The concept of metabolism in ocean biogeochemistry: departures, consistencies, and implications

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Abstract

‘Metabolism’ is a term commonly defined as the sum total of chemical processes happening within some living entity which sustains that entity. Biogeochemists use this concept somewhat differently. A stark example comes from marine contexts, where biogeochemists sometimes refer to ‘ocean metabolism’. From the standard biomedical perspective, the ocean does not seem to be the kind of thing which can possess metabolism; it does not seem to be a single living entity that is sustained by chemical processes. In the light of this puzzle, this paper does three things: first, we flesh out a distinct biogeochemical sense of metabolism, exploring how this differs from, but retains connections to, biomedical definitions of metabolism. Second, we use this to explain how the ocean can be considered metabolic without needing to be considered an organism. Finally, we explore the consequences and implications of this sense of metabolism – in scientific, epistemic and social dimensions – and of recognising biogeochemical systems, such as oceans or parts of them, as metabolic.

Keywords: Ocean metabolism, biogeochemistry, external metabolism, shared metabolism, microbial oceanography

1. Introduction

Metabolism is a foundational concept in the life sciences, invoked as a definitional internal feature of living things, and a byword for the capacity of self-maintenance in organisms (Judge & Dodd, 2020; Parke, 2023). The concept of metabolism has changed over time – something catalogued in a series of papers by Hannah Landecker (Landecker, 2011, 2013a, 2013b, 2013c, 2015, 2016, 2019) - including a recent movement towards what she has termed 'post-industrial metabolism', associated with understanding the impacts of modern lifestyles and environmental degradation on the human body (Landecker, 2013a, 2013b).

The term metabolism has also been applied to many other contexts beyond the biochemistry of organisms: as a concept for analysing societies (Foster, 1999; Landecker, 2013b), cities (Swyngedouw, 2006), industry (Erkman, 1997), ecosystems (Hutchinson & Bowen, 1947), and the ethics of multispecies interactions (Chao, 2023). In many of these cases, a metabolic perspective brings with it significant ethical import. Recognising some system as metabolic may change how we perceive and treat it. If cities, societies, or ecosystems are truly metabolic, this raises questions about how they are related to human metabolism, or the metabolism of other organisms, and whether this should impact how we interact with them. There are further connections to related questions, such as those around the definitions of life, for example, if something is metabolic, is it therefore alive? Similarly, there are potential connections to other perspectives on the environment, such as the Gaia hypothesis, or other worldviews which stress the interdependence of organisms, or the agency of environments.

But can processes happening outside of organisms really be 'metabolic'? The concept of metabolism plays roles in several related areas of the life sciences. For the purpose of this article, we will focus broadly on two clusters of usage: one related largely to the physiology of macroscopic organisms (and to disciplines like medicine and agriculture) and another related to ecological and geochemical processes associated, in large part, with microbes. In both cases, metabolism denotes a set of chemical reactions which aid in the perpetuation of life. Microbes do feature in both cases (acting as a site of convergence between these two clusters of usage), although may be conceptualised differently: medical contexts, for example, may often consider them as well-bounded individuals, whereas ecological approaches may treat them as parts of larger interactive systems (Grote, 2017; O'Malley, 2016; Schneider, 2025b, 2025a)[1].

It may sometimes be assumed that usages of the metabolism concept beyond the boundaries of individual organisms – particularly when incorporating entities which are not organisms - are metaphorical, non-scientific, or otherwise looser than the well-known biomedical sense of metabolism. Not all such cases are so easily characterised this way, however. In the last few decades, a more distributed notion of metabolism has been steadily developing in the ocean sciences: biological oceanographers and biogeochemists have taken to describing the entire ocean, or large tracts of it, as metabolic (Ducklow & Doney, 2013; Regaudie-de-Gioux, 2020; Saito et al., 2024). The ocean covers 71% of the planet's surface, with an average depth of 3.6km. The (at least) billions of microbes found per litre of seawater are increasingly recognised to act in co-ordinated ways and to be responsible for a very large chunk of the respiration and photosynthesis occurring globally (Moran, 2015). It is worth considering,

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[1] There are of course nuances here: see Grote (2017) and Schneider (2025b) for more on different traditions in thinking about microbes.

then, in what senses the ocean can be considered a metabolic entity, and what the implications of this perspective are.

In this paper we explore the notion of *ocean metabolism*, using ocean biogeochemistry as a window into the ways metabolism takes on different meanings in different areas of the life sciences and beyond. We offer conceptual analysis of the metabolism concept, reflecting on usage of this concept across the life sciences, in particular looking at biogeochemical and microbial contexts, and relating this to more well-known usages in biomedical, terrestrial and macroscopic contexts. We highlight differences and points of convergence across these areas, and explore the implications of thinking biogeochemically about metabolism, in particular, the possibility of ascribing metabolic activity to non-organismal entities. Our main purpose is to show the ways in which ‘metabolism’ has been fruitfully applied to a range of cross-cutting cases: biomedical and biogeochemical; physiological and ecological; microbial and macrobial. In short, that metabolism can be instantiated in a range of contexts (beyond singular biological entities), without rejecting the distinct features of different ways of thinking about these concepts (which can nevertheless be seen to partially converge in some areas of the contemporary life sciences). We then explore some of the implications of a biogeochemical view of metabolism, which may offer a bridge between organism-centric instances of metabolism and the other senses in which the concept has been employed elsewhere. As has been shown elsewhere in science, distinct versions of the same concept can co-exist, overlap, and differ substantially, often without notice (Chang, 2012).

In what follows, we analyse the distinctives of the notion of metabolism in use in ocean biogeochemistry, starting with a brief history and explanation of scientific notions of metabolism (section 2), and of the ocean metabolism concept (section 3). After this, we explore three sets of examples from ocean biogeochemistry, which each suggest a point of departure from more organism-focused biomedical definitions: metabolism as shared, as external, and as pluralistic (sections 4, 5 and 6). In some of these instances, there are still strong connections retained to terrestrial, biomedical, and macroscopic cases. Finally, in section 7, we explore the implications of a biogeochemical perspective on metabolism.

Alongside the marine and microbial sciences, and philosophy, we draw also on the valuable work done on metabolism in science and technology studies, and hope our analysis is of use to those interested in metabolism from a range of disciplines (for instance, when considering the degree to which *metabolism*, applied to non-organismal systems, is a 'metaphor'). Our analysis does not include in-depth investigation of the social and technological factors shaping the biogeochemical notion of metabolism, but further research on this would be of great value to better understanding the development and trajectory of the metabolism concept.

2. Metabolism

The term 'metabolism' came into usage alongside a cluster of related concepts in the mid-19th century (Landecker, 2013c). It is often strongly associated with chemical reactions involved in the production and utilisation of chemical energy by organisms, particularly the molecule ATP (Judge & Dodd, 2020). Biochemists discovered and mapped chains of metabolic reactions related to this, for example the 'Krebs cycle', a set of biochemical reactions integral to making chemical energy usable by living organisms (Kornberg, 2000; Wilson et al., 2010). These now form central parts of increasingly complex maps of interconnected biochemical reactions, which are a hallmark of discussions of metabolism in biochemical contexts (Holmes, 1991; Likić, 2006)[2].

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[2] See the IUBMB-Nicholson Metabolic Pathways Chart, freely available online, for a prominent example of this mapping endeavour (*IUBMB-Nicholson: Home Page*, 2024).

In general, scientists studying metabolism are interested in the chemical reactions which are important for the production and transformation of living things and organic matter - in particular photosynthesis and respiration - but also a variety of other processes. These investigations focus on things like how these chemical reactions work, how they sustain certain conditions (e.g. perpetuating certain bodily states), and how they change under different conditions (for example, in the presence of different chemicals).

Metabolism sits at the confluence of several disciplines. A large part of the research into metabolism has taken place in medical and agricultural contexts, and has been preoccupied with the study of particular biologically and socially important chemical reactions, in order to enable the development and maintenance of things like healthy populations of humans and appropriately developed agricultural organisms (Landecker, 2013b, 2019). Medical and physiological approaches to metabolism have often conceptualised it as follows:

- 'The sum of all the chemical and physical changes that take place within the body and enable its continued growth and functioning.' [taken from a medical dictionary] (Martin et al., 2020)

As is indicated here, metabolism denotes a set of chemical reactions used to support life, something common to the metabolism concept across contexts. Differences arise however in the question of where these chemical reactions are instantiated – i.e. what is the 'container' of metabolism? – and which biological systems are understood to be supported by these reactions, i.e. what is the 'beneficiary' of metabolism? In the medical definition above, the body is emphasised as both the container and beneficiary of metabolic processes. Given the focus of medicine on ensuring that bodies operate in particular ways, this focus is unsurprising.

However, those with a strong interest in cellular research may also invoke different sorts of biological entities when defining metabolism:

- ‘Metabolism … comprises the total of all chemical reactions that take place in the cell that are essential for life.’ [article in biochemistry journal] (Judge & Dodd, 2020, p. 607)
- ‘Enzyme-catalysed processes within cells that metabolize macronutrients, carbohydrate, fat and protein.’ [mycology article in microbiology journal] (Keller et al., 2005, p. 938).

Here, Judge and Dodd emphasise *the cell* as the container of metabolism, with the beneficiary left vague (‘life’). Keller et al. similarly invoke the cell as container, and go on to distinguish ‘primary metabolism’ as chemical processes which are indispensable for the cell, and more broadly for the growth of the organism (p.937)[3]. There are the same core concerns visible here as the previous definition, namely, how chemical processes support life and growth.

Alongside cells and bodies, definitions of metabolism are also often focused on organisms:

- ‘The sum of all chemical processes taking place within a living cell or organism’ [plant biology textbook] (Eichorn & Evert, 2012, p. G-14)

Eichorn & Evert invoke *the cell* and *the organism* as the container of metabolism, and in other parts of the text mention both the plant as a whole (p.30) and individual plant cells (p.103) as beneficiaries of metabolic processes. Already here, questions about individuation arise: it is not always clear what counts as a ‘whole plant’, nor that this will coincide with a

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[3] In contrast, s*econdary metabolism* denotes chemical processes which contribute to aspects of organisms’ lives beyond their direct survival, such as signalling to other organisms (Verpoorte, 2000). We leave this aside here, although its use within ocean biogeochemistry, along with related terms like *anabolism* and *catabolism,* is an interesting topic for future exploration.

single organism (consider, for example, plants where two species have been grafted together, or one individual plant which is then split into two) (Gerber, 2018; Yilmaz & Dupré, 2025).

What is important here is that from these definitions we can see the key kinds of entities invoked as containers and beneficiaries in this tradition of thinking about metabolism: cells, bodies, and organisms. In the context of macroscopic terrestrial organisms, particularly humans and other animals, these definitions may often line up fairly unproblematically: cells often will be found as parts of well-defined bodies which may also correspond to the boundaries typically associated with the organism (although, as with the plant case, this will not always be so).

This is a fairly restricted list of entities which metabolism can take place within, and be of benefit for, and there are potential inconsistencies: cells may not always be within an organism (e.g. single celled organisms); organisms, bodies, and cells may also be found *inside* those of *other individuals or species*; processes happening within organisms may not happen within cells (e.g. inter-cellular processes); and more broadly, demarcations of 'bodies' and 'organisms' can vary. We will not attempt here to pin down exactly what is going on here, but instead to contrast a focus on these entities with the approaches taken in biogeochemistry (which, we hope, will also shed some light on developments in more biomedical contexts too). These issues relate more generally to the question of individuation in biology, i.e. how individuals such as organisms are demarcated (Clarke, 2011; Gilbert et al., 2012; Pradeu, 2016), something we return to later.

To recap the key themes of this way of thinking about metabolism:

- Metabolism denotes a set of *chemical processes*
- It takes places within *an* entity (the 'container'), typically a cell, body, or organism

- These processes sustain and support a living thing (the ‘beneficiary’), typically, again, a cell, body, or organism[4]

Biogeochemical perspectives on metabolism, we will show, only depart from these themes in small ways, but in doing so significantly alter the relationship between biological individuals and metabolism. What is important for now is to note that these more biomedical definitions of metabolism often focus on bodies, organisms, and cells, and feature an *internal, private*, and *restricted* sense of metabolism: it is contained by, and benefits, singular biological entities.

The restricted focus on cells, bodies and organisms, and on private and internal senses of metabolism, is associated in part with the historical investigative contexts and drivers of metabolic research. The metabolism concept originated in heavy association with agriculture, animal husbandry, and calorie production through industrialization, and often entailed a strong focus on the bodies of commercially and socially important organisms, such as terrestrial animals and plants (Landecker, 2013a). Techniques such as radioisotope tracing made it easy to trace substances moving through their bodies (Creager, 2015), and the mass adoption of cell culturing techniques made cellular processes a central focus of biology (Creager & Landecker, 2009). This combination of study subjects and techniques lends itself to a focus on how energy moves through and sustains particular entities of interest (such as large terrestrial multicellular organisms), and in many cases these entities seem well-bounded and largely autonomous.

2.1 Ecological metabolism

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[4] This relation is sometimes expressed in terms of possession: organisms *have* metabolisms, this is *my* metabolism, and so on. We return to this phrasing later on.

There is another, related, trajectory of metabolic thinking which is very relevant here: ecological approaches. Paralleling the development of organism-centred metabolic approaches, ecologists have also used metabolism as a way of thinking about the movement and transformation of substances within ecosystems, communities, and populations of organisms (Creager, 2015; Mitman, 1992). This strand of thinking has often focused strongly on interactions between living entities (rather than just processes internal to them), that is, it has taken what has been called an ‘interactionist’ approach to thinking about living entities, conceiving them not just as simply autonomous individuals but also as deeply influential on one another (Mitman, 1992; Schneider, 2025b).

This approach to ecological thinking developed, in part, out of 20th century debates about the nature of ecosystems, and the degree to which they could be thought of as individual ‘superorganisms’, arbitrarily defined collections of discrete entities, or as something in between (Clements, 1916; Hutchinson, 1940, p. 268; Odenbaugh, 2019; Mitman, 1992)[5]. Despite a variety of stances on the nature of ecosystems (Creager, 2015, Chapter 10; Millstein, 2024, p. 15; Mitman, 1992), this metabolic approach to ecology became very influential (e.g. Hoellein et al., 2013; Odum, 1965; Odum & Odum, 2000), and part of a core strand of thinking in ecology which approaches ecosystems from an energetic and functional perspective (Callicott et al., 1999).

One of the clearest examples of this tradition is the work of US ecologist G. Evelyn Hutchinson, who, in a series of studies on lakes, explored the ways in which they cycled and transformed substances, explicitly describing these processes in metabolic terms (Creager, 2015, Chapter 10; Mitman, 1992, p. 140; Hutchinson, 1941). Hutchinson drew direct parallels with organismal biology, and employed similar techniques as those studying individual

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[5] There are connections here with James Lovelock and Lynn Margulis’ Gaia theory, where the entire Earth is seen as an organism, or a self-regulating system (more on this in the final section) (Schneider, 2004).

organisms. Just as within organisms, substances such as phosphorous could be traced through the lake using radioisotopes. These studies revealed surprising speed and depth of spread of the substance, pointing to a role for biological activity in cycling it through the lake (Hutchinson, 1941; Hutchinson & Bowen, 1947; Creager, 2015; Landecker, 2013c). Hutchinson's approaches, and those developed since, have explicitly used the concept of metabolism to study the cycling and transformation of substances through ecosystems (Brown et al., 2004; Testa et al., 2012).

In doing so, Hutchinson was both building on and laying further foundations for an approach to metabolism which recognised it also in *interactions* between organisms, cells, and bodies, as well as within them (Hoellein et al., 2013; Mitman, 1992). A distinct strand of thinking about the *containers* and *beneficiaries* of these metabolic processes is visible here, something also strongly connected to the study of microbes (Schneider, 2025a, 2025b).

2.2 Microbes and metabolism

A key part of these ecological approaches to metabolism is a focus on the role of microbes in these environments. Hutchinson's studies, for example, explored how plankton (small free-floating aquatic organisms) play a major role in explaining the production of energy and transformation of substances throughout lakes (e.g. Hutchinson & Bowen, 1947). More broadly, microbes are increasingly recognised as important components of ecological, metabolic, and physiological functioning across a wide range of contexts, including within individual organisms (Cockell, 2024; Michán-Doña et al., 2024; O'Malley, 2016). In the environment, microbes are recognised as the origin of Earth's oxygen-rich atmosphere, they form the basis of food webs, produce vital substances for many other lifeforms (us included - such as vitamin B_{12}, which we cannot produce in our bodies), and are integral to the movement and storage of carbon dioxide (and so influence the climate) (Tagliabue, 2023).

They are described as ‘engines of biogeochemistry’ (Falkowski et al., 2008) that set the conditions under which most forms of life have evolved and continue to exist.

On top of this, microbes have also increasingly been recognised as highly significant for development, growth, and various other important physiological processes within other organisms, and are increasingly found living in, on and with a variety of different macroscopic organisms (Gilbert et al., 2012; Michán-Doña et al., 2024). Microbes produce substances which facilitate (or disrupt) developmental processes, and enter into sustained (and sometimes inheritable) symbioses with a great many macroscopic organisms (Gilbert et al., 2012). When entities like viruses are also included, the influence of microscopic biological entities on life is even greater (O’Malley, 2016).

Changes in technologies across the life sciences, such as the development of meta-genomics and other -omics techniques (explained in more detail shortly), have driven the reconceptualization of important and intertwined biological notions such as metabolism, individual, and organism (Dupré & O’Malley, 2007; Gilbert et al., 2012; Landecker, 2011; Prieto, 2023; Schneider, 2025a). An interactionist and ecological approach to microbes has become increasing relevant also to macroscopic and organism-centric biology due to the recognition of the importance of diverse groups of microbes in shaping the biology of these organisms (Landecker, 2016; Michán-Doña et al., 2024; Schneider, 2025b). Sitting at the (re-) confluence of many of these developments, ocean biogeochemistry offers an interesting window into the development of the metabolism concept and its relevance beyond individual cells, bodies, and organisms.

3. Biogeochemistry and ocean metabolism

Marine biogeochemistry is the study of how living things regulate the movement and transformation of chemicals in the ocean, and how this interacts with geological and ecological systems (Bashkin & Howarth, 2002, p. vii)[6]. In particular, biogeochemists are often interested in processes in the sea which involve the production of energy and organic matter, and their transformation into different forms. Examples include how carbon is converted from gaseous forms into molecules for use by organisms ('primary productivity'); the roles played by chemical substances (such as iron, oxygen, phosphorous or nitrogen) in marine geological and ecological systems; how these substances move around; and the overall balance of important processes like photosynthesis and respiration in the sea.

These processes are of interest in part because they are enormously consequential: studying the physics of the ocean doesn't give the full picture of what is happening there and the implications for human life. As it turns out, ocean life, and particularly microbes, have a significant impact on the chemical composition of the ocean (Redfield, 1958; Tagliabue, 2023) (this includes also viruses (Fuhrman, 1999; O'Malley, 2016)). As a result, whether the ocean is a net producer or consumer of carbon dioxide, for example, will depend heavily on the organisms living there, and the chemical substances (often produced by other organisms) available to them (Ducklow & Doney, 2013). Modelling changes to the ocean as a result of climate change therefore requires understanding the microbial processes at play there and their key determinants (Levine et al., 2025; Tagliabue, 2023). The ocean, and the microbes inside it, also form a vital part of the systems which produce food for humans, via the movement of substances like nitrogen through the biosphere (Canfield et al., 2010; Rose et

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[6] We focus on marine contexts here, but there is no clear-cut distinction with terrestrial biogeochemistry. For example, ocean-floor sediment is often considered a marine topic, but also has connections to things like soil science (Wall et al., 2005).

al., 2024), or the production of important vitamins (such as B_{12}) for consumption by other organisms.

Biogeochemists are therefore very focused on understanding the bewildering array of plankton – floating organisms – which are often microscopic and form the bases of many of the webs of chemical inter-relation found across the planet (Durham et al., 2025). These plankton can form complex associations, including synchronised growth (blooms) which can have significant ecological impacts (such as depleting an area of oxygen or releasing large volumes of chemical substances). Communities of plankton may exist in complex symbioses with one another, including varying degrees of interdependence[7] (Bannon et al., 2022; Seymour et al., 2017; Wienhausen et al., 2024). Patterns of microbial interactions may vary across timescales and locations, including, for example, seasonal changes in availability of different chemical substances and prevalence of different species (Bannon et al., 2025; Gaudin et al., 2024). All of these patterns are the targets of biogeochemists, who seek to understand how microbes, chemistry, the ocean, and the broader earth system shape one another, often with a view to understanding human impacts on these systems and the knock-on effects of these for humans and other organisms.

An early and insightful example of ocean metabolism emerging from biogeochemical and microbial thinking comes from Alfred Redfield. Redfield showed that phytoplankton seem to regulate the proportions of chemical elements throughout the sea, keeping them at levels similar to the ratios inside their bodies (specifically the ratios of phosphorous, nitrogen, carbon and oxygen) (Redfield, 1958)[8]. These ratios are not what is to be expected by simple diffusion of substances in the ocean: the chemical composition of the ocean is actively

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[7] Interdependence is understood here to mean not just necessity for survival, but also influence on things like the type and rate of growth they experience (Bannon et al., 2022; Millstein, 2018).

[8] Phytoplankton are a varied group of small organisms unified by their ability to produce energy from sunlight and inability to swim against horizontal ocean currents.

maintained by microbes (Gruber & Deutsch, 2014; Redfield, 1933). Redfield's work catalysed the development of a whole field: the exploration of how life exercises control over the chemical features of its environment, often at large scales (Nature Geoscience, 2014; Williams, 2006). This invited further study of the *stoichiometry* of the ocean (i.e. the ratios of different chemical substances found there), and how plankton and microbes more broadly shape this, along with other important biological and physical properties (for example, the colour and darkness of the ocean depends on the prevalence of microbes and organic molecules (Davies & Smyth, 2025)).

The seeds of the ocean metabolism concept are visible here. Redfield noted that it was possible to study ocean biogeochemical cycles 'in much the same way as the physiologist examines the general metabolism of an individual organism' (1958, p.207). His work both influenced and was influenced by ecological approaches to metabolism, such as Hutchinson's work on lakes, and also provided inspiration for later concepts such as the Gaia hypothesis (Lovelock, 2003, p.769). In particular, with the advent of meta-omics technologies, this view of microbes as *constituting,* rather than just *residing within* the sea, gained increasing currency (Helmreich, 2009). Today, it is possible not only to trace chemical substances moving through parts of the environment, but understand in more detail how they relate to the living things found there. This allows increasing fulfilment of the research programme inspired by Redfield, namely, understanding the ways in which environmental and biological chemistry are intertwined (Redfield, 1958).

3.1 Ocean metabolism today

Developing out of this context, the term *ocean metabolism* has been used to refer to chemical process stretching across marine environments. To quote one study: 'Here we estimate the contribution of the benthos [ocean floor dwellers] to total deep North Pacific metabolism' … 'respiration is a large and perhaps dominant contributor to deep ocean metabolism' (Jahnke &

Jackson, 1987). Ocean metabolism here refers to chemical processes happening in the ocean - including respiration, a key process focused on in traditional biochemical metabolic science - but treats them as something which many separate organisms may contribute to. Such processes may have wide-ranging effects on the ocean: for instance, contemporary biogeochemists are concerned that changes in levels of organic substances, and associated biological activity of plankton, may be causing the ocean to darken in many places (something which may have further knock-on effects on the many marine organisms which depend on sunlight) (Davies & Smyth, 2025).

The term *ocean metabolism* has notably been invoked in debates over whether ocean gyres[9] are sites of net photosynthesis or respiration, and so whether they absorb more carbon dioxide than they emit (Ducklow & Doney, 2013). Various authors have discussed the 'the metabolic balance of', and 'net community metabolism in' gyres of the open ocean (Duarte et al., 2013, p. 551). The articles particularly focus on energy flows through the ocean, and the production and destruction of organic matter by photosynthesis and respiration. While a biologist may focus on rates of photosynthesis and respiration by (and in) a specific type of organism, the geochemist is interested in the cumulative impact of many organisms (measured in a manner divorced from those organisms) on things like carbon production or consumption. Biogeochemists seek to do both simultaneously and to draw them together.

Here some of the key elements of ocean metabolism are visible: an emphasis on connections between communities of organisms, and the idea of metabolic pathways extending across environments. Analogies with cells or organisms are sometimes made explicit:

> "By analogy to a living cell, the ocean has a collective metabolism that is based largely on its dynamic genetic blueprint, with expressed phenotypes that control

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[9] Large spiral shaped currents found in the open ocean, sometimes spanning many miles.

> fluxes of energy and matter. The microbial processes that underlie this collective metabolism are influenced by environmental forcing…" (Karl, 2007, p. 759).

The point here is not that the ocean *is like a metabolic system*. Rather, the ocean is like a cell *because it has a metabolism* (albeit a collective one). On this view, metabolic processes may suffuse oceans as well as cells.

A contemporary attempt at explicit definition of the ocean metabolism concept is provided by 'BioGeoSCAPES', at the time of writing a fledgling large-scale international scientific network, aiming to conduct large-scale co-ordinated studies of biogeochemistry around the world (BioGeoSCAPES, 2023). The project is explicitly oriented around the aim of better understanding ocean metabolism, which they define as: 'the chemical processes that occur within individual organisms and populations, as well as among communities and ecosystems' (Maldonado et al., 2018). There is clear difference here with the more biomedical definitions of metabolism surveyed earlier: these chemical processes do not seem to be possessed by or to be internal to some specific single living thing, that is, they do not seem to invoke the same containers and beneficiaries of metabolism.

There are two obvious possibilities which it is worth excluding before continuing. First, that biogeochemists might simply be taking the ocean to literally be a cell, organism, or part of the body of an organism, as in some versions of the Gaia hypothesis (Lovelock, 2003; Schneider, 2004). The examples above hopefully make clear that this is not the case, in that bodies, organisms and cells are invoked insofar as they contribute to metabolic processes, not as constituents of larger organisms which possess metabolism in a conventional biomedical sense. We return to connections with the Gaia hypothesis later in the paper.

Second, it might be tempting at this point to consider this as a case of describing external (i.e. non-metabolic) interactions between organisms *as though* they were internal (metabolic) ones within organisms. Rather than writing this off as simply loose or metaphorical usage of the metabolism concept, we seek to do something else here. Instead, we want to recognise, as others have in other contexts, that scientific concepts get used, developed and refined in distinct ways, often in association with different study systems, techniques, and aims (Chang, 2012; Haueis, 2024)[10]. There are distinct lineages of the metabolism concept at play here, and it is instructive to pay attention to different usages, including how these different senses of the concept relate to one another.[11]

To study these processes, they employ both geochemical and biological techniques, which do not always give compatible answers (Ducklow & Doney, 2013). Integrating these methods, particularly those of geochemistry and microbial oceanography, and developing new ones, has become a pressing concern for the field, and is central to understanding how the ocean will respond to and influence climate change.

3.2 Measuring ocean metabolism

Given the influence of microbes in the ocean, much of the study of ocean metabolism is concerned with microbial metabolism (O'Malley, 2016; Schneider, 2025a, 2025b; Tagliabue, 2023). Some important methods used by biogeochemists to study microbial activity are referred to as '-omics' techniques: genomics, transcriptomics, proteomics, and metabolomics (Levine et al., 2025). These labels relate to different realms of biological activity. Genomics

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[10] There is also a rich literature on the productive use of metaphor in science (Helmreich, 2020; Keller, 2020), the 'dying' of metaphors to become meaningful in a more literal sense, and the various non-epistemic reasons someone might seek to use a concept, or apply a concept from one area to another (Reynolds (2022); or see Kaiser and Morrow (2024) for an example). There are clear possible non-epistemic reasons for the use of 'metabolism' in the context of the ocean, for example as a way to communicate the complexities of the kind of multi-scale work done by ocean biogeochemists (Saito et al., 2024, p. 3). But possessing a non-epistemic function does not call into question the scientific status of a concept.

[11] It is worth noting here that the concept of ocean metabolism is not used by all ocean biogeochemists, and no doubt is used in different ways in different cases. Biogeochemistry is a diverse field, and there are a variety of possible perspectives to be taken on the nature of the Earth system, the ocean, the biogeochemical processes happening within it, and the concepts of metabolism employed in these contexts. We present one such perspective here. A more nuanced understanding would be helped by empirical investigation into the rapidly developing field of biogeochemistry (for example, through ethnography of or interviews with biogeochemists).

focuses on cataloguing the genes an organism has. Transcriptomics looks at which genes are being activated. Proteomics examines the abundance and identity of proteins, which facilitate interactions with the geochemical environment. Metabolomics attempts to measure the suite of chemicals produced during biological processes. These all serve as indicators of microbial activity.

Many organisms cannot be cultivated in a lab, or, if they can, may behave differently when they are, in part because they rely on a range of biological processes enacted by other living things in the sea. Insights into the complex biological processes in the ocean therefore require sampling it directly. Here, ‘meta-omics’ techniques are used, studying the relevant substances within an environmental sample in the same way described for organisms above (Dupré & O’Malley, 2007; National Research Council, 2007). Development in techniques for studying genes, proteins, and metabolites in the lab and the environment have driven rapid advances in our knowledge about microbes in the ocean (Helmreich, 2009; Levine et al., 2025).

Geochemical methods for tracing the movement of substances through the ocean are also important. There are various ways to do this: comparing the movement of chemicals sensitive to biological activity with those that are not, to infer the impact of biological processes (Shigemitsu et al., 2016); or by using isotopes (different forms of) specific chemical elements, such as radioactive forms of phosphorous or uncommon forms of carbon, which can show how quickly these elements move through particular systems (there is a partial overlap here again with both ecological and biomedical techniques for studying metabolism).

Biogeochemists seek to bridge the gap between these sets of methods: -omics approaches reveal the kinds of living systems present and the activity they engage in; geochemical ones show how substances move through these systems and the cumulative impact of microbial activity. Ocean metabolism is sometimes invoked in the context of this integrative move, to refer to the sets of processes at the interface of biology, geology and chemistry, which, it is hoped, will be better revealed as these methods are brought together (Saito et al., 2024)[12]. The metabolism concept at play in biogeochemistry, then, is linked to a range of methods used also in traditional macroscopic studies of metabolism (radioactive tracing, and genomic studies), but with particularly strong connections to the ecological and microbial perspectives on metabolism. We now explore some of the points of contrast and convergence between the ocean metabolism concept and the biomedical definitions explored at the start, particularly focusing on the question of which containers and beneficiaries of metabolic processes are being invoked. In the process, we show how the ocean itself has been conceived of as a metabolic entity.

4. Containers in biogeochemistry: external metabolism

If we take the label 'ocean metabolism' seriously, without simply making the ocean into one of the container entities discussed earlier (cells, bodies, organisms), how do the features of this notion of metabolism fit with the definitions offered in biochemical contexts? We suggest three senses in which biogeochemical metabolism departs from the definitions surveyed earlier (although, as we will show, there are areas of reconnection in some of these cases).

The first point of departure is from the idea of metabolism as something which only happens *within* cells, organisms, or bodies. Ocean metabolism explicitly includes processes also happening outside of these: within and between communities, populations, and ecosystems. Some versions of the Gaia hypothesis might simply say that these processes nevertheless happen inside larger organisms, e.g. the whole Earth system (Lovelock, 2003), but another

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[12] See Brigandt (2013) for more on the notion of integration in the life sciences.

option is possible: that metabolism can happen outside of organisms, cells, or bodies. Here, different kinds of metabolic container are recognised. The ocean, in this case, provides a site for metabolic processes to take place beyond cells, bodies, or organisms[13]. Biogeochemists are keen to understand these processes because of the impact they have on many living things (Tagliabue, 2023).

Organisms exchange substances with their environment in various ways: ‘leaking’ or transferring them while alive, or releasing them upon death (Morris, 2015). These processes, whether beneficial to emitters and selected for by evolution, or costless and accidental, have important impacts on the chemical environment of the ocean (Pacheco et al., 2019). Redfield showed this on a grand scale: plankton influence the ratio of phosphorous, nitrogen, carbon and oxygen throughout the ocean, bringing it in line with the ratios in their own bodies (Gruber & Deutsch, 2014). Some further examples will make this more explicit.

4.1 Vitamins and metals

Vitamin B_{12} is very important for the survival and growth of many organisms. Only a small subset of living things - many of them plankton - are able to produce vitamin B_{12}. Other organisms must therefore ultimately obtain it from these producers (Bannon et al., 2022, 2023). B_{12}-producing plankton release it, accidentally or otherwise, into the sea, constructing a chemical environment conducive to other forms of life. Additionally, some microbes make only portions of the B_{12} molecule, while other groups can stitch these portions together, collaboratively making this critical molecule available for themselves and other B_{12}-requiring organisms in the ecosystem (Weinhausen et al., 2024).

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[13] This is not to say metabolism can easily happen anywhere, nor that physical boundaries do not matter: the properties of the medium are important, hence the focus of many scientists on the ocean (rather than, say, the entire Earth) or specific parts of it (as with the ‘deep North Pacific’ or ‘ocean gyres’ examples earlier).

B_{12} production, whether by one or multiple microbes, requires particular precursor substances, such as iron and cobalt. A lack of these (or of B_{12}) can limit the rate at which other plankton can grow, even if light, heat, other nutrients, or CO_2 levels increase. These organisms are described as iron or cobalt *limited* (Bannon et al., 2022). If a B_{12}-producing organism is limited by lack of iron, it may not be able to produce B_{12} for use by other organisms, which will then not be able to grow and develop. One organism is limited by the conditions experienced by another (Bannon et al., 2022). When iron levels are increased, limitations are lifted on two groups almost simultaneously, which may have a cascading impact on other aspects of ocean biochemistry.

To follow the chain further backward: iron availability is shaped by the activities of other organisms in the area. Seawater cannot hold much iron, but some organisms in the sea produce molecules (ligands) which increase the quantity of iron it can hold, and make existing iron more available to themselves and other organisms (Hoffman et al., 2024; Moffett & Boiteau, 2024). The same is true of many other metals in the ocean, which are similarly vital to various biological processes, and are controlled by various biological processes (Bruland et al., 1991). An intricate web of these limitations fills the ocean (de Baar, 1994), and the chemistry of seawater is changed as a result. Life-sustaining chemistry, in the ocean, does not happen solely inside cells, bodies, or organisms, but also in the spaces between them.

4.2 The environment as container

The relevant point to be drawn from these cases is that there are processes important to the maintenance of life which take place outside of the cell/body/organism: external metabolism (relative to these entities), or recognition that metabolism is internal to a different kind of container, in this case, the ocean itself (or parts of it). Many such processes may happen inside well-defined living entities in some contexts, but in more diffuse and distributed ways in others. There are, for example, coupled species of ocean microbes – Prochlorococcus and SAR11 - which perform photosynthesis and respiration in concert with one another, recapitulating the internal biochemistry of a plant's leaf, but which are separated by ocean water (Braakman et al., 2017).

The inclusion, in biogeochemistry, of parts of the environment as metabolic containers, is not entirely disconnected from more traditional biomedical cases, where external processes are also often relevant. Take a canonical and early articulation of the aims of metabolic studies, from Franz Koop, a teacher of Hans Krebs (alluded to earlier as a pioneer in the study of biochemical metabolism):

> [the aim of metabolic studies is to] "present a scheme that puts together an unbroken series of equations of all of the reactions from the food stuffs which continuously supply to the organism its energy needs, all the way to the slag that again leaves the organism as energyless final oxidation products." (Holmes, 1991, via Judge & Dodd, 2020)

This quote might seem to articulate the biomedical view of metabolism that biogeochemists depart from. But the focus on food, and on an unbroken series of equations pertaining to its transformation, is important. Foodstuffs are broken down by humans: mechanically (through chewing) and chemically (by enzymes and microbes). Digestion then continues through the alimentary canal, including the stomach and intestines. The container of metabolism becomes blurry here: these areas are not within human cells. The enzymes and other digestive agents operating here are extra-cellular. On some perspectives, they are not even within the body or organism: the stomach and intestines form a tube running through the body, lined with specialised surfaces to facilitate exchange (Johnson, 2003, p. 4), making the contents of your stomach and intestines, in a sense, a part of the external environment, waiting to be absorbed into your body.

Here, paradigmatic sites of metabolic processes in a biomedical sense (mouths, stomachs, intestines) can be seen as cases where metabolism is not neatly or unambiguously contained within only cells, bodies, or organisms. In the past, biochemical conceptualisations of metabolism have also emphasised it as a process which operates across the boundaries of bodies, rather than just inside them (Landecker, 2013c), but this recognition is lost in many contemporary definitions. Developments in contemporary biology, however, point to a re-emergence of this conception, through notions such as *extended physiology*, which recognise physiological processes beyond the outer surface of the organism (Turner, 2002). Further examples of extra-bodily digestion abound: many arthropods (e.g. insects, spiders) dissolve bodies of prey by injecting enzymes into them (Cohen, 1995). Extra-cellular enzymes are also used by marine organisms as parts of energy and resource acquisition processes (Sebastián & Niell, 2004; Arnosti, 2011). A full understanding of how these organisms obtain energy from food would need to include these extra-bodily processes. So it seems that whilst biogeochemists might be keener to explicitly include other kinds of metabolic container, this is more of a difference in emphasis than some sort of fundamental disagreement with biomedical approaches.

5. Beneficiaries in biogeochemistry: shared metabolism

So both biogeochemical metabolism, and, in some cases, other senses of metabolism, may involve containers beyond cells, bodies, and organisms. A second, connected, aspect of metabolism we are concerned with here is the idea that metabolism is *private*, i.e. that metabolism supports *a specific entity,* particularly a cell, organism, or body. The definitions of metabolism included at the start of this paper typically invoke these single entities as beneficiaries. Metabolism, in traditional definitions, is something relevant to one living thing: it is the sum total of chemical processes supporting *an* organism, *a* cell, or *a* body.

But a single metabolic process may have relevance for many living things. Recognition of the ubiquity of microbes has placed these kinds of interactive processes (symbiosis, collaboration, co-ordination, competition) increasingly centre-stage in many areas of the life sciences (O'Malley, 2016, Dupré & O'Malley, 2007, 2009; O'Malley & Dupré, 2007), pushing studies of metabolism to explore processes which are relevant to multiple traditionally-demarcated organisms (Landecker, 2011).

Associations of microbes often involve complex conjunctions of biochemical processes which are equivalent in many ways to the activity inside traditional multicellular organisms. As such, some authors have argued some microbial associations should be considered organisms or individuals (Dupré & O'Malley, 2009; Ereshefsky & Pedroso, 2015; O'Malley & Dupré, 2007). Leaving the definition of organism aside here, many of these processes are the same as those labelled *metabolic* when taking place within individual organisms. The case of nitrogen fixation illustrates this further.

5.1 Nitrogen Fixation

Nitrogen constitutes 70% of the atmosphere, and is physiologically important for living things, but is particularly unreactive in its gaseous form (Canfield et al., 2010). As a result, it is very difficult to make use of for most organisms. Some plants employ specialised micro-organisms in their roots called diazotrophs to 'fix' nitrogen for them, resolving this problem (Sun et al., 2021). Perhaps these microbes are to be seen as parts of the plant, staving off recognition of truly shared metabolism for now (and see Yilmaz and Dupré, 2025, for more on the tricky question of plant individuality). But in oceans, this process is much more distributed. Diverse types of marine diazotrophs, often free-living, take inaccessible gaseous environmental nitrogen and use it to produce nitrogen-containing substances that are expelled into the water and become available to those other organisms (Sohm et al., 2011). This is known to be a major source of nitrogen to the ocean as a whole, not just to organisms in close proximity to diazotrophs.

Many organisms get nitrogen through their diet, that is, they eat organisms (or parts or products of organisms) which have previously fixed nitrogen from the air. This nitrogen is then incorporated into the bodies of the consumer organisms. The process of obtaining nitrogen, for these organisms, depends on processes happening in others. As a result, nitrogen fixation is one of the most important metabolic processes underlying the existence of life on Earth, enabling the growth and persistence of many forms of life (Canfield et al., 2010). The production and movement of nitrogen in the sea has a huge impact on many of the things living there (and elsewhere) and so is of great interest to biogeochemists (Rose et al., 2024; Zehr & Capone, 2020). This is just one of many cases of shared metabolism in microbes (Dupré & O'Malley, 2009), which are a central concern for those studying life-sustaining processes in the ocean (Tagliabue, 2023). It is not a single biological entity which benefits from nitrogen fixation, but a whole swathe of the life on the planet.

5.2 Kinds of sharing

Nitrogen is not the only such case of shared metabolism in the ocean. 'Shared' here can imply several different things, which it is worth briefly disambiguating:

1. A single metabolic process relevant to multiple beneficiaries (e.g. multiple organisms). For example, many chemical substances are broken down by a

heterogenous consortium of microbes which cannot do it alone (Morris, 2015), whilst others are built by different species working together[14].

2. Several interdependent metabolic processes which are relevant to multiple beneficiaries (e.g. organisms). For example, different kinds of marine microbes have evolved to use one another's waste products, forming a chain of sequential metabolic processes (Braakman et al., 2017; Mitamura & Saijo, 1980).

3. The same *kind* of metabolic process being instantiated in many different organisms, such as the chemical pathways involved in respiration and photosynthesis, common to many forms of life (Falkowski et al., 2008). (Here, *shared* refers to common mechanisms or processes by which the metabolism takes place, rather than to the entities which benefit.)

These types blur into one another. One metabolic process may be analysed as sequential steps (making type 1 into type 2). Common metabolic mechanisms (type 3) may contribute to some larger overall process of importance to many living things (type 1), as with instances of nitrogen fixation producing the overall cycling of nitrogen (Canfield et al., 2010). Most relevant here, however, are types 1 and 2: any given metabolic process(es) can benefit more than one entity simultaneously. Metabolic systems may compete or work together, for evolutionary reasons or accidentally (for example through 'leakiness', discussed momentarily) (Machado et al., 2021).

The degree of interdependence and integration between different biological entities, and different metabolic processes, can vary here: some species of microbes might start to make use of the products of another species, slowly stop producing it themselves, and come to

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[14] See the recent discovery that two species of microbe collaborate by producing different parts of the vitamin B_{12} molecule (Wienhausen et al., 2024).

depend on this other species (known as the ‘Black Queen Hypothesis’) (Morris, 2015). ‘Cross-feeding’, evolving through this or additional mechanisms, may be very widespread and fundamental across aquatic environments (Braakman et al., 2025). In other cases, species might simply benefit from the presence of other species, but can survive without them: for instance, some marine species, including seagrasses, may associate with filamentous ‘cable bacteria’ which provide distinct spaces for different chemical reactions to take place, and also provide centimetre-length conduits for the flow of electrons, something which enables transformation of sulphur compounds which may otherwise be damaging to nearby species (Malkin & Cardini, 2021; Scholz et al., 2021). Interdependence amongst microbes and metabolic processes is something which can vary across contexts, and change with time (Schneider, 2025b).

This is not too much of a departure from where we started: single organisms and cells can still *possess* metabolism. But joint ownership is possible, and often unavoidable: there may be multiple beneficiaries at once. Even processes associated with more standard biochemical contexts can be seen to be collaborative in this sense: digestion in the gut involves microbes which do not share our genome; an estimated 70% of our body heat (at rest) may be produced by microbes, and changing the human gut microbiome (e.g. through antibiotic exposure) can impact body temperature (Rosenberg & Zilber-Rosenberg, 2016). Digestion and temperature regulation are widely accepted examples of metabolic processes, and yet both involve collective action and collective benefit. The idea of shared metabolism is neither revolutionary or new, but is harder to ignore in dissolutely and resolutely aqueous oceanic life than in more neatly packaged terrestrial organisms.

Even in important experimental organisms such as hydra and rats, from which many insights into metabolism have been gained, metabolism is increasingly seen as a shared endeavour (Deines et al., 2017; He & Bosch, 2022; Carter et al., 2020; Landecker, 2011). So, whilst ocean biogeochemists might be more focused on shared metabolic processes - such as the movement of nitrogen through diffuse microbial communities – these kinds of processes are increasingly recognised as relevant to more biomedical cases of metabolism too.

6. A pluralistic view of metabolism

The two steps taken so far allow for a picture of metabolic processes as extended through and shared between biological entities within the ocean. But this can go a step further, with a reappraising of *the kinds of things* which can be considered beneficiaries in analysing metabolic systems. This is a step further than the previous section: not simply saying that there may be multiple simultaneous beneficiaries from the list discussed earlier (cells, bodies, organism) in any given case, but that this list itself can be expanded to include other things.

Metabolism is typically presented as something that works in service of a particular cell, organism, or body. Metabolisms sustain organisms. This focus comes from a particular investigative context where often what mattered in metabolic studies was ensuring animals, plants and humans consume the substances they need to perpetuate certain socio-economic arrangements (Landecker, 2013b). However, strands of both historical and contemporary thinking have emphasised that metabolic systems can be processes distinct from organisms (Landecker, 2013c), and act as influences on the evolution and development of the organisms they interact with (Doolittle & Inkpen, 2018). In some versions of this perspective, metabolic processes can also be seen as beneficiaries in their own right: biogeochemical cycles, such as the nitrogen or phosphorous cycles, can act as processes which recruit organisms to further perpetuate them. Here, the organisms are no more important than the processes they sustain (Doolittle & Booth, 2017; Falkowski et al., 2008; Morowitz et al., 2008), or, to phrase it another way, the organisms are conceived of interactionally, that is, the interactions between them are at least as important as the organisms themselves (Mitman, 1992; Schneider, 2025a).

In these cases, the biogeochemical environment of the organism is thereby similar to the macroscopic environment of the organism: biological entities might evolve jaws large enough to eat certain fish, or, similarly, evolve features to take advantage of the presence of oxygen or nitrogen (Morowitz et al., 2008). Insofar as these biogeochemical cycles are, at least in part, external and shared metabolic processes, metabolism can be seen to shape, constrain and afford certain ways of living (for example, by providing an oxygen-rich environment).

There are several ways to phrase the relationships here, such as through language of possession, parthood, or contribution: cells, bodies, and organisms *belong* to broader biogeochemical process; they are *part* of these process; or they *sustain* these processes[15]. Here, the relationship between the standard kinds of beneficiary and the metabolic process is inverted, or at least rebalanced. Metabolisms sometimes *have* organisms, as well as organisms *having* metabolism.

6.1 Metallomics and microbial engines

This point amounts to a larger degree of pluralism in biogeochemistry when thinking about the beneficiaries of metabolism: metabolic cycles themselves can be seen as important, and may shape and constrain biological entities which form parts of them. There are various examples of this rebalancing in biogeochemical contexts. Paleo-metallomics investigates the ways in which organism biochemistry has utilised specific metals through time. From patterns of use, it is possible to infer things about the chemical environments within which those organisms evolved (Hickman-Lewis et al., 2020). These chemical environments

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[15] Note the latter is a feature of existing definitions of metabolism: organisms do things (e.g. eating) which perpetuate their internal metabolic processes. The difference here is that they also perpetuate shared and external processes.

represent, in part, the collective metabolism of a whole range of different entities, which impact the prevalence of various metals (usually as a result of their modulation of other substances, especially oxygen and nitrogen) in the ocean at different times in history. These techniques are rooted in the idea that organisms, cells, and bodies are parts of, and instantiate, broader metabolic systems.

There is considerable stability of specific metabolic processes, like those studied in Paleo-metallomics, which may persist even beyond drastic shifts in the Earth's climate and ecology. In many cases, specific ways of doing metabolism are transferred between microbes, through mechanisms such as the swapping of genes with one another ('horizontal gene transfer'). In doing so, they demonstrate a decoupling of metabolic processes from the taxa that realise them, with microbes acting as 'engines' of biogeochemical cycles, allowing diverse taxa to instantiate the same metabolic processes (Falkowski et al., 2008). (This is an example of 'type 3' sharing in the typology we offered earlier, namely, the sharing of the same kind of metabolic system, which may also entail contribution to some larger biogeochemical phenomenon.)

The nitrogen cycle again helps demonstrate this. Early in Earth's history the movement and transformation of nitrogen around the planet was largely abiotic, driven by factors like volcanoes, plate tectonics and lightning strikes. As life developed, organisms came to play significant roles in bringing nitrogen from the air into organic molecules for use by other living things (humans also now do this on a huge scale by producing and using agricultural fertilisers). The molecular mechanisms by which microbes do this have been preserved across a variety of microbial species, which act sometimes as free-living organisms and sometimes in close symbioses with specific organisms such as legumes (Canfield et al., 2010; Sun et al., 2021).

Diverse associations of living things have therefore become involved in the long-term maintenance of the nitrogen cycle (Doolittle & Inkpen, 2018; Falkowski et al., 2008). This cycle then 'recruits' living systems which perpetuate it, and shapes the evolution and development of the living systems existing within its sphere of influence. The nitrogen cycle, on this perspective, is a shared and external metabolic system[16], but also an important entity in its own right, and not subservient to any single specific organism. Conceived this way, such metabolic processes can themselves be seen as beneficiaries of biological activity (Doolittle & Booth, 2017; Doolittle & Inkpen, 2018)[17]. It is important to note that biogeochemical cycles – such as those involving nitrogen and oxygen - are also very interdependent on one another. These extended and shared metabolic processes influence one another, pervading the world and interlocking in a way which supports a whole range of living systems, which in turn may further reinforce those metabolic processes (Falkowski et al., 2008; Doolittle & Inkpen, 2018).

Exactly which beneficiaries are picked out in a given case will depend, in part, of investigative context: ocean biogeochemists do not abandon thinking about cells, bodies, and organisms as benefitting from metabolic processes. Instead, there is an increased range of potential beneficiaries to be explored. For example, biogeochemists have studied how microbes communicate in collectives ('quorum sensing'), focusing both on the impact of this on the metabolic processes of individual microbes, but also on the potential impact on larger scale multispecies communities of microbes and the biogeochemical cycles they shape (such as the movement and storage of carbon) (Pollara et al., 2021).

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[16] The sharing here involves all three types of sharing discussed earlier: there are common kinds of metabolic process across the nitrogen cycle (type 3), but also specific instances of metabolism which benefit multiple organisms (i.e. type 1 and 2, depending on how the metabolic processes are demarcated).

[17] The broader question of the relationship between evolution and metabolism is too thorny to discuss here in detail. Understanding the nuances of a biogeochemical approach to metabolism is an important precursor step for doing this, however.

There is a much more obvious departure from standard biochemical thinking here, in that the focus on very large-scale systems with geological components leads more easily to the possibility of thinking about metabolism without a tight link to a specific organism. The list of potential beneficiaries – the things supported by metabolic processes – may include metabolic processes themselves, such as large-scale biogeochemical cycles of which individual entities are but a part. There are echoes of this perspective in some other areas of science too: biogeochemical studies of human disease (for example, the prevalence of different substances in the environment and incidence of different types of cancer) draw together human metabolism and a focus on movement of substances through the environment (Bashkin & Howarth, 2002); others have argued that humans - and human economic activity - can be fruitfully seen as part of broader global scale metabolic processes, such as the balance between and rates of heterotrophy and autotrophy across the history of the planet (Braakman et al., 2017). Holobiont theories of evolution may similarly focus on persistence of amalgamations of organisms, other biological entities, and the traits these combine to produce (Veigl et al., 2022). There still remains here, however, a larger point of departure between biogeochemical and biomedical approaches to metabolism, with regards to the kinds of beneficiary they invoke.

7. Implications: loosening tied ends

To recap, on a biogeochemical reading of metabolism: chemical processes which sustain living things (cells, organisms, and bodies) and reside within them are still recognised as important parts of metabolic processes, but this is not the whole picture. Metabolism may occur outside of these entities, including in the ocean (or any other appropriate medium) itself. Several of these entities might benefit from a metabolic process at the same time, and other kinds of beneficiaries might also be relevant, including biogeochemical cycles themselves. What counts as *internal* and *external* is not always as easy to distinguish in many cases, but this need not impede the study of metabolism[18]. Biogeochemical metabolism still denotes the chemical processes which sustain life (and, in the context of secondary metabolism, also augment it in various ways), but these processes may not be contained entirely within, or only relevant to, specific individual cells, bodies, or organisms.

7.1 Gaia, individuals and life

This perspective no doubt raises many further questions, which cannot be answered in detail here, but some of which we will briefly survey. Why should the entire nitrogen cycle be considered one process, rather than many small ones working in concert? A brief answer to this, as with individuating things like organisms (Pradeu, 2016) and species (Dupre, 2001), is that metabolic systems will be nested, overlapping, and dependent on others in varying degrees. Individuating metabolic systems depends – in part - on societal and scientific interests and techniques. Cell culturing, isotope tracing, and food production drove a focus on cells and bodies in the past, whilst newer geochemical and microbiological techniques, and concerns over anthropogenic crises, drive a refocusing on external, shared and overarching metabolic systems too, i.e. a more interactionist approach (Creager & Landecker, 2009; Landecker, 2013b, 2013c; Schneider, 2025a). Definitions of metabolism from biomedical and terrestrial contexts have focused primarily on the cell, body, or organism as the container and beneficiary of metabolism. Building on ecological and microbial approaches, marine biogeochemists have taken a more pluralistic approach to this question, allowing for a loosening of the connection between individuality and metabolism (related developments can

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[18] Much existing work is relevant here: process perspectives on biology (Nicholson & Dupré, 2018), for example, Meincke (2022) on mothers and children as bifurcating processes, which offers an example of how partially integrated living systems can be understood; Hannah Landecker's work on insides, outsides, and metabolism (2013c); and the McMenamins on the similarities between bodies and the ocean (1994) .

be seen also in debates about how to properly individuate organisms more generally (Pradeu, 2016)).

What counts as alive under this view? Unlike organism-centred versions of the Gaia hypothesis, this perspective does not necessarily entail that the ocean, or the Earth, is a single integrated organism. Such a view may still presuppose an internal, private and more restricted view of metabolism, tying metabolism closely to single organisms (Schneider, 2004). On the view we offer here, the Earth can be seen as either a single metabolic system with varying degrees of integration amongst its parts, or a series of metabolic systems which interact in various ways (see the previous point about individuation): either way, biogeochemical processes are sets of interlocking chemical processes which help sustain life.

Does this mean that (some) biogeochemists think that the ocean itself is alive? Insofar as metabolic processes sustain a version of the ocean different to that without life present (this is a key part of Redfield's discovery, mentioned earlier), the ocean is not best described by just physics. Living processes flow through and constitute the ocean, are produced by organisms within it, but also produce those organisms (and ecosystems, cells, genes, etc. too). The study of biogeochemical systems lends itself to the idea that 'aliveness' is best thought of as a matter of degree, as many have articulated previously (Dupré & O'Malley, 2009; Mariscal & Doolittle, 2020; Parke, 2023)[19], or to a focus on 'life' as a broad and diffuse phenomenon, rather than just thinking about 'living things' in the particular (O'Malley, 2016).

A final clarificatory point related to this is as follows: it is not the case that a biogeochemical perspective allows for simply any environment to be considered metabolic, but rather that

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[19] This perspective is similar to the 'ancestral state' put forward by Carl Woese as the universal ancestor of life on Earth. This metaphysically spicy soup does not feature discrete organisms but rather integrated diverse communities of cells which developed into more well-defined and bounded organisms (Woese, 1998). These kinds of entities are also invoked in debates about whether metabolic processes or reproductive processes appeared first in the genesis of life, where some authors have suggested that metabolism may have arisen before organisms (Anet, 2004).

entities other than cells, bodies, and organisms can also serve as places where metabolism can happen; that these metabolic processes can stretch across and be relevant for multiple different living things at the same time; and that entities other than cells, bodies, and organisms may also be important to consider here. It might be doubted that the ocean today has the kind of structure amenable to being described as metabolic, or as being made up of distinct metabolic systems (as with the notion of 'deep North Pacific' metabolism, mentioned earlier). Metabolism is, after all, associated with the maintenance of complex systems. The term 'structure' is often associated with rigidity, but the sea is awash with non-rigid structural complexity, such as globe-spanning ocean currents which act to convey water of different depths, temperatures and salinities around the planet (Hays, 2017). It is easy to mistake this complexity for simplicity. Sections of the Earth, such as the ocean, and sections of the ocean, such as the deep North Pacific, instantiate and produce structures and boundaries which lead people to fruitfully demarcate them as metabolic entities in their own right. The same is likely true of other important (and overlapping) biogeochemical systems, such as the atmosphere, soils, and Earth's crust (Schneider, 2025a). This is not an entirely disembodied notion of metabolism, then, but one which can be instantiated in a wider range of contexts.

7.2 The ethics of metabolism

There are some basic ethical implications to this perspective on metabolism, and in particular the idea of ocean metabolism, which we would like to highlight here. The conclusion is not a simple ecocentrism: that the ocean, or biogeochemical cycles, or a given marine ecosystem, *necessarily* possess some kind of intrinsic value. Nor is it advocation for straightforward ecological holism, i.e. an over-riding concern for large-scale conjunctions of biotic and abiotic components (i.e. ecosystems) over other potential concerns (e.g. human or non-human organism wellbeing), or advocating for rights for specific parts of the environment (such as the ocean, or rivers) (Shrader-Frechette, 1996).

But there are other important ethical implications to be drawn here. First, the ocean, and parts of it, are containers of metabolic processes. As a result, we gain an increased sense of the contingency and consequentiality of the biochemical composition of the ocean. It is an actively maintained metabolic system, and this metabolic arrangement is of enormous import. At different times, levels and ratios of substances in the ocean (e.g. oxygen, iron) have been radically different. Related factors such as acidity, dissolved gases, temperature, currents and other variables have also varied. These are not to be seen simply as background conditions for living things to exist in, but features of the ocean which are often actively shaped by and shape life.

Different chemical compositions - such as radically altered levels of oxygen - have prevailed in the past, and may again prevail in the future. These may suit different existent and future forms of life differently. Some past incarnations of the ocean would not have been chemically suitable for humans nor for the organisms and processes we care about. Future oceans likewise may not[20]. Metabolic processes in the ocean are also not simply products of organisms: they have their own inertia. The basic conclusion for how we treat the ocean is this: even without recognising it as possessing things like intrinsic value, interests, or rights, it is also clear that the ocean is not just water, and the ways we interact with it can produce surprising and consequential results beyond simply a change in the number and distribution of organisms living there: the chemistry and geology of the ocean may change too, by extension impacting the chemistry and geology of biotic and abiotic systems connected to it (including ourselves).

Second, the ocean is filled with instances of shared metabolism, including at scales above the individual organism: there are many potential beneficiaries, and kinds of beneficiaries, to be

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[20] Helmreich (2009, p.63-67) recounts a terrifying story in this vein, where we might be unwittingly engineering a great de-oxygenation event, by which we help ancient microbes retake the oceans that were once theirs.

discerned. Our newfound and nascent abilities to measure metabolites in the ocean offer potential to uncover currently unseen metabolic interactions that may be critical to determining the nature of the ocean and all it contains (Braakman et al., 2025; Durham et al., 2025). What happens to the ocean then should be evaluated not only in terms of the interests of some important individual species, nor of the entire biosphere (as is sometimes argued - whatever this would entail), nor just human desires. All of these may be relevant, but must be considered alongside the recognition that the ocean is a vast site of complex symbiosis, and of intertwined biogeochemical cycles, all of which may also be objects of concern in their own right. This perspective lends itself to views which emphasise the importance of *both* biological entities (e.g. organisms) *and* their interactions, as well as aspects of the environment considered to be abiotic (see, for instance, Millstein, (2024, Chapter 5) and Puig de La Bellacasa (2017)).

Advocates of geo-engineering risk missing these points. Treating the ocean as simply an extension of human metabolism to be modified to help solve human problems (as some current and proposed human activities seem to do), ignores that doing so may deprive other living systems – organisms, communities, ecosystems – of continued access to these shared metabolic processes, and that alterations to this shared metabolic system may ultimately end up producing a system with which humans no longer fit.

There are, of course, risks to adopting a metabolic perspective on the ocean. For some people, it might invoke a medicalisation of the ocean, as a site which can be intervened on in order to fix it, just as we might with bodily metabolic problems (see, for instance, talk about adding ‘antacids’ to the ocean (Tollefson, 2023)). This process of medicalisation of environmental problems has occurred elsewhere (Ankeny & Leonelli, 2019). But this too can also give us pause for thought about how we decide environmental interventions are safe and justified. Many aspects of medicine are highly regulated, especially areas which threaten to impact more than just the person whose body is being intervened on (consider, for example, germ-line genetic engineering (MacCord, 2024)). Recognising that we are parts of shared metabolic systems calls for similar caution when seeking to intervene on marine systems too (and, of course, when considering how our behaviour already intervenes on them).

Interactions with the ocean, then, can be examined through the lens of metabolic justice (Chao, 2023): are we treating it simply as a part of human metabolism, or are we recognising that it is a contingent and shared system of which we are only a small part? Are we recognising that interactions between biological entities can be just as important as the entities they take place between? (Schneider, 2025a). A metabolic lens offers a way to think ethically about the ocean without needing to invoke ocean rights or ocean interests (see Earth Law Center (2023) for more on ocean rights), nor necessarily to invoke a sense of intrinsic value for the ocean. (Although it is not incompatible with intrinsic value approaches: see, for instance, Millstein, 2024 (esp. chapter 5).) Importantly, thinking about the ocean, and metabolism, in this way, also offers opportunities to connect cutting edge science with a broad array of ideas, including work which is explicitly metabolic (such as emerging ideas around metabolic justice) but also other perspectives which fit with this kind of view.

7.3 Science, worldviews, and intuitiveness

An intriguing feature of this notion of metabolism is that it concords well with a variety of existing worldviews. This is despite it being driven, in part, by rapid advances in what are somewhat obscure technological developments (such as the -omics techniques mentioned in the introduction). Some existing perspectives on nature - particularly feminist and indigenous ones - have already stressed many of the themes we draw on here in relation to the environment, our understanding of it, and the nature of human-environment relations: a pluralistic and relational conception of reality, whereby there are multiple legitimate ways to understand a given system (Barad, 2007; Haraway, 1988; Todd, 2020); a respect for and recognition of the agency of non-human systems, particularly non-human organisms and environments more generally (Bennett, 2010; Watts, 2013); a recognition of the deep connections between organisms and their environments, and between components of the environment (Haraway, 2003; Warbrick et al., 2023; Enyew et al., 2021); the ways in which elements of living systems have come to adapt to a shared way of living together (Haraway, 2016; Tsing, 2015; Watts, 2013); the difficulty (and undesirability) of separating epistemological, ontological and ethical concerns (Barad, 2007; Todd, 2020).

There is not space to do justice to these connections here, but by showing that scientific practice supports a view of metabolism compatible with these notions, we hope to offer space for investigating overlaps in worldviews and exploring avenues for productive collaboration between diverse social groups. Doing so can provide benefits for both scientific practice and for groups historically marginalised by scientific processes (Ludwig, 2016; Renck et al., 2023; Wylie, 2015). Exploring these connections is a particularly important task in relation to groups which stand to suffer the most from climate change (Redvers et al., 2020; Warbrick et al., 2023).

These points of overlap also offer an example of science developing in a way which aligns well with (at least some) people's intuitions about nature. This runs counter to the idea that science becomes increasingly counter-intuitive as it gets more sophisticated, or of unambiguous distinctions between 'scientific' and 'folk' perspectives (Medin & Atran, 1999). As areas of science probe deeper into the subjects they focus on, it is sometimes supposed - particularly in the context of physics - that the resultant picture of nature will be increasingly alien to human intuition[21]. But in this case (borrowing terms from Wilfred Sellars) we can see a striking convergence (and a lack of rivalry) between the 'scientific' and 'manifest' (i.e.

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[21] Philosopher Alfred North Whitehead was particularly critical of this idea, and of counter-intuitive scientific theorising generally. For more on this, see Desmet & Irvine (2022).

common-sense) image that humans have of the world (Sellars, 1991). Scientific activities can bring theories and concepts closer to some pre-existing perspectives and intuitions held by groups of people about the nature of the environment. This implies there is a richer interplay of everyday and scientific concepts than might be sometime supposed, rather than simply seeing non-scientific concepts as impoverished versions of scientific ones (Chang, 2012).

Finally, we can return also here to the many extra-biological uses of metabolism mentioned at the start of the paper (such as the application of the label 'metabolism' to cities, societies, or industries). Given that opposition to those may be, in part, along the lines of opposition to metabolism being contained by and benefitting entities other than individual cells, bodies, or organisms, it may be possible for a biogeochemical perspective to act as a bridge between these different uses of the term. This is not to say that such uses are therefore implicitly biogeochemical, or that they are necessarily grounded in scientific evidence, but that there may be more connection between, say, the metabolism of a city and the metabolism of a human, than might be first thought. Further work exploring these connections, and which kinds of mediums can sustain or instantiate different sorts of life-sustaining chemical activity, may produce opportunities for better understanding metabolic processes at a whole range of scales.

8. Conclusion

We have argued here that ocean biogeochemistry provides a window into a different understanding of the concept of metabolism. The combination of biological (particularly microbiological) and geochemical perspectives yields a notion of metabolism as not simply biochemical processes contained within and benefiting solely an individual organism, cell, or body, but as processes which sustain, stretch across, and are related in various ways to a whole range of living things. The ocean can therefore be legitimately thought of as metabolic without needing to be seen as an organism. Instead, it is host to, and a participant in, a variety of biogeochemical processes which are produced by organisms, communities, ecosystems and their constituent parts, and which in turn shape and produce the entities supporting them. On this view, the ocean can be seen as not simply a vessel in which life takes place, but as something suffused with and constituted by life. The organism-metabolism relationship is rebalanced somewhat: organisms have metabolism, but metabolisms may have organisms too.

This has relevance too for more traditional biochemical instances of metabolism, such as energy-producing processes in macroscopic terrestrial organisms, which we have shown may also often spill out of and be shared between a range of living things, i.e. involve different kinds of containers and beneficiaries of metabolism, often in combination. In both biomedical and biogeochemical cases, connections between living systems can be very similar to those within them. There are still important differences in these traditions of thinking about metabolism however, such as the importance placed on metabolic processes as beneficiaries in their own right. No doubt there are also further interesting variations on the metabolism concept being used within biomedical, biogeochemical and other contexts too, investigation of which can shed further light on how people both conceptualise and care about the living world around them.

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