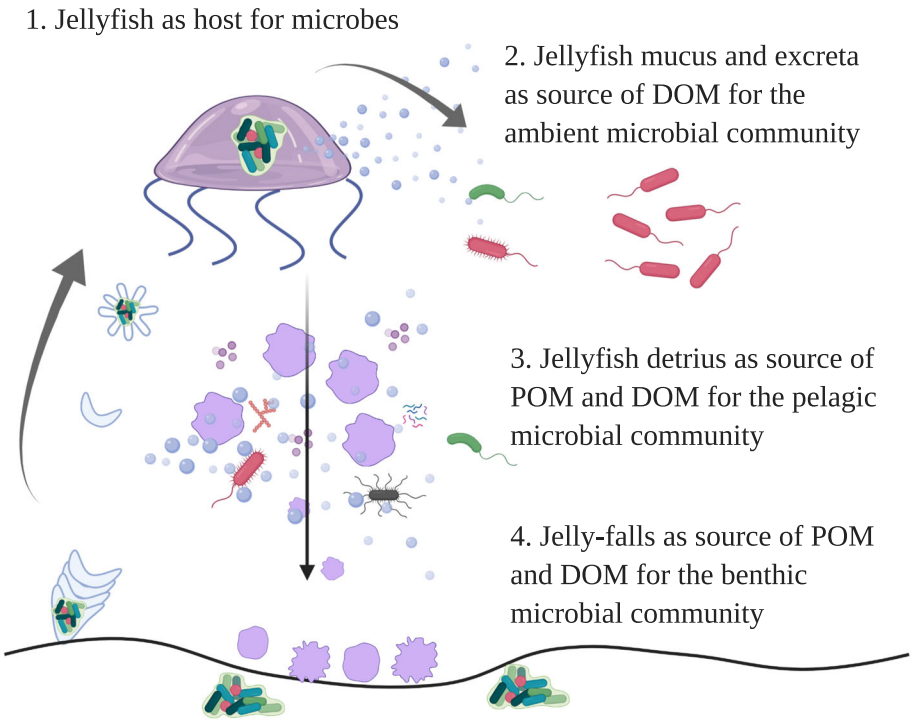

Fig. 2. Proposed links between different stages of jellyfish life cycles and the microbial community. DOM, dissolved organic matter; POM, particulate organic matter.

same time, the microbiome might benefit from constant nutrient input and other compounds from the jellyfish host and could be self-regulating the structure of the jellyfish microbiome via the production of quorum quenching molecules by specific microbes (Prasse et al. 2019). Recently, it has been suggested that the bacterial community colonizing the mucus of *A. aurita* is controlled via host-derived quorum sensing (Weiland-Bräuer et al. 2019). In addition, it has been suggested that invasive jellyfish such as the ctenophore *M. leiydi* or outbreaks of *Aurelia* sp. could serve as a vector for allochthonous (and even pathogenic) microbial species and thus affect marine food web structure and function of the invaded systems (Manzari et al. 2015; Jaspers et al. 2019, 2020). This potential role of jellyfish could be particularly important since the medusa stage drifts with ocean currents over long distances (Vodopivec et al. 2017). Also, it has been hypothesized that some invasive species were introduced into environments via ballast waters (Malej et al. 2017). Taken together, the review of the current state of knowledge on the jellyfish-microbiome reveals that this topic is severely understudied and should be studied in more detail in the future.

Living jellyfish exert top-down control and bottom-up effects on planktonic communities

During their life span, jellyfish can have a major impact on the biogeochemical state of their habitat and thus, on the dynamics of the ambient microbial community by actively and passively releasing DOM and inorganic nutrients via excretion, egestion, mucus production, and leaching from fecal pellets (Hansson and Norrman 1995; Condon et al. 2011; Steinberg and Landry 2017; Fig. 2). However, the mechanisms underlying microbial processing of released jelly-DOM, the consequences on the diversity and functioning of microbial communities remain unclear.

As the jellyfish bloom develops it might cause changes to the surrounding ecosystem. The top-down effect of jellyfish on microplankton communities has been demonstrated, although most studies focused on the adult medusa stage (Titelman and Hansson 2006; Malej et al. 2007; Riisgård and Madsen 2011; Zoccarato et al. 2016). It has been suggested that different developmental stages of jellyfish selectively prey on some microplankton groups (Wang and Xu 2013; Zoccarato et al. 2016; Xiao et al. 2019). In this way, jellyfish can reshape the marine food web structure. For example, by removing the grazing pressure jellyfish blooms can trigger an indirect cascading effect on phytoplankton and bacterioplankton communities (Turk et al. 2008; Zoccarato et al. 2016).

Besides top-down control, jellyfish can exert bottom-up effects on different micro- and bacterioplankton communities in the surrounding system. During the early developmental stage of jellyfish, excreted inorganic nutrients support rapid growth of specific phytoplankton groups (diatoms and cryptophytes; Xiao et al. 2019). Jellyfish excreta are rich in phosphorus relative to nitrogen (inorganic N : P ratio 6.9–11.4; reviewed by Pitt et al. 2009) and therefore, can support primary production, particularly in P-limited systems (coastal saline lake in Australia, Pitt et al. 2005; inland Sea of Japan, Shimauchi and Uye 2007; Yellow Sea, Xiao et al. 2019) (Fig. 2). As jellyfish blooms reach mature stages, the composition of ambient phytoplankton communities can change, which is attributed to the change in the quantity and quality of OM released by mature jellyfish (Xiao et al. 2019).

Along with the release of grazing pressure on phytoplankton via predation on crustaceous zooplankton, the material released by the different jellyfish developmental stages stimulates heterotrophic microbial production and favors blooms of copiotrophic bacterial taxa (Turk et al. 2008; Zoccarato et al. 2016). It has been demonstrated that DOM released by living jellyfish is rapidly respired, rather than fueled into bacterial biomass production by otherwise rare members of the ambient microbial community (Hansson and Norrman 1995; Riemann et al. 2006; Turk et al. 2008; Condon et al. 2011; Dinasquet et al. 2012*a*,*b*, 2013; Manzari et al. 2015; Zoccarato et al. 2016) (Fig. 2). Fecal pellets of some gelatinous zooplankton, that is, pelagic tunicates, exhibit fast sinking rates (> 2000 m d^{-1}; Turner 2002), are rich in C and N; however, degradation rates are low (Caron et al. 1989; Iversen et al. 2017). Yet, there is no information available on the composition and sinking rates of jellyfish fecal matter (Luo et al., 2020). Albeit there is limited information available on microbial processing of jellyfish mucus, jelly-DOM, and fecal matter, there is evidence that the composition, stoichiometry, and bioavailability of OM released by living jellyfish are very different to the OM stored within the jellyfish biomass and thus, could trigger very different responses of the microbial planktonic community (Pitt et al. 2009; Condon et al. 2011).

The fate of jellyfish detritus

About 10–30% of the organic carbon produced in the sunlit surface waters are exported into the ocean's interior via sinking particles, a mechanism coined the biological carbon pump (Herndl and Reinthaler 2013; Boyd et al. 2019). The biological processing of the particle-associated organic (and inorganic) matter during its sinking through the water column affects the global carbon cycle and thus the global climate. Sinking particles originating from different sources (such as from phytoplankton or zooplankton, fecal pellets, etc.) vary in complexity, molecular composition, and bioavailability (Boyd and Trull 2007; Turner 2015; Johnson et al. 2020). These sinking particles are colonized by specific populations (microbes and larger organisms) with different mechanisms to utilize particle-associated OM (reviewed by Boyd and Trull 2007; Johnson et al. 2020). In addition, different molecules are degraded at different rates generating a variety of by-products in the degradation process. Consequently, the composition of the detrital (and dissolved) matter pool changes with depth in the water column (Johnson et al. 2020).

It has been estimated that detrital matter represents ~ 30 Pg C in the world's oceans (Libes 1992). In the mesopelagic and bathypelagic ocean, detrital matter derived from the euphotic layer represents an important food source for the heterotrophic food web as it consists of relatively fresh OM, in contrast to DOM as revealed by ^{14}C radiocarbon dating (Druffel et al. 1992 for DOC; Hwang et al. 2004 for sinking POC). Most studies on detrital particles so far have focused on detritus of macroalgal and phytoplankton origin, crustacean zooplankton, and appendicularians (Anderson et al. 2017 and references therein). However, jellyfish detritus, differing in composition from detritus of phytoplankton and crustacean zooplankton, might represent a substantial fraction of the total detrital OM pool. It has been shown that the flux of jellyfish detrital OM can be substantial relative to phytodetrital fluxes in some jellyfish-dominated ecosystems such as in Norwegian fjords, where the maximum flux of jelly-POC and jelly-PON was equivalent to ~ 90% and ~ 150%, respectively, of the phytodetrital-POC and phytodetrital-PON daily fluxes to the seafloor at certain times (Sweetman and Chapman 2015; Lalande et al. 2020). During the decay of a jellyfish bloom a significant fraction of pelagic biomass incorporated by jellyfish throughout their life cycle becomes available to the interior of marine systems. This is particularly relevant on a local scale and in coastal environments where the largest jellyfish blooms are usually reported (Condon et al. 2013; Lucas et al. 2014; Lebrato et al. 2019).

Jellyfish blooms often occur seasonally and are short-lived (weeks to months), after which the populations abruptly collapse, representing an important perturbation to the marine ecosystem. A comprehensive review of environmental factors causing the collapse of jellyfish blooms (Pitt et al. 2014) lists food limitation, predation, disease (parasitism and bacterial infections), death after spawning by simultaneous loss of tentacles leading to starvation. Also, physiological stress caused by adverse physical conditions such as water temperature, low salinity, and ultraviolet radiation in shallow waters leads to the collapse of jellyfish blooms (Pitt et al. 2014). Jellyfish carcasses might have a significant impact on the environment with higher OM release rates after massive jellyfish die-off with different stoichiometry and biochemical composition than the release of OM from a living jellyfish (Kingsford et al. 2000; Miyake et al. 2005; Pitt et al. 2009).

Once jellyfish start decaying, they are in moribund state for a long time and start to passively sink through the water column. Noteworthy, larger aggregations of passive jellyfish have been observed floating at the surface in some areas, also reporting air bubbles entrapped within jellyfish bodies (Malej 1989). Sinking rates are in the range of 900–1100 m d^{-1} for Scyphozoa and between 500 and 1300 m d^{-1} for Ctenophora (Lebrato et al., 2013). However, there is a lack of information on species-specific sinking velocities as emphasized by Lebrato et al. (2013, 2019). It is reasonable to assume that carcasses of different jellyfish species, exhibiting different weight and shape sink with different speed. Also, the methodology applied to determine sinking velocities of jellyfish carcasses (e.g., using previously frozen jellyfish samples; Lebrato et al. 2013) might represent a source of error in these estimates of sinking velocities. For sinking jellyfish carcasses different routes can be envisioned: they could be either consumed, scavenged, fragmented, or degraded by pelagic (microbial) communities or massively deposited at the seafloor and eventually degraded by benthic communities (Fig. 3).

Although jellyfish were traditionally considered as trophic dead end, this paradigm has recently shifted (Hays et al. 2018). In fact, a variety of predators, including turtles, birds, fish, and other gelatinous zooplankton prey on jellyfish because of rapid digestion, low capture costs, availability, and selective feeding on energy-rich components of the jellyfish body such as gonads (Dunlop et al. 2017; Hays et al. 2018; Stenvers et al. 2020). In this way, OM incorporated into jellyfish is transferred to higher trophic levels. Nonetheless, to date there are only few published estimated on predation rates on jellyfish from models (Ruzicka et al. 2012, 2020; Chiaverano et al. 2018; Luo et al. 2020). Recently, Luo et al. (2020) estimated that on average ~ 45% of the gelatinous zooplankton production is consumed by predators. Luo et al. (2020) also emphasized that there are many unknowns with respect to gelatinous zooplankton, which needs to be further investigated to resolve the discrepancies between actually measured rates and model parameters (Luo et al. 2020). There are several reasons, however, why predators also might avoid feeding on jellyfish. This feeding avoidance on jellyfish might be due to chemical repellents (nematocysts and/or symbionts), low (diluted) nutritional quality of jellyfish or predator gut volume limitations (large quantities of water are consumed with jellyfish; Bullard and Hay 2002). In addition, their transparency and diel migrations make jellyfish less visible and elusive for predators (Bullard and Hay 2002).

If not consumed, intact jellyfish corps continue sinking through the water column as jelly-falls (term coined by Billett et al. 2006; Lebrato and Jones 2009; Lebrato et al. 2011; Sweetman and Chapman 2011) and the OM contained within their biomass could be transferred in a cascade to different members of the marine food web. Potential scavengers, such as macrofauna and megafauna, might fragment jellyfish bodies, as experimentally shown (Sweetman et al. 2014), with no significant depth effect on mean scavenging rates (Dunlop et al. 2018). In addition, fragmentation of jelly carcasses during sinking could also occur under turbulent conditions in the upper mixed water column, as previously reported for different size-ranges of particles in the ocean (Briggs et al. 2020 and the references therein). This process could be more common in the case of more fragile jellyfish species and in certain ecosystems under specific conditions and could be one of the reasons why large depositions were never reported in some jellyfish-dominated environments such as the Northern Adriatic Sea. Scavenging and fragmentation of carcasses would result in jelly-particles of varying sizes. The smaller the particle

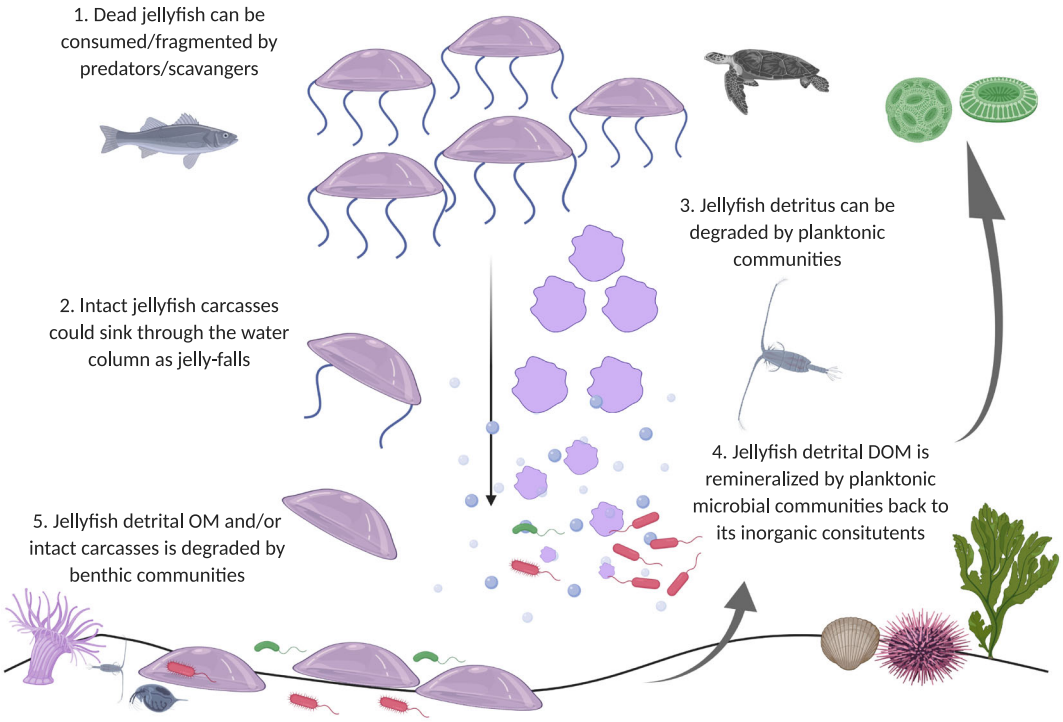

Fig. 3. The possible fates of jellyfish detritus.

the higher is its surface-to-volume ratio, affecting its sinking velocity and potentially enhancing the remineralization rate of jellyfish particles by microbes (Frost et al. 2012; Briggs et al. 2020). The resulting range of differently sized jellyfish-derived particles could be hitchhiked by different microorganisms, which transform certain constitutes of jelly-OM to become accessible to other organisms such as detritivorous zooplankton (Mayor et al. 2014). Eventually, microbes could solubilize a certain fraction of jelly-POM to DOM for subsequent assimilation.

Jelly-OM not consumed by the pelagic biota is deposited at the seafloor, a phenomenon observed mainly in some coastal systems (Lebrato et al. 2012). Whether this massive deposition takes place in the open ocean also remains unknown. Importantly, most of these are records of cnidarian carcasses, while as emphasized by Luo et al. (2020), there are no records of benthic depositions of ctenophores. If deposited at the seafloor, jellyfish carcasses would be either scavenged (Sweetman et al. 2014; Dunlop et al. 2017, 2018) or degraded and remineralized by the benthic community (Lebrato and Jones 2009; West et al. 2009; Chelsky et al. 2016; Sweetman et al. 2016; Dunlop et al. 2017). It has been shown that the degradation rate by the benthic community may change as a function of water column O_2 availability (Billett et al. 2006; Sweetman and Chapman 2011, 2015).

However, about half of the jellyfish detrital matter is composed of POM, while the other half is in the form of DOM, which is rapidly leaching into the ambient water and is therefore exclusively accessible to microbes (Tinta et al. 2020). Large jellyfish detrital particles are accessible to large organisms such as scavengers and zooplankton (Mayor et al., 2014) and subjected to physical forces fragmenting the jelly-POM into slow-sinking particles. In contrast, jelly-DOM might be consumed and degraded solely by pelagic microbial communities and thus retained in the pelagic food web (Tinta et al. 2020).

Hence, how much of jellyfish biomass is recycled in the water column and how much of it actually reaches the seafloor depends on many factors, such as the initial jellyfish biomass and its specific density, the jellyfish species and its biochemical composition determining its bioavailability. Also, the depth where the jellyfish die-off, the predation and fragmentation rates and thus, the sinking velocity, remineralization rates, ambient seawater temperature and water column structure, and the composition and functional capacity of the marine food web determine the fate of jellyfish detrital matter.

The flux of jellyfish carbon (jelly-C) and its transfer efficiency to different depths of the open ocean was estimated using available jellyfish biomass data, vertical migration data measured in the field, published sinking rates, vertical temperature profiles and empirically determined jellyfish decay rates (Titelman et al. 2006 for *Perphylla perphylla*; Iguchi et al. 2006 for *Nemopilema nomurai*; Sempere et al. 2000 for salps) of

jelly-C (coined *jelly-C microbial decay ratio*) (Lebrato et al. 2019). It was estimated that between 59% and 72% of jellyfish biomass production reaches 500 m, 46% and 54% reaches 1000 m, 43% and 48% reaches 2000 m, 32% and 40% reaches 3000 m, and 25% and 33% reaches 4500 m depth (Lebrato et al. 2019) in the open ocean. Luo et al. (2020) used a different approach resulting in different estimates of jellyfish biomass and its production, as discussed above. This resulted in a nonpredation mortality (carcasses) estimate of 25% of gelatinous zooplankton production (Luo et al. 2020). Combined with the much greater fecal matter flux, total gelatinous zooplankton POC export at 100 m was estimated to amount to 1.6–5.2 Pg C yr^{-1}, equivalent to 32–40% of the total global POC export (Luo et al. 2020). The fast-sinking gelatinous zooplankton export resulted in a high transfer efficiency of 38–62% to 1000 m depth, and 25–40% to the seafloor. Both studies show that jelly-C is an important component of the global biological soft-tissue pump, potentially playing an important role as a food source for the food web of the ocean's interior (Lebrato et al. 2019). However, both studies (Lebrato et al. 2019; Luo et al. 2020) had to make several assumptions due to the lack of available experimental data on the influence of temperature, sinking rate, fragmentation, and size on the remineralization rates of jellyfish detritus (Lebrato et al. 2019).

Microbial decay rates of jellyfish detritus

A major potential source of bias in the models of Lebrato et al. (2019) and Luo et al. (2020) in estimating jelly-C flux and export efficiency from the euphotic layer into the ocean's interior is its dependence on only few estimated microbial decay rates of jellyfish biomass in the water column. The temperature dependence of microbial decay rates was only determined in a few studies, such as for *N. nomurai* off Sado Island Japan (Iguchi et al., 2006), *P. perphylla* at Lurefjorden, Norway (Titelman et al. 2006) and *Thalia democratica* and for other salps in the NW Mediterranean Sea (Sempere et al. 2000). The decomposition of jellyfish carcasses and detritus and its effect on the surrounding system after the collapse of blooms was also subject of other studies (Tinta et al. 2010, 2012, 2016, 2020; Blanchet et al. 2015; Chelsky et al. 2016). Thus far, published studies provide decay rates for only a limited number of jellyfish taxa from only a few systems (Table 1). The reported jellyfish decay rates vary substantially, potentially depending on jellyfish species and the size of individuals and the environmental conditions, for example, ambient seawater temperature and/or the habitat (pelagic vs. benthic) where the decay takes place (Table 1). We argue, however, that uniform microbial decay rates for jellyfish cannot be applied globally, due to different ecosystem characteristics and different species-specific features of jellyfish. Even more important, most of the reported jellyfish decay rates cannot be solely attributed to microorganisms, that is, bacteria and archaea, due to the experimental designs applied. In these studies, the exclusion of larger organisms playing a role in the decomposition process was not assured or the parameters that would allow accurate determination of microbial community growth were not measured. For example, to study jellyfish decay rates, jellyfish are commonly isolated in a net, bag or bottle together with ambient seawater in a setup that allows for colonization of both microbes and larger organisms (i.e., mesh size of 5–10 mm; Titelman et al. 2006) or using ambient seawater potentially containing organisms other than microbes (West et al., 2009; Frost et al., 2012). Also, some studies focused solely on the degradation of jellyfish biomass at the sediment surface (West et al., 2009; Chelsky et al. 2016; Sweetman et al., 2016; (Guy-Haim et al. 2020), while others focused on the degradation process in the water column (Titelman et al., 2006; Tinta et al., 2010, 2012, 2016, 2020).

All these different approaches make the results of these studies difficult to compare and reveal the need to apply more standardized and comprehensive approaches to address the problem (Table 1). In particular, if one wants to incorporate the recycling rates of jellyfish-derived OM (i.e., carbon and nitrogen) into biogeochemical budgets, the decay rates of carcasses in the water column need to be determined to reliably estimate how much of jelly-OM is eventually exported into the ocean's interior and finally deposited at the seafloor. One of the key factors determining the fate of jellyfish detritus, the link between microbes and jellyfish detrital matter, is of particular relevance.

Microbial processing of jellyfish detritus

Only a few studies so far have designed experiments to actually study microbial degradation of jellyfish biomass in the water column and measured the parameters directly linked to microbial growth, that is, bacterial abundance, production, respiration and community structure, aside from concentrations of dissolved organic and inorganic matter (Titelman et al. 2006; Tinta et al. 2010, 2012, 2016, 2020; Blanchet et al. 2015). Other studies have, in addition, focused also on the response of specific, culturable bacterial strains to jellyfish detritus (Titelman et al. 2006; Tinta et al. 2012; Blanchet et al. 2015). None of these studies, however, applied an experimental design that allows determining the microbial decay rate of jellyfish biomass (i.e., the decrease of jellyfish biomass wet or dry weight solely due to microbial degradation). Tinta et al. (2020) studied the microbial consumption of different compounds of the jelly-DOM pool (i.e., DOC, total dissolved nitrogen, free and combined AAs and inorganic nutrients). However, also this study provides no information on the microbial degradation of jelly-POM (Tinta et al. 2020). Different studies used jellyfish biomass in different forms to set up the experiment (i.e., homogenized carcasses, freeze-dried material or just certain fractions of jelly-OM). Moreover, jellyfish biomass used in most of these experiments was not representative for natural populations. For these experiments, jellyfish were either kept in captivity prior to the experiment or only few individuals and even only pieces of individuals

Table 1. Studies analyzing jellyfish decay rates together with experimental designs, jellyfish species, study area and parameters describing the decay rate of jellyfish carcasses.

Publication	Study area	Aquatic layer	Jellyfish species	Experimental design	Parameters	Jellyfish wet weight	Seawater temp.	Jellyfish decay time	Decay curve y = wet weight. x = days, k = decay coefficient/rate	Decay coefficient	Jellyfish turnover time
Hansson (1997)	Gullmarsfjorden, Sweden	Pelagic zone	*Aurelia aurita*	Intact whole jellyfish immobilized in nets in large tanks in situ	Decrease of wet weight over time	149–428 g	15–17°C	4.9 d	n.p.	n.p.	n.p.
Iguchi et al. (2006)	Sado Island, Japan Sea	Surface water (2.5 m depth)	*Nemopilema nomurai*	Umbrella parts of jellyfish incubated in surface water tank, deep water tank and at the sea floor in situ	Decrease of wet weight over time expressed as residual ratio	955 g	8°C	8 d	$y = e^{-kt}$	0.513 d^{-1}	n.p.
		Deep water from 334 m incubated in a tank at 10 m depth				884 g	2.7°C	14 d		0.215 d^{-1}	
		Sediment				2000 g	n.p.	5–8 d		n.p.	
Titelman et al. (2006)	Raunefjorden, Norway	Pelagic zone	*Periphylla periphylla*	Suffoxated jellyfish caracasses were incubacted in situ for 7 d in net with mesh size of 5–10 mm	Decrease of wet weight over time	42 ± 8.14 g	10–12°C	4.1–7 d (95% of inital WW was degraded in first 5 d)	$y = 42.08(\pm 0.91)\ e^{-1.12(\pm 0.22)x}$	1.12 d^{-1}	n.p.
						121 ± 12.3 g			$y = 121.2(\pm 1.4)\ e^{-0.716(\pm 0.056)x}$	0.72 d^{-1}	
						223 ± 12.3 g			$y = 222.6(\pm 1.6)\ e^{-0.666(\pm 0.031)x}$	0.67 d^{-1}	
						300 ± 361 g			$y = 299.3(\pm 4.1)\ e^{-0.844(\pm 0.031)x}$	0.84 d^{-1}	
West et al. (2009)	Coastal lagoon (Smiths Lakes), New South Wales, Australia	Sediment	*Catostylus mosaicus*	10 L of sediment and 1 whole freeze/thawed jellyfish were incubated for 9 d in 60 L mesocosm with continuous flow of water in the dark (the cut off size of organisms is not clear)	Visual observation of jellyfish tissue decomposition	1600 g	~ 30°C	9 d	n.p.	n.p.	0.02 d^{-1} to 0.05 d^{-1} (calculated by Sweetman et al. 2016)
Song et al. (2012, publication is in Chinese)	Chinese Sea	n.p.	*Nemopilema nomurai*	n.p.	n.p.	5000 g	n.p.	6–7 d	n.p.	n.p.	n.p.
Frost et al. (2012)	Mouth of the Steinhatchee River Florida's west coast	Pelagic zone	*Chrysaora quinquecirrha*	Pieces of healthy individuals were incubated with 200 mL of ambient seawater (the cut-off size of organisms is not clear, but visible zooplankton was removed) for 200 h (8.3 d) under light and dark cycle	Decrease of wet weights over time	9.6–19.6 g Whole animals of 39.6–47.0 g	~ 22°C	5–8 d (half-life of 3 d) 92–100% decomposed in 8 d	$y = 13.3e^{-0.299x}$	0.29 d^{-1}	n.p.
Qu et al. (2015)	Huiquan Bay in Qingdao, jellyfish were collected from Jiaozhou bay. China	Pelagic zone sediment	*Cyanea nozakii*	Processed jellyfish pieces placed on the sediment/or in the water and incubated in plastic tube with 200 μm prefiltered ambient seawater	Visual observations	800 g	Laboratory conditions, temperature of incubation not clear	14 d	n.p.	n.p.	n.p.

(Continues)

Table 1. Continued

Publication	Study area	Aquatic layer	Jellyfish species	Experimental design	Parameters	Jellyfish wet weight	Seawater temp.	Jellyfish decay time	Decay curve y = wet weight. x = days, k = decay coefficient/rate	Decay coefficient	Jellyfish turnover time
Chelsky et al. (2016)	Coastal lagoon in New South Wales, Australia	Sediment	*Catostylus mosaicus*	Benthic chamber incubations with sediment, pieces of killed jellyfish and overlaying water were incubated in situ. The netting was coarse (3 cm) to allow bacterial colonization and scavenging by benthic fauna and small fish,	Decrease of wet weight over time	1200 ± 50 g	~ 23°C	68% ± 1.4% left after 1 d, 52.4% ± 3.5% left after 2 d 33.7% ± 1.1% left after 3 d	n.p.	n.p.	n.p.
Sweetman et al. (2016)	Fanafjorden, Norway	Sediment	*Periphylla periphylla*	Sediment chamber with 0.2 pre-filtered overlaying water and pieces of thawed jellyfish incubated under laboratory conditions in the dark	Turnover time of jellyfish biomass	8.6 ± 0.1 g	~ 8°C	Jelly-C decay rate: 435 mg C m^{-2} d^{-1}	n.p.	n.p.	0.016 d^{-1}

were collected in the natural environment and used in the experiments. The common conclusion from the above studies is that jellyfish-OM is a high-quality substrate for bacteria and supports rapid growth of specific, potentially pathogenic, bacterial phylotypes that preferentially use N moieties of jelly-OM (mainly the protein fraction), leaving C-enriched jelly-OM in the system.

The concept of *detritosphere* was coined by Biddanda and Pomeroy (1988) describing the microenvironment around detrital particles in which specific microbial communities thrive following specific succession patterns. The detritosphere of both phytoplankton (Pomeroy and Deibel 1980) and crustacean and noncrustacean (rotifiers) zooplankton (Fukami et al. 1985; Tang et al. 2009; Bickel and Tang 2010; Bickel et al. 2014) was studied. However, most studies focused on the succession of bacterioplankton populations over seasonal cycles including the dynamics after the decay of phytoplankton blooms (Teeling et al. 2012, 2016; Buchan et al. 2014; Needham and Fuhrman 2016), while bacterioplankton succession patterns following the decay of zooplankton blooms are scarcely reported (Bickel et al. 2014; Kolmakova et al. 2019). The microbiome of gelatinous zooplankton (Tinta et al. 2019; Jaspers et al. 2019 and references therein) was investigated and to some extent also the changes of the ambient bacterioplankton community composition during gelatinous zooplankton blooms (Riemann et al. 2006; Condon et al. 2011; Dinasquet et al. 2012*a*,*b*, 2013) were studied. In contrast, the detritosphere of gelatinous zooplankton and the microbial processing of this OM source in the water column have received less attention (Titelman et al. 2006; Tinta et al. 2010, 2012, 2016, 2020; Blanchet et al. 2015). These studies report a rapid decrease of *Alphaproteobacteria* and an accompanied increase of *Gammaproteobacteria* (representing from about 40% to more than 90% of the jellyfish-degrading community (Tinta et al. 2012, 2016, 2020; Blanchet et al. 2015). Thus, *Gammaproteobacteria* are the first group of Bacteria responding to jelly-OM, followed by a succession of Bacteroidetes presumably growing on more complex and less-labile jellyfish OM (Condon et al. 2011; Tinta et al. 2012; Dinasquet et al. 2013; Blanchet et al. 2015).

The bacterial communities thriving on jellyfish detritus exhibit rapid growth rates, from 0.2 d^{-1} (Table 2, (Tinta et al. 2010) up to 7 d^{-1} (Titelman et al. 2006)) depending on the jellyfish species, environmental conditions and ecosystem characteristics. This is higher than bacterial community growth rates reported for the ocean (0.1–1 d^{-1}, Arístegui et al. 2009). Altogether this indicates that microbial growth on jellyfish detritus in the water column can be rapid. It has been shown that a consortium of opportunistic bacteria can rapidly consumed almost the entire pool of *A. aurita*'s proteins (> 98%), AAs (~ 70%) and DOC within ~ 1.5 d, indicating a rapid turnover of jellyfish-DOM including soluble proteins (Tinta et al. 2020). However, the basic parameters, such as how much of jellyfish detrital matter is respired by bacteria and is therefore lost for the system and how much of

Table 2. Degradation of *Aurelia aurita* s.l. by ambient microbial communities with experimental details, ambient seawater temperature, concentrations of NH_4^+ and PO_4^{3-} in the ambient seawater, bacterial growth rates (μ), and accumulation rates of NH_4^+ and PO_4^{3-} per g jellyfish (wet weight) per day.*

								Accumulation rates	
Publication	Days	Ecosystem	Jelly-enrichment g L^{-1}	T °C	NH_4^+ μmol L^{-1}	PO_4^{3-} μmol L^{-1}	μ d^{-1}	NH_4^+ μmol g^{-1} d^{-1}	PO_4^{3-} μmol g^{-1} d^{-1}
Tinta et al. (2010)	18	N Adriatic	30	14	0.5	0.1	0.76	0.29	0.02
	4	Big Lake, S Adriatic	15	17	0.3	0.11	0.66	0.64	0.02
	3	Big Lake, S Adriatic	15	10	0.19	0.03	0.48	0.25	0.01
	7	Big Lake, S Adriatic	5.5	19	0.32	0.15	0.37	0.56	0.02
	7	Big Lake, S Adriatic	3.1	11	0.43	0.04	0.22	0.37	0.02
Tinta et al. (2012)	22	N Adriatic	12.5	11	0.82	0.17	0.46	0.69	0.03
Tinta et al. (2016)	3	Black Sea, coastal	12.5	24	2.22	0.56	1.22	0.93	0.06
	4	Black Sea, off shore	11.5	24	0.71	0.07	0.91	1.43	0.05
Blanchet et al. (2015)	22	NW Mediterranean	37.5	18	6	0.5	1.44	0.12	0.01
Tinta et al. (2020)	3.5	N Adriatic	2.5	25	2.5	0.02	2.16	2.8	0.15

*The dry weight was assumed to amount to 4% of the wet weight.

this OM pool is incorporated into bacterial biomass and thus potentially returned to the system via, for example, bacterial grazers remain largely unknown. Recently, a bacterial growth efficiency of 65% ± 27% was obtained for a jellyfish-degrading microbial consortium (Tinta et al. 2020), which exceeds substantially the bulk growth efficiency of oceanic surface water bacteria (15% ± 12%) and coastal bacterioplankton (27% ± 18%) (del Giorgio and Cole 2000). The high bacterial growth efficiency indicates that the jelly-DOM, which represents about half of the detrital jellyfish OM can be exclusively and efficiently incorporated into bacterial biomass. This has important implications for the fate and flux of jellyfish-derived OM and for marine ecosystem functioning and its biogeochemical state. It implies that a substantial amount of jellyfish detrital matter (~ 50%) is degraded and incorporated into planktonic bacterial biomass, which is efficiently retained in the pelagic food web. Hence, the amount of jelly-OM reaching the seafloor is efficiently reduced by microbial degradation in the water column.

In contrast, the study of Condon et al. (2011) found that most DOM released by living jellyfish such as mucus is respired by bacteria and thus, lost from the system rather than incorporated into bacterial biomass. As stated above and also by Condon et al. (2011), there is a major difference between DOM released by jellyfish while alive (i.e., colloidal material with a C : N ratio of 26 ± 32 : 1; Condon et al. 2011; Dinasquet et al. 2013) and OM in jellyfish biomass and detritus (C : N ratio of ~ 4.5 ± 0.1 : 1 and rich in proteins). In addition, the composition, stoichiometry and thus the bioavailability of jelly-derived DOM might be species specific (i.e., jelly-DOM of *A. aurita* (Tinta et al. 2010, 2012, 2020; Blanchet et al. 2015) vs. *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi* (Condon et al. 2011; Dinasquet et al. 2013). Yet, the findings of Tinta et al. (2020) contrast those of Blanchet et al. (Blanchet et al. 2015) studying the response of the bacterial community from a coastal lagoon to the DOM fraction of *A. aurita* reporting a bacterial growth efficiency < 20%, while Tinta et al. (2020) determined a bacterial growth efficiency for *A. aurita* DOM of ~ 65%. This implies that the overall environmental conditions might affect the microbial response to jellyfish detritus, as the study of Tinta et al. (2020) was performed with water collected from a coastal oligotrophic system (northern Adriatic) while the study of Blanchet et al. (2015) was conducted in a eutrophic lagoon. Also, Blanchet et al. (2015) used jellyfish detrital DOM (< 0.2 μm fraction) of juvenile medusae kept in captivity, while Tinta et al. (2020) used subsamples of whole freeze-dried jellyfish detrital OM pooled from 27 moribund individuals sampled during senescent phase of jellyfish bloom.

As a result of microbial degradation of jellyfish detrital matter, NH_4^+ and PO_4^{3-} are generated, regardless of the jellyfish species and ecosystem features (Titelman et al. 2006; Tinta et al. 2010, 2012, 2016, 2020; Blanchet et al. 2015) (Table 2). By comparing the accumulation rate of NH_4^+ per g jellyfish wet weight from different experiments using the same jellyfish species (i.e., *A. aurita*) from different ecosystems at different environmental conditions, significant correlations were found between bacterial growth rates and ambient seawater temperature ($r = 0.72$, $p < 0.05$), and the concentration of NH_4^+ in the ambient water ($r = 0.67$, $p < 0.05$) and the accumulation rate of NH_4^+ ($r = 0.71$, $p < 0.05$) (Table 2, Fig. 4). Also, a significant correlation was found between the accumulation rate of NH_4^+ per g jellyfish matter and the ambient seawater temperature ($r = 0.70$, $p < 0.05$) (Table 2; Fig. 4). This suggests that regardless of the ecosystem and state of jellyfish material (e.g., homogenate vs. freeze-dried material) the accumulation rate

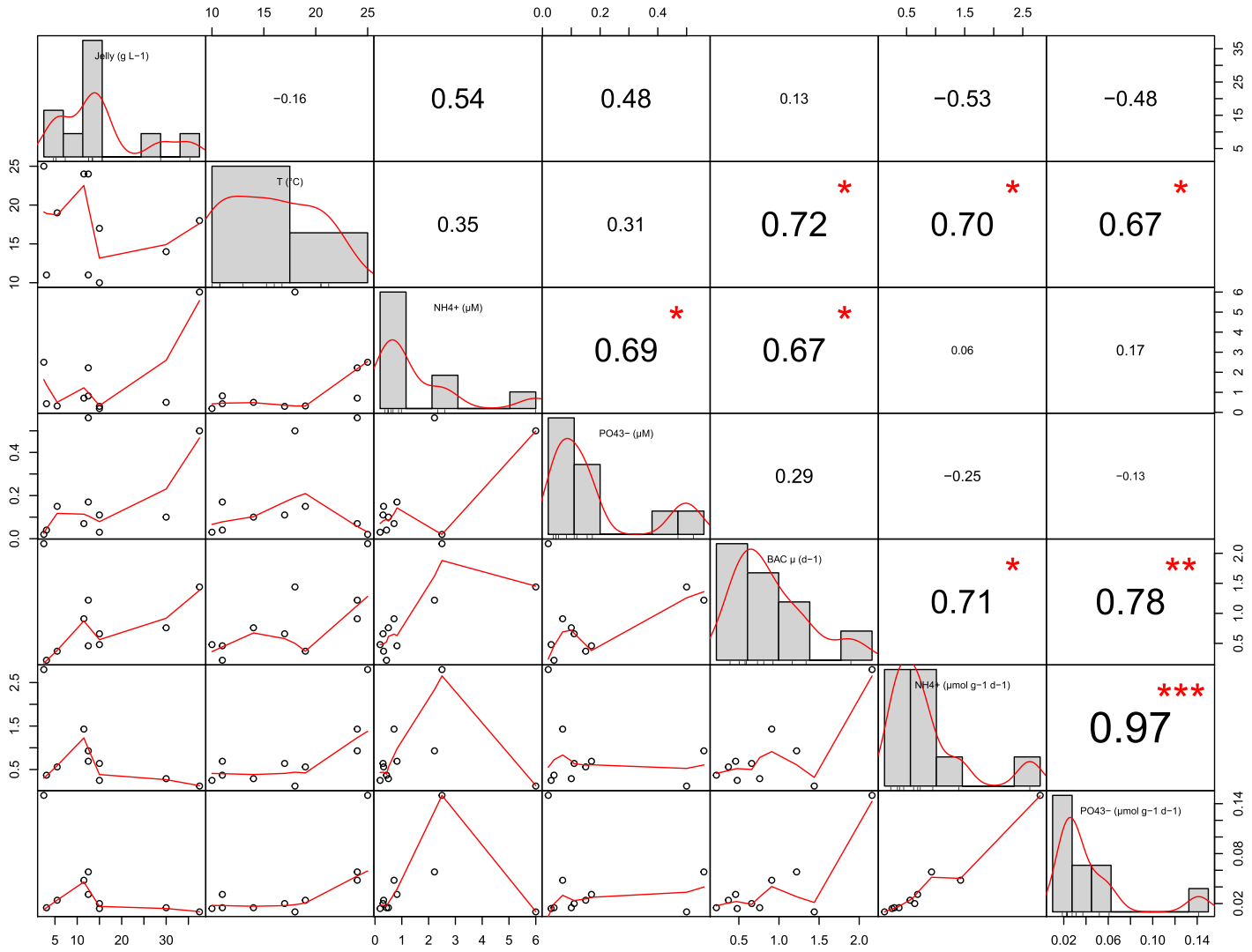

Fig. 4. Histograms of variables with matrix visualizing Pearson's correlations and their significance (*p*-values 0.001, 0.01, 0.05 are marked with symbols "***," "**," "*", respectively) among wet weight of jellyfish (Jelly, g L^{-1}), ambient seawater temperature (*T*,°C), ambient concentration of NH_4^+ and PO_4^{3-} (μmol L^{-1}), bacteria growth rates (BAC μ, h^{-1}), accumulation rate of NH_4^+ and PO_4^{3-} per g jellyfish (wet weight) per day (μmol g^{-1} d^{-1}) based on data from studies listed in Table 2.

of NH_4^+ per g of jellyfish matter, as a measure of the degradation of the proteinaceous, N-rich fraction of jellyfish detritus, correlates with bacterial growth rates, which depends on ambient seawater temperature, in turn, affecting bacterial metabolism. The accumulation of PO_4^{3-}correlates with the bacterial growth rate (r = 0.78, $p < 0.01$) and ambient seawater temperature (r = 67, $p < 0.05$), with important implications for the surrounding ecosystems, that is, fueling primary production, in particular in P-limited coastal ecosystem (Table 2; Fig. 4).

In summary, the microbial decay of jellyfish blooms might alter the functioning and community composition of marine food webs, ultimately also affecting human health via supporting growth of potential pathogens (Basso et al. 2019; Tinta et al. 2019). In addition, microbial remineralization of jellyfish-derived DOM may have an important impact on the marine carbon, nitrogen and phosphorus cycle and oxygen conditions, in particular, during the decay of major jellyfish bloom events in coastal ecosystems. However, major players within the jellyfish degrading microbial community, their metabolic activities and functional traits and the exact processes and mechanisms of microbial jelly-OM transformation and microbial remineralization rates of different jellyfish-derived compounds remain largely unknown.

Future challenges

The above-described state of knowledge emphasizes the need to study jellyfish as an important but inadequately characterized source of OM and to investigate the fate of jellyfish-derived OM in the ocean. In particular, the link between

jellyfish and microorganisms as final recipients and recyclers of the oceanic DOM has to be addressed more intensively. Ultimately, this knowledge will improve our understanding of the implications of jellyfish blooms on marine biogeochemical cycles, to predict the response of marine ecosystems to this natural and/or anthropogenic perturbation and to more accurately incorporate jellyfish into global biogeochemical budgets and its flux through the oceanic water column and its ultimate deposition at the seafloor. By reviewing the current state of knowledge on jellyfish—microbe interactions, we recognized several gaps to be addressed in the future.

1. The effort to comprehensively monitor the abundance of jellyfish global biomass should increase in the future, by increasing sampling effort and via the implementation of newly developed tools for in situ observations.

2. The biochemical complexity of the OM encapsulated in and released by the vast diversity of different jellyfish species remains to be fully explored and the investigations have to be scaled down to the molecular level, that is, the scale relevant for microbes mediating biochemical reactions (e.g., by screening of jellyfish and ctenophore transcriptomes and proteomes). Also, as jelly-OM most likely represents a significant fraction of the global ocean's DOM pool, the molecular level analyses of this largely unidentified organic material per se will contribute to our understanding of the complexity of the ocean's DOM pool.

3. Due to compositional and stoichiometric differences of OM stored in jellyfish biomass and released by living jellyfish, the two jelly-OM pools (POM vs. DOM) should be treated as separate entities in terms of their implications for biogeochemical cycles and functioning of marine ecosystem.

4. The fate of jellyfish detritus in the ocean depends on several factors that remain to be fully elucidated. This knowledge will improve the flux estimates of jellyfish carbon and nitrogen to different depth layers of the oceanic water column and allow us to better constrain the amount of jellyfish biomass deposited at the seafloor and hence determine its impact on the benthos.

5. The large differences in the biochemical composition and life style of different jellyfish species as well as the specific characteristics of the habitats they inhabit suggest that a universal jellyfish-OM (microbial) decay rate cannot be applied on a global scale. This highlights the necessity to expand our explorations to different jellyfish species from diverse marine environments in a more standardized and comprehensive way.

6. The link between jellyfish-derived OM and microbes has to be further investigated using state-of-the-art approaches in marine microbial ecology, coupling -omics with the characterization of the OM pool at the individual compound level. This will provide a better understanding of the metabolic networks operated by the jellyfish-OM degrading microbial community and of the implication of microbial processing of jellyfish-derived OM for the biogeochemical state and functioning of marine ecosystems.

Data availability statement

All data needed to evaluate the conclusions of the paper are present in the paper. Additional data related to this paper may be requested from the authors.

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Conflict of Interest

None declared.

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