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Missing links in the study of solute and particle exchange between the sea floor and water column

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Abstract:

Exchanges of solutes and solids between the sea floor and water column are a vital component of ecosystem functioning in marine habitats around the globe. On the coastal shelf, their influence is especially vital given that shallow water depths facilitate connectivity throughout the entire water column, down to the seafloor. This review explores particle and solute exchange processes, the different mechanisms through which they interact at the ecosystem level, as well as their interdependencies. Throughout the wide range of solute and particle exchange processes, each of them is highly dependent on the characteristics of the physical, chemical and biological environment within which it takes place. Exchange is driven directly by a number of factors, which are identified in this review and may be moderated by others, such as currents, granulometry, nutrient and matter inputs, as well as living organisms. In turn, the occurrence of exchanges can influence adjacent environments and organisms. Major gaps in the present knowledge include the temporal and spatial variation in many of the processes driving benthic/pelagic exchange processes and the variability in the relative importance of individual processes caused by this variation. Furthermore the accurate assessment of some anthropogenic impacts is deemed questionable due to a lack of baseline data, and long-term effects of anthropogenic actions are often unknown. It is suggested that future research should be transdisciplinary and at ecosystem level wherever possible, and that baseline surveys should be implemented and long-term observatories established in order to fill the current knowledge gaps.

Main text:

More than 70% of the Earth's surface is covered by water. If the water were to be removed, marine sediments would cover more global surface area than all other ecosystems combined (Snelgrove *et al.*, 1999). This marine benthos (sea floor) can have extremely varied geological, physical and chemical characteristics and supports a diverse range of life forms. It also acts as an important source and sink of energy and matter which are exchanged with the overlying water (Morris and Howarth, 1998). Thanks to new technologies, tackling formerly inaccessible areas of the ocean, it is now known that the benthos is an important asset of marine ecosystems globally, which is tightly coupled with other marine environments (*e.g.* Marcus and Boero, 1998; Navarrete *et al.*, 2005). In this review, this connection of benthic and pelagic (water column) environments will be explored by assessing exchange processes between the two.

A wide diversity of physically and biologically mediated benthic/pelagic solute and particle exchanges (hereafter "B/P exchanges") exists. The potential for, and nature and magnitude of, B/P exchanges depends strongly upon the physical characteristics of the sediment, such as its grain size, cohesion, permeability and porosity (Kalnejais, Martin and Bothner, 2010). A sediment bed may be described as cohesive when it contains at least 10 - 30 % clay and / or silt content, particles which are less than 63 µm in grain size; and non-cohesive otherwise (Winterwerp, 2011). Permeable sediment can be defined as having a permeability of greater than 10^{-12} m^2 (see Huettel, Berg and Kostka, 2014). While cohesion mostly affects particle exchange processes, more permeable environments have larger solute exchange potentials. Sediment properties may in turn be modified through physical and biologically mediated sediment mixing and ventilation, thereby passively and actively altering exchange rates (N Volkenborn *et al.*, 2010). In many cases the effects of biological processes are particularly influential in the absence of large-scale physical disturbances (*e.g.* Widdows *et al.*, 1998;

Andersen and Pejrup, 2002; Paarlberg *et al.*, 2005). For instance, the degree of cohesion and fluidizations of sediments may fundamentally reflect the activity of its biological community (Widdicombe and Austen, 1999). In turn, biological communities are often shaped by their physical and chemical environment as many organisms occupy specific niches (Snelgrove, 1999).

In addition to biogenic and physical influences on B/P exchanges, anthropogenic (human) interventions can also play an important role. The effects of anthropogenic interaction with the marine environment are often synchronous and can act synergistically, making it difficult to put preventative and counter-active measures in place (Caddy, 2000). Impacts are not only concentrated in coastal shelf areas where anthropogenic activity is prevalent, but can be spread further (Martín *et al.*, 2008). For example, the form and extent of effects of bottom trawling on benthic communities is also dependent on the respective sediment types they occur in, which also in themselves affected by this activity (Hiddink *et al.*, 2006; Queirós *et al.*, 2006; Hale *et al.*, 2017).The relative impact of anthropogenic interferences compared to naturally occurring processes on B/P exchanges can thus be hard to quantify, as the two can have similar consequences (Pusceddu *et al.*, 2005) but cause different effects on different types of organisms? (*e.g.* on meiofauna: Schratzberger *et al.*, 2009; and macrofauna: Fang *et al.*, 2019).

In the course of this review, the complexity of particle and solute B/P exchange processes, as well as particular driver interactions will be explored. Solute and particle exchanges will be reviewed individually, with solute exchange subsections designed to highlights the main drivers of exchange, and particulate exchange subsections structured to highlight downward and upward directed exchange processes. Interdependencies between solute and particle specific processes will be explored using the example of organic matter cycling, which is a biologically vital process that crucially depends on both types of exchange. Knowledge gaps in the current research will be highlighted throughout each section and finally reviewed in combination with recommendations for future research.

1. Solutes

Solutes in the marine environment can broadly be defined as substances dissolved in sea water. Throughout the water column, solutes may be transported through eddy and molecular diffusion (Boudreau 2001), as well as convection (Webster *et al.*, 1996). When biologically important elements such as Oxygen (O_2), Carbon (C) and Nitrogen (N) are in solution, they are readily available for processes such as respiration, photosynthesis, calcification, diagenesis, and direct nutrient uptake (all of which will be elaborated upon below), which is why their transport across the pelagic and the benthic environments, and exchange between the two, are essential.

O_2 is perhaps the most biologically important solute moving across the sediment-water interface. The depth to which O_2 penetrates the sediment controls the depth-distribution of O_2-dependent biogeochemical oxidation reactions, such as nitrification and sulphide oxidation (Rysgaard *et al.*, 1994), as well as the oxidisation of organic matter (OM; Cai and Sayles, 1996). On the whole, the availability of dissolved oxygen in sediment drives aerobic OM degradation rates, a reduction of the concentration of dissolved organic C, and can decrease molecular dissolved OM diversity (Seidel *et al.*, 2015). O_2-driven diagenesis (mineralisation, dissolution and geo-polymerisation during burial; Lindqvist, 2014) is intensified in the presence of marine organisms, which produce enzymes that catalyse those reactions (Lindqvist, 2014). In the absence of biological interactions, the penetration depth of O_2 in the sediment has been shown to depend on the O_2 concentration in the overlying water (Revsbech and Jorgensen, 1980; Rasmussen and Jorgensen, 1992). Anthropogenic disturbance, such as trawling, can cause a reduction in dissolved O_2 (Tiano *et al.*, 2019). The displacement of the oxygenated sedimentary surface layer through trawling equipment lessens biogenic O_2 consumption and causes deeper O_2 penetration depths in the affected areas, thereby effectively changing the sedimentary biogeochemical environment (Tiano *et al.*, 2019).

Nutrients are another ecologically important solute group in the marine system, as their availability and cycling throughout the environment can be limiting to many organisms (*e.g.* Howarth, 1988). Intermittence in nutrient concentrations in the water column, and thus at the sediment water interface, is driven, among other processes, by seasonal changes in temperature (Pomeroy and Deibel, 1986), fluvial and terrestrial input (Justic *et al.*, 1995; Burnett *et al.*, 2003; Milliman and Farnsworth, 2013), water column mixing, and sea bed resuspension. The latter is often initiated by stochastic storm events (Corte *et al.*, 2017). Temporal patterns of denitrification and nutrient flux dynamics also depend upon the sediment type, as sandy sediments exhibit seasonal changes primarily driven by temperature and irradiation, while silty sediments are additionally influenced by aforementioned stochastic resuspension events (Seidel *et al.*, 2015) and meteorologically induced upwelling events (MacIntyre, 1998). The resulting supply of nutrients from the benthos to the pelagic environment is a crucial factor controlling phytoplankton blooms at times of the year when the water column is not stratified in non-eutrophic systems, as the mixing of water from depth and surface layers can place nutrients from benthic sources within reach of the pelagic organisms (Barnes *et al.*, 2015). This, in turn, fuels zooplankton productivity and can give rise to knock-on effects throughout the entire marine food web (Eloire *et al.*, 2010). Increased pelagic productivity, on the other hand, leads to increased nutrient influx rates to the benthos from sinking OM, which is why the benthic community and its activity typically flourish in response to large seasonal plankton blooms (*e.g.* Queiros *et al.*, 2015; Tait *et al.*, 2015). Other nutrient sources to benthic sediment-water interactions include atmospheric input

(Krishnamurthy *et al.*, 2010), anthropogenic terrestrial sources (Justic *et al.*, 1995; Burnett *et al.*, 2003), dredge-spoil dumps (*e.g.* Harvey, Gauthier and Munro, 1998), as well as the addition of dead cells and faecal pellets from pelagic organisms, sinking onto the sea floor (van Duyl *et al.*, 1992). The relative impact of each of these depends on factors such as proximity to the coast and the extent of local pelagic primary productivity, and lateral transport fuelled by circulation patterns can alter their relative importance (*e.g.* Walsh, 1991; Williams and Follows, 1998). Most of the organically available nutrients near the seafloor are extracted and processed diagenetically by the benthic microbial community, or directly consumed by deposit and suspension feeding fauna, degrading and mineralising the floccules' contents. The latter can generally be described as the return of nitrogen (N) and phosphorous (P) to inorganic forms after having been incorporated in organic molecules, or (re-)mineralisation (Williams and del Giorgio, 2005). Within the sediment, diagenesis is fuelled by the enrichment of the sediment matrix with O_2 (Emerson and Hedges, 2003).

The B/P exchange of not only O_2 and nutrients but of all solutes is governed by a number of direct and indirect drivers (Figure 1), and the current understanding of each in the literature will be detailed throughout this section.

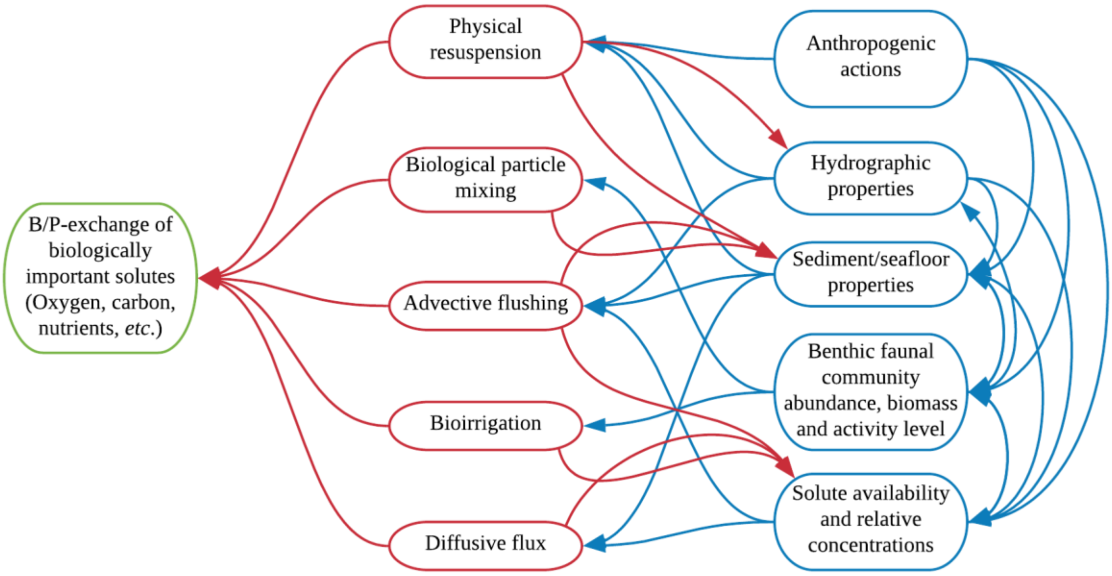

Figure 1: Flowchart of direct (red) and indirect (blue) drivers of solute B/P exchange (green); arrows indicate which factors affect others and are colour-coordinated with the driver they originate from.

It is difficult to definitively determine the relative importance of the different driver groups and important factors within each on B/P, as they can be highly variable across spatial and temporal scales. Seasonal variation, for example, can cause shifts in the relative importance of biological and physical influences (Howarth *et al.*, 1993; Schlüter *et al.*, 2000); biogenically induced spatial variation in sediment properties can cause differences in the main drivers of solute B/P exchange on both small (Wethey and Woodin, 2005) and large (Fang *et al.*, 2019) spatial scales. This variability constitutes a knowledge gap which has to be filled on a situational basis, specific to the system, location and time period of each study within which such processes are investigated. For the purposes of this review, the main drivers of solute B/P exchange are therefore elaborated upon in no particular order.

1.1 Diffusive flux

Water close to the sediment surface within the benthic boundary layer is directly affected by friction at the seabed, which promotes solute transport *via* diffusion. Cohesive sediments, with high clay content, tend to be more difficult to percolate due to a generally smaller degree of permeability, thus impeding the flux of solutes (Yang and Aplin, 2010; though this is not necessarily true for cohesive environments with low clay content, see *e.g.* Winterwerp and Kesteren, 2004). In such conditions, molecular diffusion of pore-water solutes across the sediment-water interface prevails, leading to more gradual solute fluxes (Berner, 1980; Forster *et al.*, 1999) in the form of ion transfer between pore water and near-bottom water or as a result of the reactivity of solid surfaces (Kalnejais, Martin and Bothner, 2010). Other physical environmental variables, such as pressure differentials driven by tides, have been shown to lead to short-term temporal variability of diffusive fluxes (Van Der Kamp and Gale, 1983). The potential depth of diffusive processes is, theoretically, only limited by time. In some cases, however, diffusive distances can be altered, driven, and extended through an increase in sediment permeability, promoted by benthic biological activity. Sedimentary O_2 uptake, for instance, is only a function of physical penetration depth, which is determined by time in the absence of biological activity and organic matter (Revsbech and Jorgensen, 1980). What is hitherto unknown is whether there are ways in which biological or anthropogenic interactions may be directly inhibitive of solute diffusion across the sediment-water interface. As diffusion does not necessarily occur in isolation from other drivers of solute exchange, a differentiation between relative contributions of each driver would be of interest to correctly quantify each pathway. However, while the balance between, for example diffusive and advective solute B/P exchange, may be calculated in theory (Anderson and Cherry, 1979; Taigbenu and Liggett, 1986), in-situ measurements that take both into account and clearly differentiate between their respective contributions have so far not been successful.

1.2 Advection and physical resuspension

Abiotically driven fluctuations into (and out of) the sediment matrix can also occur through mechanically-driven water transfer into and out of the sediment pores. With increasing shear stress and turbulence, benthic boundary layer thickness typically decreases (though there are some exceptions) and with it the resistance of solute transfers into and out of the sediment (Lohse *et al.*, 1996b). This decline continues into the top sediment layers (Ahmerkamp *et al.*, 2017). In turbulent conditions, under strong enough shear stress or in the presence of sediment surface obstacles, solute transport is prevalent through advection and physical resuspension. Obstacles can include protruding solid objects (rocks, shells, *etc.*), man-made structures, biogenic sediment structures (*e.g.* polychaete tubes) or simply a three-dimensional bedform, all of which lead to pressure differentials that drive water through the sediment and significantly enhance the exchange of solutes (Huettel and Gust, 1992; Ziebis, Huettel and Forster, 1996; Hutchinson and Webster, 1998). The flushing action from advective processes can winnow smaller particles from the sediment matrix, leading to an overall coarser environment which can be percolated more easily (Malarkey *et al.*, 2015) and the less cohesive and more permeable the seabed is, the more likely is the occurrence of active ejections of solutes into the water column through physically driven advective currents (Lohse *et al.*, 1996a; Cook *et al.*, 2007). Resuspension events, driven by either biological activity or abiotic interactions, can enhance solute exchange processes through an increase of the sediment surface area availability for dissolution through placement of particulates in the water column, re-oxygenation of formerly diagenized elements, and the direct flushing out of interstitial water (Morse, 1994; Morin and Morse, 1999; Saulnier and Mucci, 2000; Kalnejais, Martin and Bothner, 2010). Turbulent hydrodynamic forces close to the sea bed thus catalyse the oxygenation of the surface sediment layers through partial resuspension as well as flushing action (Malan and McLachlan, 1991; Couceiro *et al.*, 2013). And B/P solute exchange through physical processes, such as advection and resuspension, further contributes to the breaking down of OM and subsequent supply of biologically important solutes (Franke *et al.*, 2006). In intertidal sandy areas, for example, which typically contain low concentrations of particulate OM due to seasonal hydrodynamic removal (POM; Rusch, Huettel and Forster, 2000), pore-water nutrients may be supplemented through advective flushing (Seidel *et al.*, 2015).

Clearly, although there already is a large body of literature covering physically-driven solute exchange processes, there are still areas requiring further exploration. Temporal variability of advective transport, for instance, is poorly understood and has therefore so far not been taken into account in most studies (Cook *et al.*, 2007). As the hydrographic drivers of advection and resuspension may be consistent (*e.g.* currents), and/or regularly occurring (*e.g.* tidal flow), and/or stochastic in nature (*e.g.* storm events), even in-situ measurements only capture a snapshot of events, and the potential overlap between time-scales impedes our ability to differentiate between them. Long-term monitoring of physically-driven B/P solute exchanges may offer a solution to this, though so far this has not been undertaken. The extent to which boundary layer flow dynamics impact physically driven solute B/P exchange has also yet to be definitively quantified, especially in an in-situ context, including physical and biological interactions.

1.3 Bioirrigation and biological particle mixing

Biological mediation of solute exchange across the sediment-water interface is constant and inherent to sedimentary life, but in environments in which physically mediated transport is minimal, processes such as faunal flushing of pore waters can determine the rate and characteristics of B/P exchange of solutes (Mermillod-Blondin and Rosenberg, 2006; Volkenborn *et al.*, 2010). In addition, the sediment depth to which solutes are transported biologically can be multiple times that which may be reached through purely physical means

(Volkenborn *et al.*, 2010). The biological exchange of solutes can take the form of bioirrigation, the active displacement of liquid and solutes by benthic organisms (Volkenborn *et al.*, 2007a) linked to respiration, metabolite excretion, and other individual-based processes; or bio-advection, the induction of additional pore water through burrowing organisms' physical activity into the surrounding sediment (Volkenborn *et al.*, 2012). Biologically mediated exchange rates strongly depend on the characteristics of the associated faunal and microbial community (see *e.g.* Waldbusser *et al.*, 2004). Both bioirrigation and bio-advection are at least equally as important as, and often largely exceed, the rates of molecular diffusion in the upper sediment layers of biogenic environments (Berg *et al.*, 2001). The large spatial extent to which the hydraulic forces generated by bioadvectors and bioirrigators propagate through the sediment can lead to effects which far exceed the immediate vicinity of their burrows (Wethey and Woodin, 2005). This can in some instances have significant effects at the landscape scale (Fang *et al.*, 2019), though more often it leads to small-scale spatial variation with hot-spots of altered oxygenation nutrient and carbon concentrations in the immediate vicinity of the bioirrigative activity. The release of O_2 from root systems in submerged macrophytes can even create three-dimensional spatial variability of variable diffusion potential and solute distribution (Sand-Jensen, Prahl and Stokholm, 1982).

Pore-water O_2 content in particular is typically increased through bio-advection (N Volkenborn *et al.*, 2010; Volkenborn *et al.*, 2012) as many burrowing animals actively oxygenate the surrounding sediment by ventilating their burrows with bottom water (Volkenborn *et al.*, 2007a). Due to this, the thickness and volume of the sedimentary oxidising phase is largely extended, thus ameliorating conditions and promoting the occurrence of other aerobic life forms (Mermillod-Blondin and Rosenberg, 2006; Glud, 2008). This can in some cases lead to seasonal variations in O_2 availability linked to organisms' own seasonal life-cycle processes (Glud *et al.*, 2003). Significant variation is also observed between sediment types (Hicks *et al.*, 2017) . Through the particle movement and disruption of sediment layering, biogenic particle mixing (bioturbation) strengthens B/P coupling as it increases fluxes of nutrients, metals, C, O_2 and other micro-particles which would otherwise remain buried (Caliman *et al.*, 2007; Hale *et al.*, 2017). At the local scale, the presence of infaunal bioturbators has been shown to increase natural denitrification rates by at least 160% (Gilbert, Stora and Bonin, 1998). Generally, N-mineralisation rates are faster in more permeable substrates and may be enhanced by macrofauna influence, irrespective of organic enrichments, due to the O_2 enrichment (Hansen and Kristensen, 1998; Huettel, Berg and Kostka, 2014). The associated modified supply of nutrients can also strongly affect microbial community structure (Yingst and Rhoads, 1980). This can be traced back to a combination of factors, one of which is the input of macrofaunal metabolic waste products which provides additional sources of nutrients to microbial communities (*e.g.* Reichardt, 1988) thereby adding to the overall flux and cycling of solutes, and their bio-catalysing effects on the microbial community (*e.g.* Yazdani Foshtomi *et al.*, 2015). The polysaccharide protein lining the burrows of many invertebrates has a filtering effect on the water flushing across and through it, affects exchange processes by preferentially selecting against anionic solutes due to their own net negative charge (Aller, 1983). Burrowing macrofauna can in some cases actively culture the microbial community associated with their burrows which then in turn affects the rates and direction of solute exchange within the burrows (Kristensen, 1988). Fishing pressure can passively affect C and nutrient fluxes mediated by benthic macrofauna by altering the community composition, though these effects are mediated by sediment type and the kind of fishing gear deployed (Hale *et al.*, 2017). Changes in benthic community can also be induced through the installation of offshore wind farms (Coates *et al.*, 2014) and other solid substrates or through dredging (*e.g.* Thrush *et al.*, 1995). Sources of pollution can affect benthic community diversity (*e.g*. Kingston, 1992) and thereby also passively lower biogenic B/P solute exchange rates.

Due to many organisms' temporally variable behaviours, rates of biologically mediated solute transport can vary on scales of minutes to seasons (*e.g.* Schlüter *et al.,* 2000). Despite this seasonality being a well-studied phenomenon, there is an important consideration that has thus far not been investigated: The assumption and assessment that in some areas physical pressures are strong enough to drown out the effects of biological processes (as assumed in *e.g*. Andersen *et al.*, 2002; Paarlberg *et al.*, 2005) may not be true at all times as the balance may swing the other way during biologically active seasons. This is a crucial knowledge gap which warrants further research. Spatial variability too should be considered more often when assessing the relative importance of physical *versus* biological drivers of B/P exchange, as small scale patchiness and large scale B/P exchange budgets may differ.

2. Particles

In contrast to solutes, particles are not transported uniformly as they occur in a variety of materials, sizes, shapes and concentrations. Particle exchange between benthic and pelagic environments may be driven by water flow, occurring regularly (such as through currents or tides); stochastically (such as through storm events and faunal activity); or *via* direct disturbance of the sea bed through biological activity or anthropogenic interference. Biologically and physically mediated particle transport processes often occur simultaneously and non-independently from one another, on separate or concurrent spatial and temporal scales. Within the sediment, particle reworking occurs mainly through sources of biotic and abiotic mixing rather than resuspension and deposition. The main drivers of exchange between the seabed and the water column can be grouped into upward transport from the benthos to the pelagic environment, in the form of resuspension; and downward transport from the pelagic environment to the benthos through deposition (Figure 2). These two routes include various biological, physical and anthropogenic pathways, which will be elucidated in this section.

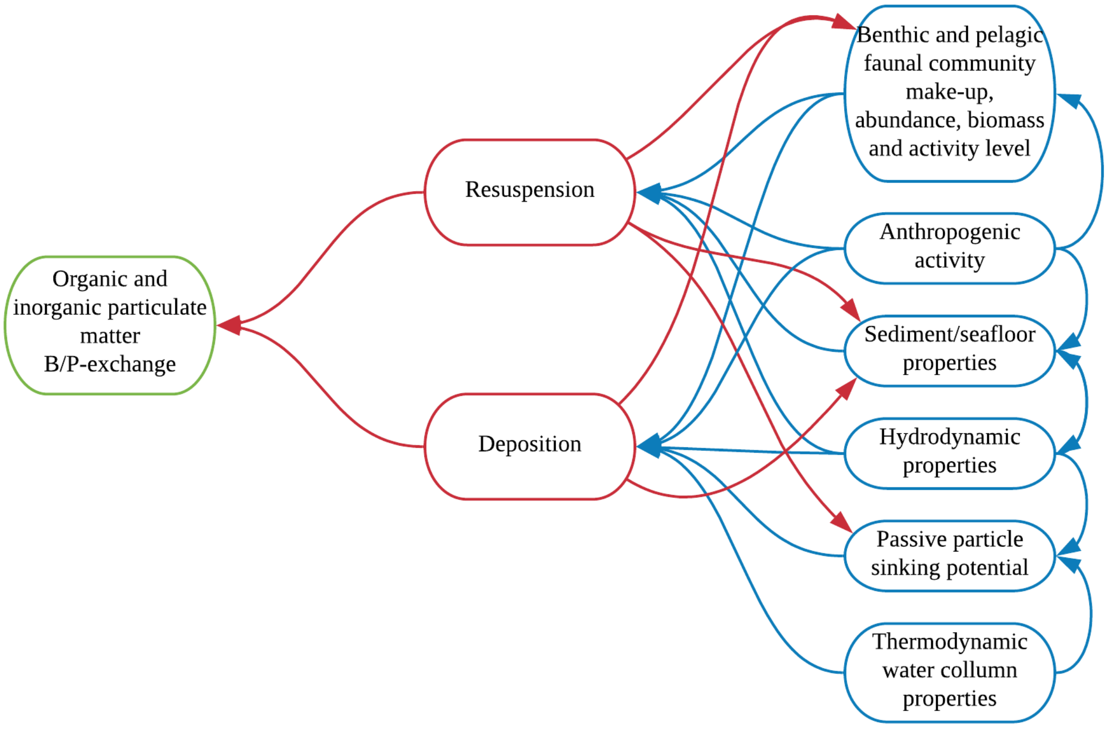

Figure 2: Flowchart of direct (red) and indirect (blue) drivers of particle B/P exchange; arrows indicate which factors affect others and are colour-coordinated with the driver they originate from.

As previously mentioned, the relative importance of individual drivers of B/P exchange is context dependent. The occurrence of large phytoplankton blooms (*e.g* Zhang *et al.*, 2015) or dredge-spoil dumps (*e.g* Moon *et al.*, 1994), for example, leads to an abundance of suspended material, the sinking of which is likely to locally dominate particle exchange processes. In storm-heavy seasons, or during the occurrence of extreme stochastic storm events, on the other hand, upward particle fluxes are likely to be dominant (*e.g* Madsen *et al.*, 1993). Outside of such extreme events, the relative importance of physical and biological drivers of

B/P exchange is dependent on location (*e.g.* Dellapenna, Kuehl and Schaffner, 1998). This situation and location dependence of the relative importance of B/P particle exchange drivers constitutes yet another gap in our knowledge of these processes. Past studies may be used to estimate each driver's importance to warrant its inclusion in future studies, though this assessment has to be made in each instance, taking into account the scale, location and timing of the sampling effort, as well as the occurrence of extreme events close to the time of sampling (Hewitt *et al.*, 2007). Because of this complexity, and for the sake of simplicity, these drivers of particle exchange are reviewed subsequently moving focus from the water column and towards the sediment, without necessarily reflecting their relative importance.

2.1 Downward flux and deposition

Throughout the water column, particles stay in suspension when the ascending vertical components of turbulent eddy velocity fluctuation are greater than the corresponding particle settling velocity (Komar, 1976b, 1976a). Physical and chemical barriers in the water column, for instance in the form of haloclines and thermoclines, can change and inhibit the rates at which matter fluctuates from the water column to the benthos and *vice versa* (*e.g.* Biggs and Wetzel, 1968; Qiao et al., 2011). While dissolved matter can still readily diffuse across the thermocline (*e.g.* Emerson et al., 1997), particulate matter up to a critical negative buoyancy threshold is unlikely to cross a thermodynamic barrier. In the majority of cases, the deposition of particles occurs in combination with other processes; turbulence and upward-mixing can make the settling process considerably unpredictable (Winterwerp and Kesteren, 2004). Mass settling flux may thus be defined as a product of matter concentration and settling velocity (Manning and Bass, 2006). The latter is mainly affected by the size and density in which OM flocs occur (Maa and Kwon, 2007) while the former depends on the rates at which particles are supplied through resuspension or release within the water column. In cohesive sediment settling conditions, high concentrations of suspended particles may flocculate while in suspension (Einstein and Krone, 1962; Stolzenbach and Elimelech, 1994). Flocculation is a constant yet dynamic balance of aggregation and disaggregation (Tsai, Iacobellis and Lick, 1987) driven by physical or chemical attraction, and particle polydispersity (Sun, Xiao and Sun, 2017). The typical primary source of cohesion and hence flocculation is the effect of salinity on charged clay particles through mass-attractive London-van der Waals forces and electrostatic bonding, though this may not be the most important factor driving flocculation in a biological context (Parsons *et al.*, 2016). Flocculated particles are relatively large in size and tend to settle more readily than primary particles, depending on their size and density, but may be broken up again easily by applied shear stress (Winterwerp, 2011). Regardless of particle size or nature, materials can be moved around the water column through turbulent water flow and trapped in biological (*e.g.* Gambi, Nowell and Jumars, 1990) or man-made (*e.g.* Simons and Şentürk, 1992) near-bottom structures. Lateral transport throughout water bodies can be hard to track and only some studies attempt to trace the origins of suspended matter collected in sediment traps (*e.g.* Narita, Harada and Tsunogai, 1990). There is much to discover yet about the sources of suspended particulates and the pathways they take through the water column.

Biological drivers of particle deposition can act both actively and passively. Some zooplankton groups, such as Copepods, migrate vertically through the water column on a diurnal basis. The transport of organic matter through diel vertical migration constitutes an active downward transport, as organisms come towards the upper water layers to feed at night and return to deeper water where the organic matter is returned to the system in the form of excretions, or as decaying carcasses (Packard and Gómez, 2013). The presence of organic matter and micro-organisms suspended in the water column (generally termed ‘marine snow’) can enhance benthic community metabolism rates and nutrient mineralisation (van Duyl *et al.*, 1992). Marine snow aggregates can include any combination of dead and living matter of highly variable spatial complexity, density and consequently, sinking rate (Alldredge and Gotschalk, 1988). It serves as a microhabitat and food source to pelagic organisms during its sinking (Lundgaard *et al.*, 2017) and is a source of organic matter to benthic organisms (*e.g.* Townsend *et al.*, 1992). In low turbulence, fluff-like organic matter which is not immediately incorporated into the sediment matrix may form a layer which rests on the sediment surface along with fine sediment particles (termed nepheloid layer; *e.g.* Durrieu De Madron *et al.*, 2017). Within this layer, particulates may be transported laterally across large distances and even exported off the continental shelf (Inthorn *et al.*, 2006). Particle residence times within the nepheloid layer can be vast and warrant further study.

Deposition of particulate matter on the seafloor is catalysed by roughness elements which result in interfacial flow dynamics, and cause descending vertical sweeps (Huettel, Ziebis and Forster, 1996). Biogenic structures, such as bivalve byssal structures and seagrasss blades, can trap suspended particles, reduce near-bed water velocity and increase turbulence in the benthic boundary layer (*e.g.* Widdows, Brinsley and Salkeld, 1998). In addition, filter feeders can actively move water, and the particles suspended in it, towards the sea floor, causing increased particle fluxes towards the benthos, preventing subsequent resuspension through ingestion, trapping in structures (such as tubes and gills), and pelletization of the descended matter (*e.g.* Widdows, Brinsley and Salkeld, 1998; Denis, Desroy and Ropert, 2007). Selective sediment particle processing, through the actions of biodiffusing bivalves for example, can lead to long-lasting changes in granulometry over large spatial scales, thereby changing the environment and creating specific habitats for other organisms (Montserrat *et al.*, 2009). Around mussel beds, biodeposition is further catalysed and accelerated through the production of pseudo-faeces, which leads to an increase in annual deposition of sediment, C and nutrients (Kautsky and Evans, 1987). Macroalgae and seagrasses have been shown to shield the sea bed from turbulence and lower water velocities, thereby increasing net deposition rates (Fonseca *et al.*, 1982; Gambi, Nowell and Jumars, 1990). The rate at which this filtering of suspended material flowing through the fronds occurs depends strongly upon the morphology of the macrophytes (Hendrick, Hutchison and Last, 2016). Obstacle-induced flow turbulence can effectively filter suspended particulate matter from the water column by driving parts of the flow through the sediment matrix, thus leading to their deposition within the sediment (Hutchinson and Webster, 1998). B/P exchange may further be affected by animals that increase sediment cohesion by building protruding tubes and byssal mats. These act similarly to sea grass and algal fronds by altering the flow and trapping sediments when they occur in high densities. *Lanice conchilega* presence for example, can lead to a reduction in erosion potential when occurring in high enough densities (Denis, Desroy and Ropert, 2007; Borsje *et al.*, 2014). The addition of small particles to the sediment matrix through active or passive filtering may lead to a change in sediment granulometry and, effectively, cohesion (*e.g.* Widdows *et al.*, 2000; Volkenborn, Polerecky, Hedtkamp, van Beusekom, *et al.*, 2007b). During the deposition of already cohesive sediments, though particles of all sizes may be deposited (Lau and Krishnappan, 1994), a sorting process can occur thus leading to vertical and horizontal particle size gradients (Mehta, 1988).

The availability of depositable particulate material in the water column may also be affected by anthropogenic structures and actions, including dredge-spoil dumping (Moon *et al.*, 1994; Pilskaln, Churchill and Mayer, 1998; Mikkelsen and Pejrup, 2000) and the installation of off-shore wind farms (Baeye *et al.*, 2011; Coates *et al.*, 2014; Dannheim *et al.*, 2019). Although the former constitutes a rapid and intense input of non-native particulate matter to the water column, this does not always affect the benthic community or local sediment properties directly (Smith and Rule, 2001). It can however introduce additional organic carbon and new species to the dredged site (Morton, 1977; Wildish and Thomas, 1985) which is likely to have knock-on effects on the biogeochemical composition of the affected environments and B/P exchange potentials. Although some monitoring studies have investigated short to medium term effects of dredge-spoil dumping on drivers of B/P exchange, few of these studies include an adequate assessment of the benthic environment prior to the commencement of the dumping and the number of long-term monitoring studies to date is insufficient to draw meaningful conclusions. Other activities, such as active bottom fishing practices (dredging, trawling), can also cause increases in SPM. For instance, trawling can increase SPM concentrations up to six times that of the background levels (Tiano *et al.*, 2019). In the case of offshore wind farms, SPM plumes up to five times the background level in concentration have been shown to be generated through tidal resuspension of fine grained materials accumulated and produced by epifauna associated with the wind farms' solid structures (Baeye and Fettweis, 2015). The changes in granulometry and organic matter content in the sediment (Coates *et al.*, 2014) are mostly attributable to the fauna's filtering activity and the production of faeces and pseudofaeces which can lead to a shift in microbenthic community structure and diversity. Additionally, the solid structures constituting the wind turbine's foundations introduce roughness elements to the water column, thereby creating eddies, vortexes and turbulent flow dynamics and increasing the probability of resuspension (Grashorn and Stanev, 2016). Considering the extensive coverage of offshore wind farms in some areas, such as throughout the North Sea, this change in circulation, seafloor community and sediment properties may constitute shifts in B/P exchange pathways at large spatial scales.

In contrast to several well-studied offshore wind farms impacts, such as seabird collisions, settlement of encrusting fauna and flora, and electromagnetic disturbances, not much research has been carried out to test their effects on B/P exchange processes (Dannheim *et al.*, 2019). Furthermore, the investigation of anthropogenic impacts often happens in retrospect and the addition of more baseline studies would undoubtedly add much to our understanding of anthropogenic impacts on particle deposition.

2.2 Upward flux and resuspension

Particle deposition is rarely final, as particulates can be eroded away from the sediment surface. Generally speaking, the erosion of non-cohesive sediments is constant with applied shear stress and a product of fluid stresses and grain stresses only affected by the excess shear stress, bed roughness, grain size and orientation, particle sorting and packing and bed configuration (Julien, 2010). On an exclusively physical basis, low level forces applied to the sediment lead to rolling or sliding of particles along its surface, medium levels prompt a hopping motion called saltation, and strong forces cause particles to be drawn from the bulk sediment into complete suspension. In turbulent environments, particles exchange momentum with the surrounding fluids and are thereby swept across or ejected from the sediment surface (Gordon, 1974; Kassem *et al.*, 2015). Physical erosion patterns in cohesive environments depend strongly upon the way in which the bed was originally formed (Ariathurai and Arulanandan, 1978). Erosion processes in cohesive environments are depth-limited and erosion rates are reduced in deeper layers, due to the consolidation of particles with depth (Aberle, Nikora and Walters, 2004). There are three different types of physical erosion (Amos *et al.*, 1992, 1997) and all three may be displayed in parallel in cohesive sediments, making the process notoriously hard to model.

An additional factor which complicates our understanding of the erosion process is the interference of biotic elements. The extracellular polymeric substances (EPS) produced by marine biofilms, for example, reduce the sediment surface roughness and frictional drag, thereby increasing cohesion (Sutherland, Amos and Grant, 1998). EPS distribution throughout the sediment is one of the key components controlling bed form dynamics where it appears in high enough concentrations (Malarkey *et al.*, 2015). There are other biological mechanisms affecting sediment erosion and resuspension such as animal tracking, grazing, (Nowell, Jumars and Eckman, 1981; Borsje, Vries and Boer, 2008; E Kristensen *et al.*, 2012) and faecal pellet production (Andersen and Pejrup, 2002) affecting bed roughness as well as resuspension potentials.

Benthic organisms can also drive transport that counters gravimetric deposition by actively ejecting OM and sediment grains into the water column during feeding and other activities, as well as their gametes and larvae to initiate pelagic stages in their development (*e.g.* the polychaete burrowers *Nereis virens*; Bass and Brafield, 1972). Other organisms known as ecosystem engineers modify, maintain and create habitats by causing physical state changes in biotic or abiotic materials, thereby modulating resource availabilities directly and/or indirectly (*e.g.* reef-building bivalves and macrophytes; Jones, Lawton and Shachak, 1994). The extent to which different areas of the ecosystem in question are impacted depends upon the strength and nature of the respective engineering species (Bouma *et al.*, 2009; Meadows, Meadows and Murray, 2012). They may for example alter their environment and change flow dynamics around the sea bed, thereby altering erosion and deposition rates in various ways (Coleman and Williams, 2002) and thus dictating the sediment type present in an area (Ginsburg and Lowenstam, 1958). Increases in bulk sediment grain size and permeability caused by the bioengineers then promotes altered B/P exchange rates (Ziebis, Huettel and Forster, 1996). Erosion thresholds may also be affected, in some cases seasonally varying between increase and decrease (Grant and Daborn, 1994; Paarlberg *et al.*, 2005). These and other biologically-mediated particle movements can affect particle distributions from micro to landscape scale (Van Hoey *et al.*, 2008; Montserrat *et al.*, 2009).

Bioturbation (the biogenic movement of particulate matter throughout the sediment matrix) can play an important role in localised particle displacement (Berg *et al.*, 2001) as well as landscape scaled effects on particle distributions by affecting sedimentary structure, biogeochemical gradients and fluxes, and the composition of associated communities of auto and heterotrophs (Van Hoey *et al.*, 2008; Bouma *et al.*, 2009; Montserrat *et al.*, 2009). Each bioturbating species may affect particle exchanges differently, depending on their functional traits, mediated by species performance in response to the environment in which they occur (*e.g.* Mermillod-Blondin *et al.*, 2004; Solan *et al.*, 2004; Maire *et al.*, 2006; Braeckman *et al.*, 2010; Ouellette *et al.*, 2012), sediment characteristics (Bernard *et al.*, 2019) and temporal patterns such as seasonal cycles (Queirós *et al.*, 2015). The main impacts bioturbation activity has on upward B/P exchange processes, are a) that it generally destabilizes the sediment, lowering critical erosion and resuspension thresholds in the process (Widdows, Brinsley and Elliott, 1998; De Deckere, Tolhurst and De Brouwer, 2001) and b) the biogenic physical ejection of particulate matter into the water column (Davis, 1993). Co-occurrence of bio-stabilizing and destabilizing organisms is known to have variable effects on sediment matrix properties (Queirós *et al.*, 2011). Such duality may even exist within the effects of a single species, such as has been shown in the deposit-feeder *Peringia ulvae*, which destabilizes sediment surfaces through grazing whilst simultaneously excreting pellets with increased settling velocity compared to the original sediment, thereby having both destabilizing and stabilizing effects (Andersen and Pejrup, 2002). In some cases, an organisms' effect on sediment erosion thresholds may even reverse in sync with seasonal environmental changes, leading to alternating stabilisation and destabilisation of the surrounding sediment (*e.g.* Grant and Daborn, 1994). Overall, the magnitude at which biological processes affect sediment transport and solute exchange is tightly dependent upon the density of active organisms and the magnitude of their effects relative to that of ecosystem attributes or processes also affecting transport of sediment and solutes (Queirós *et al.*, 2011; Erik Kristensen *et al.*, 2012). The net effect of co-occuring biostabilizing and destabilizing benthos, and how this balance may shift on different temporal and spatial scales, has thus far only been investigated in small, location-specific studies and should be investigated at the ecosystem-level.

Once buried, particles may be stored and consolidated or recycled (Graf and Rosenberg, 1997). Within the benthic matrix, the complex materials which are not permanently buried are broken down chemically *via* oxidation and biologically by benthos and bacteria, allowing them to re-enter the cycling of elements. In permeable sediments, even living microphytes may be advectively flushed into deeper sediment layers and trapped there, leaving them to be mineralized more swiftly than they would be at the sediment surface when they die, thereby fuelling the recycling of nutrients and C (Ehrenhauss *et al.*, 2004). Advective flushing of particulate OM throughout permeable sediment distributes it evenly, thereby alleviating concentrated hot spots and spreading the OM to a larger microbial community (Franke *et al.*, 2006). Diagenetic reactions vary in speed and consequently, affect the environment on different scales: very slow reactions occur mostly at depth and are of importance at geological time scales, while rapid ones define the biogeochemical conditions of the benthic boundary layer without having interfered in the sediment matrix at any significant depth (Aller, 2014). The major roles biological processes play in mineralization do not only extend to the direct impacts of microbes which catalyse and drive the process itself but also the effects of larger organisms which modify OM burial rates and contribute to its break-down through grazing (Tait *et al.*, 2015; Queirós *et al.*, 2019). The translocation of particles and potential homogenisation of surface sediment layers as well as the introduction of fresh O_2 and OM to deeper layers by bioturbators, bioirrigators and even benthivores is a crucial determinant of diagenetic processes (Lindqvist, 2014).

Direct anthropogenic causes of particle resuspension include dredging, trawling, mining, anchoring and many others. Repeated dredging can lead to long-term modification of local sediment properties and particle and solute transport rates at the dredged site (Moon *et al.*, 1994; Pilskaln, Churchill and Mayer, 1998; Mikkelsen and Pejrup, 2000) and the use of trawls and similar types of mobile fishing gear can have comparable effects (*e.g.* Palanques, Guillén and Puig, 2001; Jennings and Kaiser, 2006). The removal of fine-grained particles from continental shelves through anthropogenic resuspension on a global scale is estimated to be up to six times as large as it would be through purely natural causes of resuspension, closely matching the input of fine-grained material from riverine sources (Oberle, Storlazzi and Hanebuth, 2016). On a local level however, this may not be the case (*e.g.* Schoellhamer, 2002; Ferré *et al.*, 2008). Mobile fishing gear can furthermore lead to the removal or disruption of micro and macro-phytic communities that would otherwise inhibit resuspension, as well as modification of the benthic macrofauna community composition (Hiddink *et al.*, 2006; Hiddink, Jennings and Kaiser, 2006), and burial of sediment surface chlorophyll a content (Tiano *et al.*, 2019). Biogeochemical impacts of trawling are more pronounced in naturally muddy than in sandy environments (Sciberras *et al.*, 2016), although some sandy sediments are likely to occur due to long-term granulometry changes resulting from chronic bottom trawling pressure (Hiddink *et al.*, 2006). Long-term biogeochemical changes of seafloor habitats associated with anthropogenic interactions, and associated shifts in B/P exchange processes remain, thus far, largely unknown. This is, amongst other reasons, due to a lack of data on baseline conditions collected prior to anthropogenic intervention.

3. Interactions and inter-dependencies

Most of the B-P coupling processes described in this review are difficult to consider individually, as they either interact very closely with others or have a wide range of effects and dependencies, making them hard to assign to any one section. Each is part of a feedback mechanism and interacting with others, thereby producing the overall effect on sediment and water column structures which results in altered rates of sediment and solute transport (Borsje, Vries and Boer, 2008). The combination of interacting processes and the scales at which they affect exchanges between the benthic and pelagic zones varies in accordance with the respective physical and biological environmental conditions, the "ecological context" (Queirós *et al.*, 2011).

Most biologically important processes are dependent on both solute and particle B/P exchanges and interactions. The cycling of organic matter for example, which benthic heterotrophs mediate. Most OM in the marine environment originates from primary producers such as phytoplankton, seaweeds and other macrophytes, which require light and nutrients in solution to grow, the latter being especially important during times and in locations of nutrient depletion (*e.g.* Davis *et al.*, 2019). During phytoplankton growth cycles, both dissolved and particulate OM (DOM and POM) specimens are produced and introduced to the environment surrounding the plankton (Biddanda and Benner, 1997). Each of these OM compounds may be utilized differently, as detailed in the previous sections of this review. While POM may be consumed by secondary producers and then exported towards the benthos, either passively through incorporation in faecal pellets and marine snow floccules, or actively through the vertical migration of the consumers, DOM may stay in suspension. Depending on the hydrological circumstances, the DOM may be fully utilized and degraded by the microbial community within the water column (Mari *et al.*, 2007). Throughout this process, DOM and POM are in constant interaction through a variety of pathways which are complex enough to warrant entire review papers by themselves (*e.g.*Mecozzi, Pietroletti and Conti, 2008; He *et al.*, 2016). Once the OM reaches the sea floor, however, it is utilized by macro and micro-fauna, and/or mineralized by the benthic microbial community (Gooday and Turley, 1990). Both pathways are linked and require an oxidising environment to function, which is where B/P exchange of dissolved O_2 plays an important role (Snelgrove *et al.*, 2018). This brief excursion details only a part of the OM cycling process and highlights how inextricably interlinked solute and particle B/P exchange pathways of C, O_2, nutrients and many more elements are. Due to the complexity of the marine system and associated observation or experimentation, there are still many questions in want of an answer, offering a guiding direction for future research.

4. Future direction

Historically, the exchange of particles and solutes, which were seen as two separate pools of resources, was studied one-dimensionally and often in isolation from other ecosystem processes. This review highlights the shortcomings of this treatment of solutes and particles as separate entities instead of inseparably interwoven parts of the same exchange pathways (see *e.g.* Kristensen *et al.*, 2012). It should be noted that some fields, such as diagenetic research, the assumption of an integrated solute/particle framework has been the status-quo for decades (Berner, 1980), but this has not been the case in many fields, and especially, in benthic ecology. These differences in approach could in many instances be attributable to a lack of interdisciplinary collaborations that require bridging in future work. A separate consideration of solutes and particles may be necessary in the exploration of specific transport mechanisms, but as B/P processes are typically affected by many types of exchanges simultaneously, such one-dimensional studies can only ever represent basic foundational elements on which a higher understanding is built. Rediscovering the ecological complexity and applying it in areas other than diagenetic research will thus lead to a better holistic understanding and predictive ability, regarding both drivers and consequences of B/P exchanges. The insight that observations at the ecosystem level are too complex to be approached in the way most empirical ecological studies have done in the past, is nothing new (Lawton, 1999) and a change of perspective has already been suggested (Thrush *et al.*, 2009). Detailed guidelines have been suggested to aid scientists in their study design in order to allow the extrapolation of empirical study results to broader temporal and spatial scales (Hewitt *et al.*, 2007). This includes advice such as consideration of contextual natural history to estimate expectable heterogeneity, integration of correlative and manipulative study elements, inclusion of iterative measurements between integrative studies, use of continuous explanatory variables during the analysis stage, and finally, the integration of in-situ data and model outputs (Hewitt *et al.*, 2007). Time-series data have been assessed as one of the most useful tools to provide broad scale temporal context to ecosystem processes (Thrush, Pridmore and Hewitt, 1996) such as B/P exchange. Our review highlights that although the awareness of a need for ecosystem-level approaches clearly exists, and individual B/P exchange processes are often well-studied, not all pathways have been explored equally well in the past and the multidimensional, transdisciplinary approach is still not used as the foundation of B/P exchange research, at large. Some gaps, such as the lack of objective rank-ability of the respective relative importance of drivers of solute and particle B/P exchanges require exactly the kind of temporal and spatial ecological context described in the previous paragraph. Information on individual driver processes cannot be balanced or compared with one another without coherent scale and contextual information. Furthermore, while some studies hint at parts of different exchange pathways across the sediment-water interface (*e.g.* Berner, 1980; Glud, 2008; Aller, 2014), there is generally a distinct lack of information regarding the exchanges themselves, and their importance in the greater ecosystem context, as noted in recent work (*e.g.* Middelburg, 2017). The consequence of this shift in perception is that when dissecting any B/P exchange pathway into its individual processes, it becomes apparent that often not all processes involved are well known well enough to allow for the accurate quantification of the entire pathway. Thus, even when consideration of the environmental spatial and temporal context permits a classification of drivers of exchange by relative importance, not all may be known in enough detail to be of use.

Examples of parameters into which more research should be invested are for example the effects of biological and anthropogenic actions of the diffusion of solutes other than O_2, in-situ observations of interactions of boundary layer dynamics with physical drivers of B/P exchange, potential seasonal dominance of biological drivers of B/P exchange over physical ones, lateral particulate matter transport, and residence times within the nepheloid layer.

Embracing the ecosystem as a whole, regardless of the discipline in which individual pieces of research were undertaken, is a vital step towards improved benthic-pelagic understanding (Widdows *et al.*, 2000; Kristensen, 2001; Griffiths *et al.*, 2017) and an in-depth understanding of individual drivers and processes is key to this. However, in order to integrate studies from various fields as is often necessary when investigating ecosystem level pathways, such as B/P exchanges, some caution must be exercised. Middelburg (2017) summarizes the different approaches of various disciplines well on the example of organic carbon cycling by pointing out areas of disagreement *versus* overlap, and accumulating elements from each discipline to form a complete picture of current knowledge on the topic.

Collaborative research efforts must move past multidisciplinary approaches in which individuals or teams from different disciplines independently research the same environment, only to later collate their findings, to truly transdisciplinary working practices which take elements of the various disciplines into account from the start. The ideal next step in gaining a deeper understanding of B/P exchange in coastal marine ecosystems will be to fully acknowledge the complexity and interdependencies of the processes involved in individual pathways. This will lead towards a more precise measure of real life ecosystem scaled processes, such as elemental cycling, gas exchange, quantification and subsequent mitigation of anthropogenic influences, and much more. Measuring this complexity in real systems will doubtlessly be a challenge, but it could also be the stepping stone to a deeper understanding of the marine environment at local and global scales, providing us with the means to better study, conserve and protect it. With ongoing environmental change, be it anthropogenic or natural, we will thus be able to make more accurate assessments of the state of the marine ecosystem functioning, and take appropriate actions to conserve it.

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